

The biology of giant ostracods (Crustacea, Cyprididae), a review focusing on the Mytilocypridinae from Australian inland waters

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ABSTRACT

This study uses published and unpublished data to create a comprehensive and up-to-date synthesis of available information on a little-known group of invertebrates, namely, non-marine giant ostracods (cypridids ≥ 3 mm long). Approximately 8% of the ~1000 living cypridid species are identified as 'giant'. They occur in a range of subfamilies, in all zoogeographic regions, except Antarctica, and mainly in small standing-water ecosystems. Only those in the subfamily Mytilocypridinae are reasonably well studied. This subfamily is endemic to Australia and comprises a diverse range of giant species (~29 species in 6 genera), mainly in temporary habitats, mostly salt lakes, including in extreme conditions. We evaluate the current taxonomy of the Mytilocypridinae, analyse patterns in the field distributions and abiotic tolerances of species, and review the general biology of these ostracods. We also identify those species most in need of consideration in conservation planning, highlight critical gaps in knowledge and show how these ostracods could serve as useful models for testing ecological and evolutionary theories. The results of this study can be used to inform conservation planning for giant ostracods and direct further study of these unique invertebrates, which are an important component of the biodiversity of small standing-water ecosystems.

Keywords: aquatic invertebrate, *Australocypris*, conservation, *Mytilocypris*, ostracod, salinity tolerance, salt lakes, taxonomy.

Introduction

Historically, conservation studies have tended to focus on conspicuous, charismatic, iconic or economically significant taxa or settings, resulting in a biased perspective on threats to biodiversity and on the structure and function of biological systems in general (e.g. Di Marco *et al.* 2017; Troudet *et al.* 2017). Taxa and settings that have been identified as overlooked include aquatic invertebrates (Collier *et al.* 2016), small standing-water ecosystems (e.g. wetlands, ponds and small lakes; Bolpagni *et al.* 2019) and inland saline waters (Saccò *et al.* 2021). It is important that conservation planning focuses more on these taxa and settings and is supported by scientific studies (e.g. Di Marco *et al.* 2017; Troudet *et al.* 2017; Bolpagni *et al.* 2019). Accordingly, this study synthesises available information on a little-known group of invertebrates, namely, 'the giant ostracods', especially those in the subfamily Mytilocypridinae, which are an important component of the communities of small standing-water ecosystems, both freshwater and saline, in Australia (see below).

The term 'giant ostracod' is typically used to describe those ostracod species in the family Cyprididae that are 3 mm or more in length (De Deckker 1977; Martens 1986; Halse and McRae 2004), although the term has also been applied to unusually large marine ostracods in other groups (e.g. Fenwick 1984). The information presented herein pertains only to the former, which comprise ~8% of the ~1000 living, non-marine species of Cyprididae (Martens 1986; Halse and McRae 2004; Karanovic 2012). It is likely that additional species of giant ostracod remain to be discovered, especially in regions where giant ostracods are common but poorly studied (e.g. the Afrotropical region, see below). Also, size data are not yet available for some species in taxa that include giant species, e.g. in the tribe

Megalocypridini and the genus *Chlamydotheca* Saussure (Martens and Behen 1994; Karanovic 2012).

Giant ostracod species occur in a range of subfamilies and in all zoogeographical regions, except Antarctica (Fig. 1). The number of giant species is highest in southern parts of the Afrotropical region (Meisch et al. 2019), followed by the Australasian region, and lowest in the Palearctic and Oriental regions (Fig. 1). The subfamily Megalocypridinae has the most species, all but one of which are from the Afrotropical region (Fig. 1). The Mytilocypridinae is also diverse, but all species are from Australia (Fig. 1). Like the Mytilocypridinae, the Hungarocypridinae and Liocypridinae exclusively comprise giant species, but the total number of species in these two subfamilies is small (Fig. 1). The Liocypridinae is only found in the Afrotropical region (Fig. 1), whereas the Hungarocypridinae is represented in the Australasian (by *Hungarocypris asymmetrica* Victor & Fernando in Sulawesi; Victor and Fernando 1981), Palearctic and Oriental regions. Giant ostracods represent only a small

minority of species in the other subfamilies in which they occur (Fig. 1). There are also giant species in the genera *Cypriconcha* Sars (Cole 1960; Delorme 1969) and *Amphicypris* Sars (Fontana and Ballent 2005), which have not yet been assigned to any subfamily (Meisch et al. 2019). The above taxonomic data show that gigantism has evolved on multiple occasions in the Cyprididae.

As is the case for the Cyprididae in general (Meisch et al. 2019), most giant ostracod species inhabit freshwater (Table S1), but some, including most mytilocypridinids, are from inland saline waterbodies (e.g. saline wetlands, coastal and inland salt lakes; De Deckker 1981a, 1983a; Halse and McRae 2004). Most species have been collected from small, shallow or temporary standing waterbodies, although some occur in large permanent lakes or rivers (see Supplementary Table S1). The evolution of gigantism in the Cyprididae has been linked to reduced predation pressure (e.g. due to a general absence of fish) in temporary (Martens et al. 2007) or high-salinity waters (De Deckker 1983a).

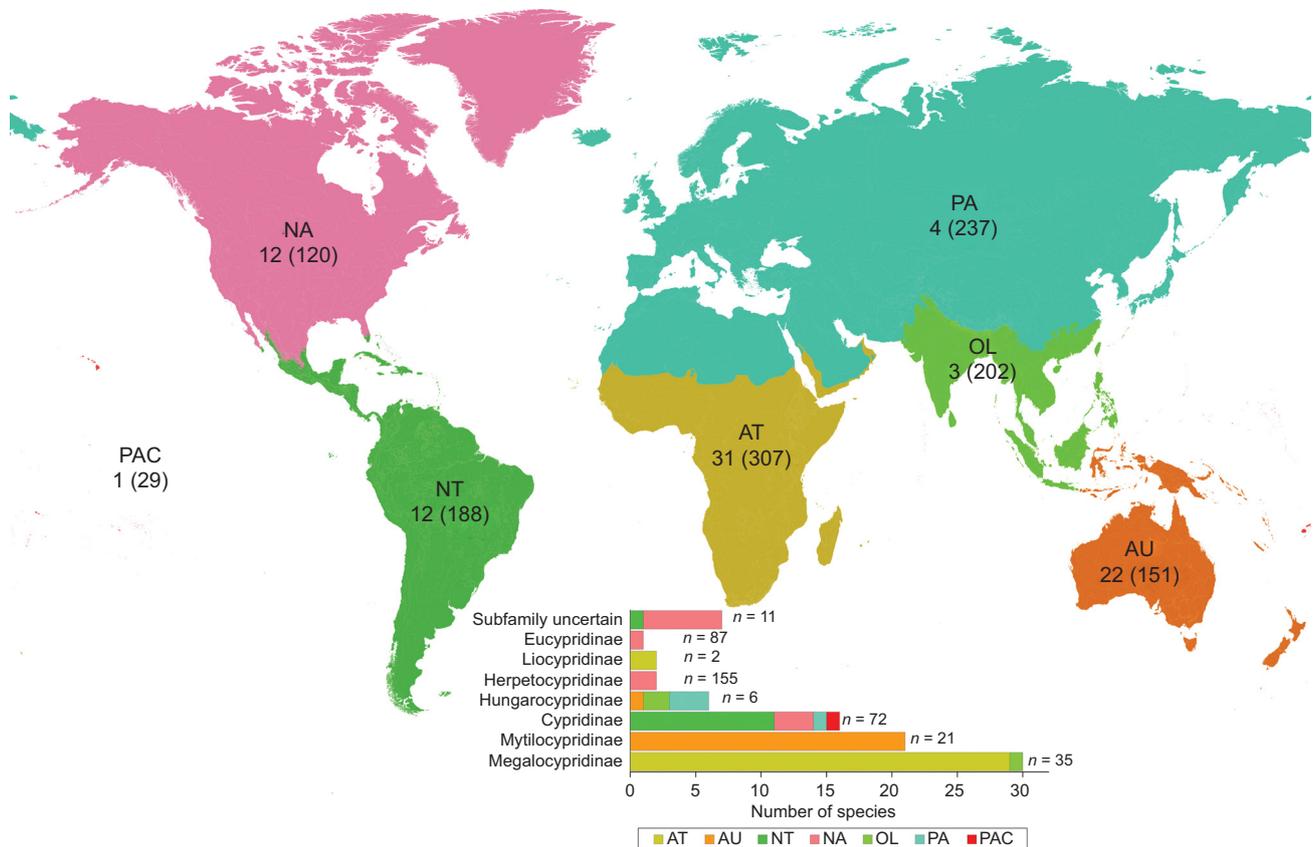


Fig. 1. Approximate number of species of non-marine giant ostracod (length >3 mm) in different subfamilies in different zoogeographical regions, as well as the total number of non-marine Cyprididae ostracods occurring in each region (in parentheses). *n*, number of total species in each subfamily. Only extant described species are included. Overall cypridid numbers were determined from the global checklist of non-marine ostracod species in Meisch et al. (2019). Sources of information about giant ostracod are provided in Supplementary Table S1. Key to zoogeographical regions: AT, Afrotropical; AU, Australasian; NT, Neotropical; NA, Nearctic; OL, Oriental; PA, Palearctic; PAC, Pacific Oceanic Islands.

Information on the biology of giant ostracod species is mainly restricted to small amounts of morphological, distributional and habitat information in limited taxonomic studies, which has been summarised above and in Table S1. An exception is the Mytilocypridinae ostracods, which are well studied, especially with respect to their taxonomy (De Deckker 1974, 1976, 1978, 1981b, 1982; Finston 2002; Halse and McRae 2004; Finston 2007) and some aspects of their ecology (De Deckker and Geddes 1980; De Deckker 1981a, 1983a; Martens 1985a, 1985b; Martens *et al.* 1985; Radke *et al.* 2003; Pinder *et al.* 2005). This subfamily has no known close relatives (i.e. its recent evolutionary history is unknown) and consists of a diverse array of giant species, which are found only in Australia (Halse and McRae 2004). A few species are restricted to temporary fresh or low-salinity waterbodies, but most are found in salt lakes (defined herein as enclosed bodies of water with a salinity normally $>3 \text{ g L}^{-1}$), where they are a key component of the ecology (see De Deckker 1981a, 1983a). Salt lakes are innumerable in Australia; $>80\%$ of lakes and wetlands are saline, and most are shallow and temporary (Timms 2005). Many giant ostracod species show a tolerance to, or even an affinity for, hypersalinity ($>50 \text{ g L}^{-1}$; Hammer 1986) and other extreme conditions (Halse and McRae 2004; Lawrie *et al.* 2021). For example, *Australocypris bennetti* Halse & McRae has been collected from a salinity range of $25\text{--}282.1 \text{ g L}^{-1}$ (Halse and McRae 2004; A. Pinder, unpubl. data) and a pH range of $2.7\text{--}9.06$ (Halse and McRae 2004; Supplementary Table S2). Like several other invertebrate taxa (e.g. *Parartemia* Sayce, some *Daphnia* Müller and *Coxiella* E. A. Smith), the Mytilocypridinae appears to have undergone a significant radiation in inland saline environments (or their precursors) in Australia (Lawrie *et al.* 2021).

The aquatic habitats of Mytilocypridinae (and other) ostracods are being affected by a range of human-related activities (e.g. see Davis *et al.* 2003; Timms 2005; Kirono *et al.* 2012). Temporary waterbodies, both freshwater and saline, in southern Australia are typically holding water less often and may fill less predictably as precipitation decreases and evaporation increases in association with anthropogenic climate change (Timms 2005; Jellison *et al.* 2008; Atkinson *et al.* 2021). The salinity of waterbodies is also increasing (Williams 1995; Halse *et al.* 2003; Kirono *et al.* 2012; Lawrie *et al.* 2021), even in deep permanent lakes because water levels are receding (Kirono *et al.* 2012). Secondary salinisation, which is caused by a rise in saline ground water (e.g. as a result of the clearing of deep-rooted trees or irrigation) is another major threat (Timms 2005). Secondary salinisation has dramatically altered the physical and biological properties of waterbodies in some areas (Jellison *et al.* 2008), particularly in south-western Australia, where up to 30% of the landscape is predicted to be severely affected (Taylor and Hoxley 2003; Timms 2005), placing many freshwater and halophilic invertebrate species at risk of regional extinction (Davis *et al.* 2003; Halse *et al.* 2003;

Lyons *et al.* 2007; Jolly *et al.* 2008). Mining is a threat to some salt lakes, either because of physical disturbance of dry lakebeds or the discharge of highly acidic or highly saline water into the lake (Williams 2002; Timms 2005). Mernagh *et al.* (2016) assessed the mineral potential of Australian salt lakes and identified six regions with a high potential for potash, lithium or boron mining. They noted that some of the lakes in these regions included sites of cultural and conservation significance. Other habitat threats include fish introductions in low-salinity lakes (Khan *et al.* 2002; Khan 2003; P. De Deckker, pers. comm., August, 2022), various types of pollution, groundwater extraction and diversion of surface flows (Williams 2002; Timms 2005; Gregory 2007).

The implications of the above-described habitat degradation for Mytilocypridinae ostracods have not been assessed. To make such an assessment, it is important to evaluate what is known about the biology of these ostracods, but currently relevant information is spread over many sources, including some unpublished material (see Methods for details). This study therefore synthesises published and unpublished information on the biology of Mytilocypridinae ostracods. The findings are used to (1) evaluate the current taxonomy of this group, (2) document important patterns in the geographic and environmental distributions of species, (3) review the general biology of these ostracods, (4) evaluate the conservation status of each species, and (5) highlight gaps in knowledge and recommend directions for future studies. The study also highlights the value of these ostracods for studying ecological and evolutionary theories.

Methods

The information used in this study comes from the following three main sources: (1) peer reviewed published articles, government reports and PhD theses; (2) a dataset held by the Department of Biodiversity, Conservation and Attractions (DBCA), Government of Western Australia; and (3) previously unpublished data held by the first author (M. Rahman), which are presented in Table S2.

Relevant articles on Mytilocypridinae ostracods were identified using Google Scholar, Scopus, and Science Direct databases, with various combinations of the following search terms: 'ostracod', 'ostracoda', 'giant ostracod', 'large ostracod', 'non-marine ostracod', 'saline lake', 'salt lake', 'salt lake Australia', 'Australocypris', 'Mytilocypris', 'Trigonocypris', 'Caboncypris', 'Repandocypris', 'Lacrimicypris'. Mytilocyprinid species names, and their synonyms, compiled from Halse and McRae (2004), were also used as search terms. Multiple searches were conducted between June 2019 and December 2020. These searches identified 60 peer-reviewed journal articles, 25 government reports and 4 PhD theses with relevant information. Although Geddes *et al.* (1981) was

found in the search, their data were excluded because the species identifications for *Australocypris* De Deckker in Western Australia are uncertain in view of the taxonomic revision of Halse and McRae (2004).

The DBCA dataset pertains to giant ostracods collected from sites in Western Australia between July 1994 and June 2020. It contains information on the location (latitude and longitude) of collection sites and associated environmental data, including water salinity and pH. Some of the data are unpublished but some are included in articles that were found in the above searches. The latter were used only once in this study. Unidentified species in the database were excluded from analyses. Raw data on the co-occurrences and salinity range of species in the Eyre Peninsula, summarised in Timms (2009a), were kindly made available by Brian Timms. The sources of geographical and environmental data for specific species are given in the Supplementary Table S3.

Maps showing the distribution of giant ostracod species across states, drainage basins and climatic regions in Australia were constructed using QGIS (ver. 3.22.0, see <https://qgis.org/en/site/index.html>) software. Information on drainage divisions (see <http://www.bom.gov.au/water/about/river/BasinAuxNav.shtml>) and climate zones (see <http://www.bom.gov.au/climate/how/newproducts/images/zones.shtml>) was obtained from the Bureau of Meteorology of Australia. Graphs and figures showing geographic and environmental data were prepared using Microsoft Office 365 and R (ver. 4.2.1, see <https://cran.r-project.org/bin/windows/base/>).

In this article, salinity data are expressed as grams of inorganic dissolved salt per litre of water. The following conversions were used to generate salinity data in these units when the source article reported a related measure. (1) Salinity data in grams per kilogram or parts per thousand were regarded as the same as grams per litre, although it is recognised that they are not identical (Williams and Sherwood 1994). (2) Total dissolved solids (TDS) data were multiplied by a correction factor of 0.91 (Bayly and Williams 1966) to take into account the fact that the former include dissolved organic matter as well as salts (Williams and Sherwood 1994). (3) Conductivity data were converted into salinity (g L^{-1}) using the equation developed by Williams (1986). Although this formula is recommended only for data $<100 \text{ mS cm}^{-1}$ (Williams 1986), it was also used to convert measurements exceeding $>100 \text{ mS cm}^{-1}$ when there was no other way to obtain salinity data (e.g. because TDS data were not reported). In such cases, this would have resulted in underestimates of the actual salinity values.

For simplicity, unless stated otherwise, the term ‘salt lake’ refers to inland waterbodies and coastal lakes with a salinity normally in excess of 3 g L^{-1} , and the term ‘giant ostracod’ refers specifically to Mytilocypridinae ostracods in the remainder of this article unless stated otherwise. All data for *Australocypris hypersalina* De Deckker have been reported under *A. insularis* (Chapman) De Deckker, because the former is a synonym of the latter (see below). Similarly,

data for *Mytilocypris minuta* De Deckker and *M. tasmanica chapmani* McKenzie are reported under *M. mytiloides* (Brady) McKenzie.

Taxonomy and phylogeny

The Australian endemic subfamily Mytilocypridinae contains 21 described species in 6 genera (Halse and McRae 2004; Fig. 2). De Deckker conducted much of the initial taxonomic work on this group, identifying 15 species in 4 genera (De Deckker 1974, 1976, 1978, 1981b, 1982). Halse and McRae (2004) conducted the most recent taxonomic revision of the group, adding two new genera and eight new species (Supplementary Table S4). In that revision, *M. praenuncia* and *M. tasmanica tasmanica* were separated on the basis of only subtle differences in the bursa copulatrix and might represent the same species (see Finston 2000; Halse and McRae 2004). Recent species checklists, i.e. Martens and Savatnalinton (2011), Karanovic (2012) and Meisch et al. (2019), have essentially followed Halse and McRae’s (2004)

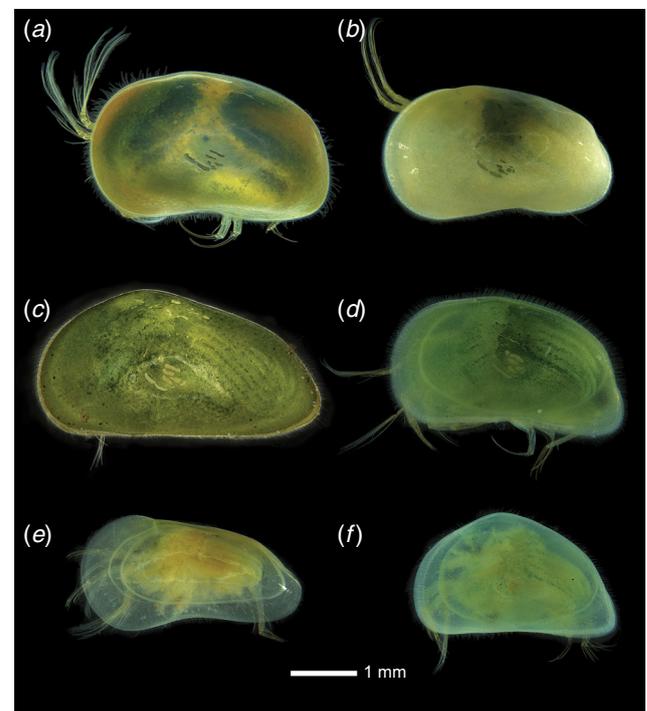


Fig. 2. Photographs of males of one species from each of the six genera of Mytilocypridinae ostracod. (a) *Australocypris robusta* De Deckker (from Willaura, Victoria), (b) *Caboncypris nunkerii* De Deckker (from Womarden, Western Australia), (c) *Lacrimicypris kumbar* Halse & McRae (from Lake Pleasant View, Western Australia), (d) *Mytilocypris ambiguosa* De Deckker (from Red Lake, Mordalup, Western Australia), (e) *Repandocypris austinensis* Halse & McRae (from Lake Carnegie, Western Australia), (f) *Trigonocypris globulosa* De Deckker (from Lake Bryde, Western Australia).

Table 1. Comparison of major characters of *A. dispar* against those of the genera *Australocypris* and *Caboncypris*.

Character	<i>Australocypris</i> (De Deckker 1978)	<i>Caboncypris</i> (De Deckker 1982)	<i>Australocypris dispar</i> (De Deckker 1981b)
Shape of carapace	Subrectangular to subtriangular, with smooth pseudo-punctate valves	Smooth to pseudo-punctate shell, ellipsoidal in lateral view	Pseudo-punctate, subrectangular carapace
Colour and ornamentation of shell	Valves pale yellow to pale green with two darker patches extending laterally and ventrally	Valves nacreous brown with one darker patch	Nacreous brown with one darker patch
Selvage	Narrow and marginal on both valves	Broad selvage in both valves and placed far away from outer edge	Selvage faint and between edge of valve
First leg of male	Hook shaped extremity of prehensile palp of male 1st leg broad and long	Prehensile palp of male 1st leg short and not hook shaped	Prehensile palp of male 1st leg short and not hook shaped
Zenker organ	Number of rosettes ~75	Number of rosettes more than 60	Number of rosettes 67
Claws of furca	Almost equal in size	Terminal claws unequal	Unequal claws with anterior one 0.66 longer, and anterior seta slightly longer than posterior one
Rake like organ	Usually nine irregular, stout teeth, variable among animals	Six to seven teeth plus a bifid one	Seven short and stout teeth plus one inner bifid one on each rake

revision, except for some minor details (see Table S4 for details). Because the overall morphological features of *A. dispar* more closely match those described for *Caboncypris* than *Australocypris* (see Table 1), we suggest that *A. dispar* is a type of *Caboncypris*.

The following new or undescribed species have been discovered since the revision of Halse and McRae (2004): (1) two undescribed species of *Mytilocypris*, namely, *Mytilocypris* ‘moojari’ from the Goldfields region (Quinlan *et al.* 2016) and Pilbara region (Pinder *et al.* 2010) and ‘*M. n. sp. 1*’ from Lake Carnegie (M. Rahman and A. Pinder, unpubl. data); (2) *Lacrimicypris* sp. nov. from a seasonal claypan in the Wheatbelt region (Pinder *et al.* 2013) and a wetland in the Perth Metropolitan region (A. Pinder, unpubl. data); (3) two undescribed species of *Caboncypris*, namely, ‘*C. n. sp. 1*’ from the Esperance region (Table S2) and ‘*C. n. sp. 2*’ from the Eyre Peninsula in South Australia (specimen provided by Patrick De Deckker); and (4) three undescribed species of *Australocypris*, namely, ‘*A. n. sp. 1*’ from the Wheatbelt region (Table S2), ‘*A. n. sp. 2*’ from the Esperance region (Table S2) and ‘*A. n. sp. 3*’ from the Great Southern (A. Pinder, unpubl. data, and Table S2).

Thus far, genetic assessment of species boundaries in giant ostracods is available only for *Mytilocypris*. Of the eight species that were recognised at the time, Finston (2000) found fixed allelic differences at allozyme loci for five (*M. ambigua*, *M. henricae*, *M. praenuncia*, *M. splendida*, *M. tasmanica tasmanica*), but no fixed differences among the other three (*M. mytiloides*, *M. minuta* and *M. tasmanica chapmani*). Also, the overall genetic differences between *M. praenuncia* and *M. tasmanica tasmanica* were small and may reflect geographic variation within a single species (see Finston 2000). Subsequent field (Finston 2004) and laboratory (Finston 2007) studies strongly suggest that *M. mytiloides*, *M. minuta* and *M. tasmanica chapmani* are a single morphologically variable species. The three morphotypes can be distinguished by differences in carapace size and shape,

but these differences are largely determined by the salinity of the environment (Finston 2004). On this basis, Halse and McRae (2004) synonymised *M. minuta* and *M. tasmanica chapmani* to *M. mytiloides*.

Neither the broader phylogenetic relationships of the Mytilocypridinae nor those among the composite genera and species have been studied. Establishing these relationships is needed to validate the current taxonomy and develop our understanding of the origin and evolutionary history of these unique ostracods.

Habitat type

Giant ostracods are found mainly in seasonal (fill seasonally) and episodic (fill irregularly) waterbodies (Halse and McRae 2004). They also occur in permanent waterbodies, but essentially only in those that have salinities greater than the tolerance level of fish predators (De Deckker 1983a). For example, *A. robusta* is found in some of the large permanent crater lakes in western Victoria (De Deckker 1983a). Although some species are strictly or partly freshwater species (see below), giant ostracods are a conspicuous and diverse component of the fauna of salt lakes in Australia (De Deckker 1981a, 1983b). Of the species that occur in salt lakes, most occur only in naturally saline waterbodies, but *Australocypris insularis* (Pinder *et al.* 2005) and unspecified *Mytilocypris* species (Pinder *et al.* 2002) also occur in waterbodies affected by secondary salinisation.

Diversity and distribution

The most diverse genera of giant ostracod are *Australocypris* and *Mytilocypris*, which have seven described species and respectively three and two undescribed species, notwithstanding that *A. dispar* may really be a species of

Caboncypris (see above). *Caboncypris* is the next-most diverse with two described and two undescribed species, and possibly also *A. dispar*. The other three genera (*Lacrimicypris*, *Repandocypris* and *Trigonocypris*) each have only two known species. These data could change as more species are discovered and information on phylogenetic relationships of genera and species becomes available. The remaining information in this section considers only described species, i.e. the undescribed species mentioned in the taxonomy and phylogeny section are excluded.

Giant ostracods are mainly known from southern Australia (Halse and McRae 2004), probably because most salt lakes occur in this region (Williams 2002; Halse and McRae 2004). On a state-by-state basis, the total number of species of giant ostracods progressively declines from Western Australia to South Australia to Victoria to Tasmania and is lowest in New South Wales and Queensland (Fig. 3c). Six of the species in Western Australia are endemic to this state, compared with only one or no endemic species in other states (Fig. 3c). Small ostracods, *Parartemia* brine shrimp, *Coxiella* gastropods show similar decreases in species richness in salt lakes as one moves eastward from Western Australia (see Lawrie et al. 2021). There are no reports of giant ostracods from the Northern Territory or the Australian Capital Territory.

We have also considered the breakdown of species richness across drainage divisions (Fig. 3a, 4), which may be the foci of evolution for these ostracods. The highest numbers of species occur in the South West Coast (13 species) and South Western Plateau drainage divisions (11 species; Fig. 3a), which are located fully (former) or partly (latter) in Western Australia (Fig. 4). The next-highest occurs in the Murray–Darling Basin drainage division (10 species; Fig. 3a), mainly owing to a high number of species recorded from the well-studied Paroo River wetlands (Timms 1993; Watts 1999). The South West Coast drainage division also has the highest number of endemic species (three species; Fig. 3a). The Lake Eyre Basin and Carpentaria Coast are the only other drainage divisions with endemic species and they have one species each (Fig. 3a).

Finally, from the perspective of climate zones (Fig. 4), temperate and grassland zones have more species than desert and subtropical areas (Fig. 3b). There are one or two endemic species in each of the temperate, grassland and desert zones, but there is none in the subtropical zone (Fig. 3b). The desert zone is reasonably unsampled and so could contain a high proportion of undescribed species (Halse and McRae 2004), although waterbodies in this zone usually only fill episodically (Roshier et al. 2001), which may limit species richness (see Williams and Geddes 1991).

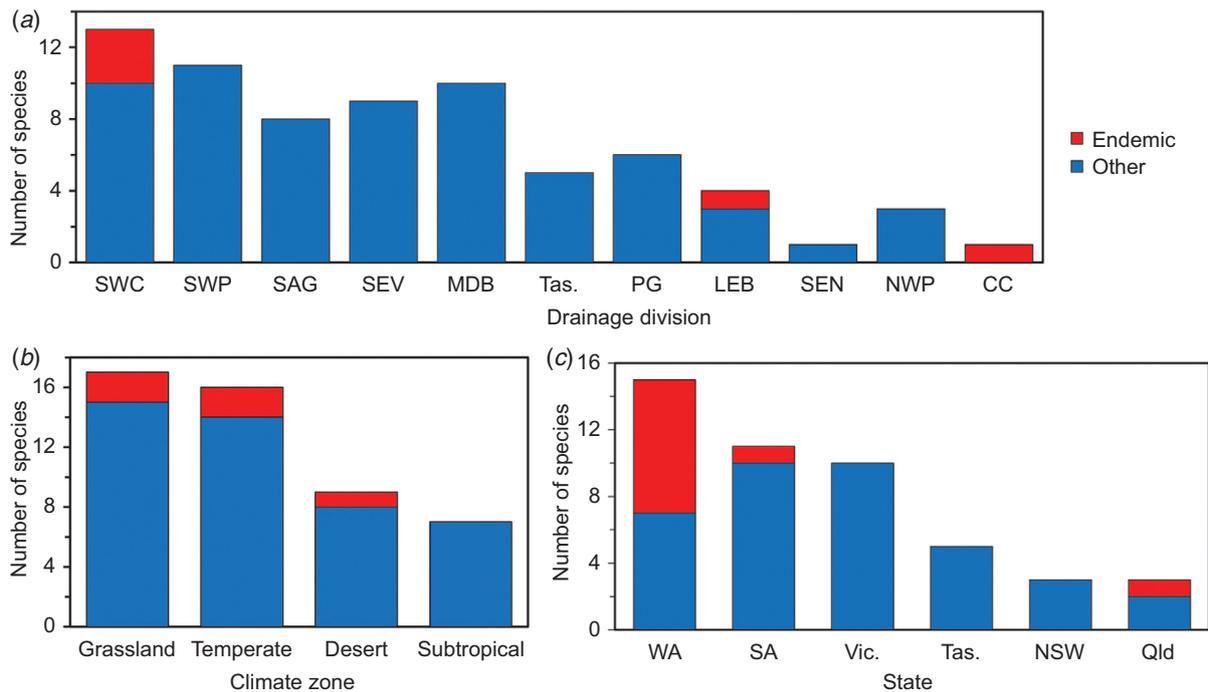


Fig. 3. Number of endemic and non-endemic species of Mytilocypridinae ostracod in different (a) drainage divisions, (b) climate zones, and (c) states of Australia. Only described species are included. Key to states: WA, Western Australia; SA, South Australia; NSW, New South Wales; Qld, Queensland. Key to drainage divisions: NEC, North East Coast; SEN, South East Coast (NSW); SEV, South East Coast (Victoria); Tas., Tasmania; MDB, Murray–Darling Basin; SAG, South Australian Gulf; SWP, South Western Plateau; SWC, South West Coast; PG, Pilbara–Gascoyne; NWP, North Western Plateau; TTS, Tanami–Timor Sea Coast; LEB, Lake Eyre Basin; CC, Carpentaria Coast.

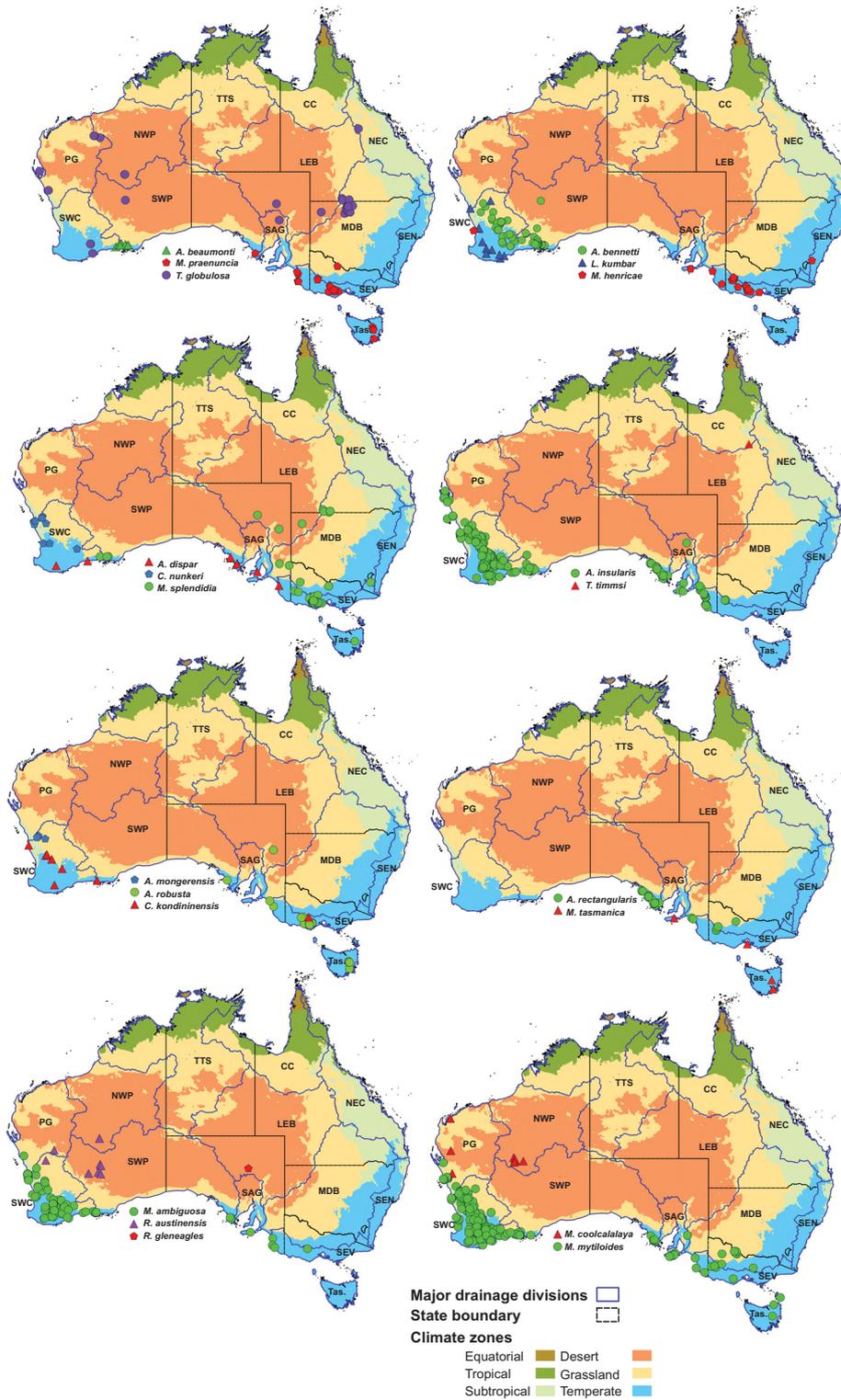


Fig. 4. Species distributions of Mytilocypridinae ostracod across drainage divisions, climate zones and states in Australia. Only described species are included. Key to drainage divisions as per Fig. 3. Source of geographical information can be found in Table S3.

The basis for high species richness and endemism in giant ostracods in southern Western Australia is likely to be

multi-faceted. A range of other taxa with desiccation-resistant life stages from small standing waterbodies also

have overall more species and more endemic species in Western Australia than they do in other parts of southern Australia. These taxa include anostracans (Timms 2012, 2014), cladocerans (Hebert and Wilson 2000), copepods (Maly and Bayly 1991), Spinicaudata (Timms 2006) and *Coxiella* gastropods (Lawrie et al. 2021).

The opportunities for speciation in giant ostracods and other taxa with desiccation-resistant life stages may be high in southern Western Australia because there are vast numbers of temporary waterbodies that collectively encompass multiple climate zones and show considerable variation in salt content and hydrological cycle (see Geddes et al. 1981, who promoted these ideas as a part of the explanation for high species richness in *Parartemia* in this region). Also, Western Australia has a long history of geological stability with repeated climatic variations, which may have promoted speciation in these ostracods and other invertebrates inhabiting temporary waterbodies (Geddes et al. 1981; Timms 2006, 2013; Timms et al. 2009). Phylogeographic studies are needed to deduce how giant ostracod species have responded to palaeoclimatic events (see Byrne 2008).

There is considerable variation in the ubiquity and abundance of giant ostracod species. We have identified six distributional categories, ranging from species that are widespread and very common to species that are known only from one site or a few sites in the same area (see Table 2, see also Fig. 4 for maps of species distributions). *Australocypris insularis* and *Mytilocypris mytiloides* are, by far, the most commonly encountered species, with each being recorded from more than 200 sites (Table 2, Supplementary Fig. S1) from throughout southern Australia, although only the latter species has been found in Tasmania (Table 3, Fig. 4, S1). *Trigonocypris globulosa* is notable because it is very

Table 2. Distributional categories for Mytilocypridinae ostracods.

No.	Category	Examples
1	Very common and found in two or more states	<i>A. insularis</i> , <i>M. mytiloides</i>
2	Common and found in two or more states	<i>T. globulosa</i> , <i>M. splendida</i> , <i>M. praenuncia</i> , <i>M. henricae</i> , <i>M. ambiguosa</i> , <i>A. robusta</i> , <i>A. rectangularis</i>
3	Rare and found in two states	<i>C. kondininensis</i> , <i>M. tasmanica</i> , <i>A. dispar</i>
4	Common in Western Australia but not found elsewhere	<i>A. bennetti</i>
5	Rare but widespread in Western Australia	<i>L. kumbar</i> , <i>M. coolcalalaya</i> , <i>R. austinensis</i> , <i>C. nunkeri</i>
6	Only reported from one site or a few sites in the same area	<i>R. gleneagles</i> , <i>T. timmsi</i> , <i>A. beaumonti</i> , <i>A. mongerensis</i>

Only described species are included. Very common, known from at least 200 sites; common, known from at least 20 sites; rare, known from fewer than 20 sites (see Fig. S1). Maps of the distribution of each species can be found in Fig. 4.

geographically widespread, occurs in all four climatic zones and is the only species that is widespread in central Australia (Table 3, Fig. 4). *Repandocypris gleneagles* Halse & McRae and *T. timmsi* De Deckker are at the other extreme, each having been reported from a single site only (Table 3, Fig. 4, S1).

The reasons why some species are more common and widespread than other species in the same genus is not known but similar variation has been reported for some other invertebrate taxa from inland Australian waters (see Lawrie et al. 2021). When considering this pattern in *Parartemia*, Williams and Geddes (1991) suggested that the evolution of adaptations that support colonisation might be favoured in some species (resulting in widespread species), whereas selection for local adaptation might be favoured in others (resulting in narrowly distributed species). Williams (1984) suggested that a relatively wide distribution of *Parartemia* in some species was related to broader ecological tolerance and relaxed selection rather than a greater dispersal ability. It would be worthwhile to test these ideas by using giant ostracod species.

Information on the distributions of giant ostracod species is more detailed than that for most invertebrate species in inland Australian waters (e.g. see Lawrie et al. 2021, for a recent review of salt-lake taxa). Nevertheless, sampling is incomplete, particularly for rare species and remote regions. Also, most information is based on *ad hoc* sampling, which may not have captured the full complement of species that inhabit a waterbody, such as, if the abundance of a species varies with time. Some information may also be based on outdated taxonomy. For example, *A. robusta* De Deckker has been reported from two sites in Western Australia, Lake De Courcy and Lake King (Geddes et al. 1981); however, these reports predate Halse and McRae's (2004) taxonomic revision. Recent data indicate that *A. bennetti* is the species in Lake King (Halse and McRae 2004), and probably also Lake De Courcy (M. Rahman, unpubl. data). Reports of *A. robusta* in Western Australia are, therefore, unconfirmed and so have not been included in the diversity and distributional data presented herein (see Fig. 4). Similarly, our data also exclude an unconfirmed report of *A. rectangularis* De Deckker from Lake Dundas (see Halse and McRae 2004), which is the only report of this species in Western Australia.

Ecology

Salinity range

Lacrimicypris is known only from freshwater (Halse and McRae 2004; Table 3). *Trigonocypris* has one species (*T. timmsi*) reported from one freshwater site (De Deckker 1976) and another (*T. globulosa*) that occurs in sites ranging from freshwater to hypersaline water (Table 3). *Caboncypris kondininensis* Halse & McRae and *C. nunkeri* have been found

Table 3. Geographic distribution, salinity, and pH ranges of Mytilocypridinae ostracod species of Australia.

Species	Distribution			Salinity (g L ⁻¹)	pH
	Drainage division	Climate zone	State		
<i>Australocypris beaumonti</i>	SWC, SWP	Temperate, grassland	WA	26–84.4	7.87–9.4
<i>A. bennetti</i>	SWC, SWP	Temperate, grassland, desert	WA	25–282.1	2.7–9.06
<i>A. dispar</i>	SWC, SWP, SAG, MDB	Temperate	WA, SA	3.1–128	7.68–9.24
<i>A. insularis</i>	SWC, SWP, PG, SAG, MDB, SEV	Temperate, grassland, subtropical, desert	WA, SA, Vic.	2–200.2	3.74–10.5
<i>A. mongerensis</i>	SWC	Grassland	WA	10–77.5	7.94–10.2
<i>A. rectangularis</i>	SAG, MDB	Temperate, grassland	SA, Vic.	45.2–198.4	7.5–8.9
<i>A. robusta</i>	MDB, SEV, Tas., LEB	Temperate, desert	SA, Vic., Tas.	4.4–288	7.5–10.1
<i>Caboncypris kondininensis</i>	SWC, SWP, SEV	Temperate, grassland, subtropical	WA, Vic.	2–15.5	7.3–9.2
<i>C. nunkeri</i>	SWC	Temperate, grassland, subtropical	WA	0.1–35.8	6.9–9.16
<i>Lacrimicypris kumbar</i>	SWC	Temperate, subtropical, grassland	WA	0.1–0.8	6.18–9.92
<i>Mytilocypris ambigua</i>	SWC, SWP, PG, SAG, MDB, SEV	Temperate, grassland, subtropical,	WA, SA, Vic.	0.5–64.6	6.9–10.2
<i>M. coolcalalaya</i>	PG, NWP	Grassland, desert	WA	0.1–3.2	7.4–9.95
<i>M. henricae</i>	Rottneest Island ^A , SAG, MDB, SEV, SEN	Temperate, grassland	WA, SA, Vic., NSW	1.5–20	8.7–10.6
<i>M. mytiloides</i>	SWC, SWP, PG, SAG, MDB, SEV, Tas.	Temperate, grassland, subtropical, desert	WA, SA, Vic., Tas.	1.3–172.9	3.86–11.1
<i>M. praenuncia</i>	SWP, MDB, SEV, TAS	Temperate, grassland	SA, Vic., Tas.	4–51.1	8.5–10.1
<i>M. splendida</i>	SWC, SWP, MDB, SEV, Tas., LEB	Temperate, grassland, desert	WA, SA, Vic., Tas., NSW, Qld	0.3–77.4	6.9–9.8
<i>M. tasmanica</i>	SAG, SEV, Tas.	Temperate	Vic., Tas.	4–9	–
<i>Repandocypris austinensis</i>	SWC, SWP, PG, NWP	Grassland, desert	WA	3.4–117	8.2–9.58
<i>R. gleneagles</i>	LEB	Desert	SA	42–51	–
<i>Trigonocypris globulosa</i>	SWC, SWP, PG, SAG, MDB, LEB, NWP	Temperate, grassland, desert, subtropical	WA, SA, NSW, Qld	0.7–122	8.2–10.6
<i>T. timmsi</i>	CC	Grassland	Qld	–	–

Only described species are included. De Deckker (1976) reported that *Trigonocypris timmsi* was collected from freshwater, but no water-quality data were found for the species. No pH data were found for *Repandocypris gleneagles* and *Mytilocypris tasmanica*. Key to drainage divisions and states as per Fig. 3. The source of the data is given in the Table S3.

^ARottneest Island is not included in any drainage basin.

in freshwater to low-salinity water respectively (up to 15.5 g L⁻¹) and freshwater to moderately saline water (up to 35.8 g L⁻¹; Table 3). Six of the seven *Mytilocypris* species are found mainly or exclusively in salt lakes (see Table 3); the remaining species, *M. coolcalalaya* Halse & McRae, is known only from freshwater and low-salinity water (Halse and McRae 2004; DBCA dataset). *Australocypris* (six or seven species, depending on the status of *A. dispar*) and *Repandocypris* (two species) are found only in salt lakes (see Table 3). These data suggest that the giant ostracods have transitioned from freshwater to saline water on multiple independent occasions.

Most salinity records for giant ostracods are based on field measurements and suggest that most species have very broad and often overlapping salinity tolerances (Table 3). Eight species have been found at salinities greater than 100 g L⁻¹ and two at salinities greater than 200 g L⁻¹ (Table 3), placing them among the most salt-tolerant ostracods in the world (see De Deckker 1981a; Lawrie et al. 2021). At the other extreme, aside from the strictly freshwater *Lacrimicypris*, there are four giant ostracod species that have been found only

at salinities less than 20 g L⁻¹ (Table 3). The overall salinity range in giant ostracods, particularly in the more salt-tolerant species, is large, for example, extending from 4.4 to 288 g L⁻¹ in *A. robusta* (Table 3).

Estimates based on multiple individual data points provide more nuanced information about the usual salinity distributions of species than do those based on maximum and minimum values. Such estimates show that *Australocypris* species tend to occur at higher salinities than do species in other genera (Fig. 5). The median salinity record is highest (~100 g L⁻¹) for *A. rectangularis* and *A. bennetti* (Fig. 5). The median salinity for 'A. dispar' (22.8 g L⁻¹) is the lowest of the *Australocypris* species (Fig. 5), which is interesting in view of the possibility that this could be a species of *Caboncypris* (see above). Among the *Mytilocypris*, the common and widespread species, *M. mytiloides* has the highest median salinity record at ~19 g L⁻¹ (range 1.3–172.9 g L⁻¹; Fig. 5). By contrast, median salinity (~48 g L⁻¹, range 2–200.2 g L⁻¹) for the common and widespread *A. insularis* is among the lowest for *Australocypris* (see Fig. 5).

Aladin and Potts (1996) investigated osmoregulation in a broad range of ostracod species, including *Mytilocypris praenuncia*, which has been recorded from salinities of 4–51 g L⁻¹ in the field (Table 3). This species was capable of hyperosmotic regulation when raised in water with salinity of <8 g L⁻¹ and of hypo-osmotic regulation when raised in water within the salinity range of 20–48 g L⁻¹. The salinity of haemolymph and the water medium was near isosmotic at salinities in between. The mechanisms of osmoregulation were not fully resolved but mitochondria-rich cells located in the non-calcified zone of the inner carapace layer appear to be important. These cells are responsible for excreting salt in hypo-osmotic regulation and may be the site of salt uptake in hyperosmotic regulation (Aladin and Potts 1996). Osmoregulation in other species of giant ostracod is probably similar to that in *M. praenuncia*.

pH range

The pH of freshwater ecosystems in Australia generally varies between 6.5 and 8 (Hobday and Lough 2011), with some exceptions (Pinder et al. 2013). The pH of most of Australian salt lakes is also near neutral (Mernagh et al. 2016), although, overall, it varies from 1.4 (Benison and Bowen 2015) to 11.0 (Williams 1998). A high proportion of lakes in the Wheatbelt and Goldfields–Esperance regions of Western Australia

are classified as moderately acidic (pH 4–6) or extremely acidic (pH 1.5–3.9), reflecting the acidic groundwaters in these regions (Benison and Bowen 2015). Acidic lakes tend to have their own unique but depauperate fauna compared with neutral–alkaline lakes (Pinder et al. 2004; Timms 2009b). Some have only recently become acidic as a result of rising groundwater (Pinder et al. 2005).

Most giant ostracod species are found only in neutral–alkaline water (Table 3, Fig. 6). Four species, namely *C. nunkeri*, *M. ambigua*, *M. splendida* and the freshwater *L. kumbar*, occur mainly in neutral–alkaline waters but are occasionally also found in slightly acidic conditions (Table 3, Fig. 6). *Australocypris insularis* and *M. mytiloides* also occur mainly in neutral–alkaline waters, but overall are distributed over a very broad range of pH, including highly acidic waters (Table 3, Fig. 6). *Australocypris bennetti* is common in both acidic and alkaline waters (Fig. 6) and is represented by different morphological forms in each (Halse and McRae 2004). Whether these different morphs reflect genetic or ecophenotypic effects is unclear. In general, ostracod species are rarely found in a pH of <5 (e.g. see Ruiz et al. 2013), and the occurrence of giant (and other) ostracods in low pH waters is surprising, because the acidic water is expected to dissolve the calcite carapace (De Deckker 2002). The mechanisms that giant ostracods use to survive in such extreme environments are not known.

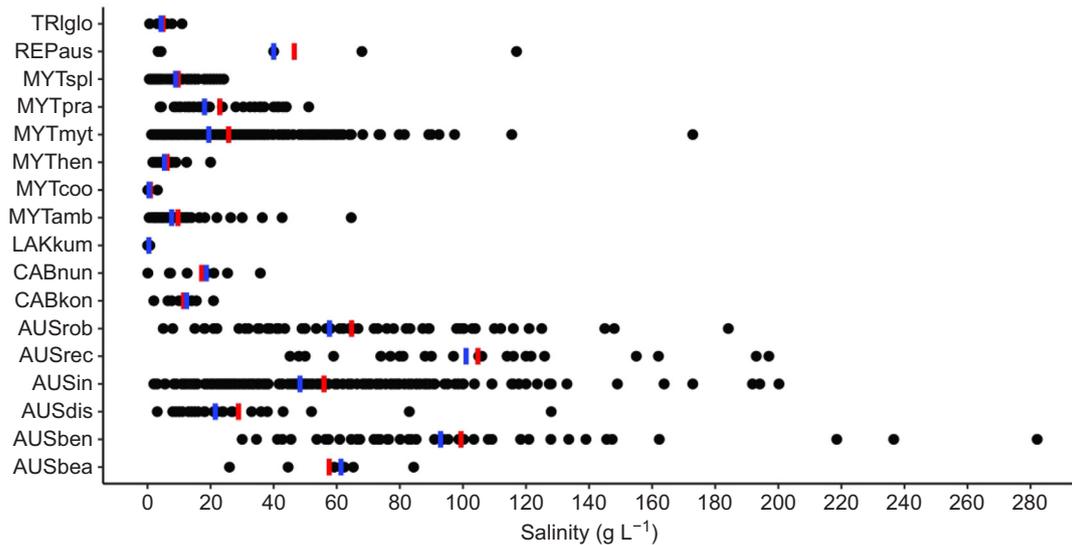


Fig. 5. Salinity distributions of selected species of Mytilocypridinae ostracods on the basis of field data. The red lines indicate mean values and blue lines indicate median values. Only those species for which there were at least five independent data points, are included. For *T. globulosa*, only data from Western Australia are included because only salinity ranges are reported for this species outside of Western Australia. In cases where multiple data points were available for a single waterbody in the same year, only the maximum salinity value was included. Data reported as salinity ranges, instead of the exact values, were not included. Key to species: AUSbea, *Australocypris beaumonti*; AUSben, *A. bennetti*; AUSdis, *A. dispar*; AUSin, *A. insularis*; AUSrec, *A. rectangularis*; AUSrob, *A. robusta*; CABkon, *Caboncypris kondininensis*; CABnun, *C. nunkeri*; LAKkum, *Lacrimicypris kumbar*; MYTamb, *Mytilocypris ambigua*; MYThen, *M. henricae*; MYTmyt, *M. mytiloides*; MYTpra, *M. praenuncia*; MYTspl, *M. splendida*; REPaus, *R. austinensis*; TRlglo, *Trigonocypris globulosa*.

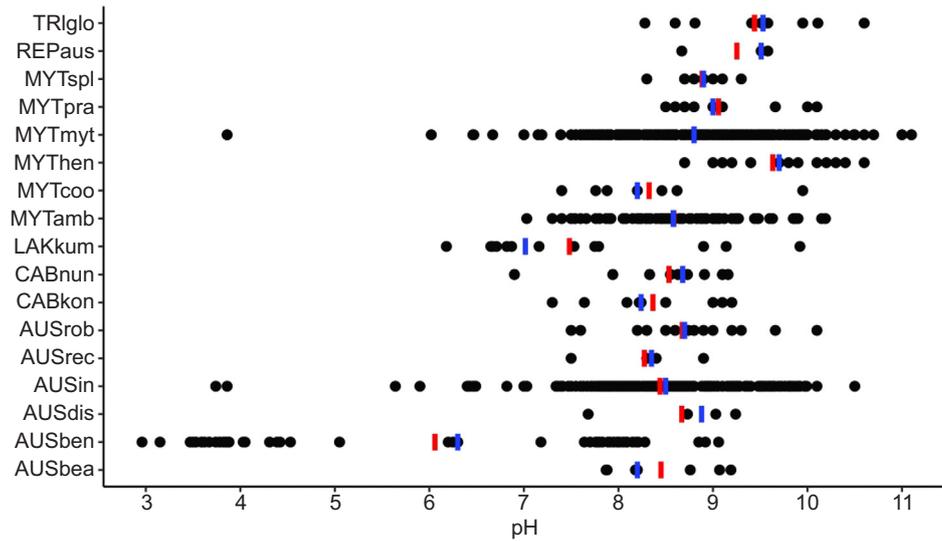


Fig. 6. pH ranges of selected species of Mytilocypridinae ostracods on the basis of field data. The red lines indicate mean values and blue lines indicate median values. Data reported as pH ranges, instead of the exact values, were not included. Key to species as per Fig. 5.

The above-mentioned salinity and pH data for giant ostracods are based on field records. These records may overestimate the salinity or pH tolerance of some species because they do not consider whether individuals can survive long term or reproduce in the conditions. They are also based mainly on the adult stage of the life-cycle, which may be tolerant of a broader range of conditions than are other life stages (see Geddes 1976, who suggested this for *Parartemia*). Conversely, the field data are likely to underestimate the true extent of variation in other species that have been subject to limited spatial or temporal sampling. For example, prior to this study, *A. mongerensis* Halse & McRae was known only from a single site at a salinity of 11 g L⁻¹ (Halse and McRae 2004) but we have found this species at another three sites in salinities ranging from 21 to 78 g L⁻¹ (Table S2).

Experimental data indicate that salinity tolerance in *M. henricae* is almost twice as high under laboratory conditions as field records (Martens (1985b), indicating that the relationship between the physiological tolerances and field distributions of giant ostracods is probably complex. Outside of a critical range, salinity is probably not a crucial factor in determining the field distributions of species (Williams *et al.* 1990). Radke *et al.* (2003) undertook a detailed analysis of the relationship between the distributions of a range of giant and small ostracods species and the ionic composition of salt lakes in south-eastern Australia. They concluded that ostracods could be separated into four groups according to their preferred water chemistry, which in part reflected the salt content and pathway of solute evolution (e.g. ratios of Ca²⁺ to alkalinity) of the water. Giant ostracod species were represented in all four groups. The three species of *Australocypris* that were included in the study (*A. rectangularis*, *A. insularis*,

A. robusta) all fell into different groups, whereas the five species of *Mytilocypris* were placed into two groups, one including *M. mytiloides* and *M. ambiguosa* and the other including *M. henricae*, *M. splendida*, and *M. praenuncia* (which also included *A. robusta*). Bayly (1969) proposed that salinity tolerance in some species of calanoid copepods from Australian salt lakes increased at a higher pH and was potentially linked to ionic proportions, particularly carbonate and bicarbonate, as well as salinity. The same might apply to giant ostracods.

Co-occurrence of species

Co-occurrence of giant ostracod species, particularly congeners, appears to be relatively rare (Table 4), although a mix of different species from up to three different genera has been collected from some sites (Cale *et al.* 2004; Table S2). *Australocypris* and *Mytilocypris* are the most relevant genera for understanding patterns of co-occurrence because they include a range of species with overlapping geographic distributions. Species of both genera, especially *M. mytiloides* and *A. insularis*, have been collected from many of the same sites across southern Australia (e.g. De Deckker and Geddes 1980; De Deckker and Williams 1982; Radke 2000; Cale *et al.* 2004, Timms 2009a, 2009b; Pinder *et al.* 2012; Cale and Pinder 2018). However, there are very few reports of co-occurring *Australocypris* species (De Deckker 1983a; Table 4), except that *A. insularis* and *A. rectangularis* were often found together on the Eyre Peninsula in South Australia (B. V. Timms, unpubl. data). *Mytilocypris* species, especially *M. mytiloides* and *M. ambiguosa*, appear to co-occur more often than *Australocypris* species, but less often than *Mytilocypris* species do with other genera (Table 4, Fig. 7). Congeneric

Table 4. Incidence of co-occurrences of *Australocypris* and *Mytilocypris* species in different waterbodies.

Source	Number of waterbodies sampled	<i>Australocypris</i> present	<i>Mytilocypris</i> present	<i>Australocypris</i> co-occurring with <i>Australocypris</i>	<i>Mytilocypris</i> co-occurring with <i>Mytilocypris</i>	<i>Australocypris</i> co-occurring with <i>Mytilocypris</i>
DBCA dataset	228	110	147	1	28	42
Timms (2009a)	40	32	6	23	0	6
Present study	150	100	57	2	0	21

Only described species are included.

species of some other types of salt-lake invertebrates (e.g. *Parartemia*) also rarely coexist (Timms 2012).

Co-occurrence of giant ostracod species may sometimes be overlooked, especially because the relative abundance (and therefore the collectability) of different species in a waterbody can vary through time (Halse and McRae 2004). Nevertheless, the rarity of reports for well-sampled taxa such as *Mytilocypris* and especially *Australocypris* is too low to be explained entirely by missed data. Because many giant ostracod species have very broad and overlapping physicochemical tolerances (see above), the rarity of co-occurrence is unlikely to be fully explained by differences in the physicochemical properties of waterbodies. Dispersal limitations are also an unlikely cause, given that many congeneric species have overlapping geographic distributions and co-occurrence of species from different genera is more common. Predation has been identified as a major factor excluding co-occurrence between congeners in the copepods *Boeckella* Guerne & Richard and *Calamoecia* Brady in Western Australia (Maly and Maly 1997). Predation and competition could be important in explaining the low rate of co-occurrence between congeneric giant ostracods (De Deckker 1983a).

General biology

Locomotion

Giant ostracods are active swimmers and use antennae for propulsion (De Deckker 1983a). They usually swim near the bottom and some species of *Australocypris* have been observed to burrow a few millimetres into soft sediment on lake floors (De Deckker 1983a). Anecdotal observations on specimens in aquaria suggest that individuals of *A. robusta* may prefer to burrow in ‘clayey’ rather than sandy sediment (De Deckker 1974). They also suggest that *M. henricae* and *M. splendida* swim less, and with the posterior well below the anterior, than do *A. robusta*, *A. insularis* (= *A. hypersalina*) and *T. globulosa* (De Deckker 1978). De Deckker (1978) proposed that swimming is more energetically expensive in *Mytilocypris* species because the tapering of the posterior of the carapace is more extreme and so adds weight without fitting soft tissue (except possibly for testes).

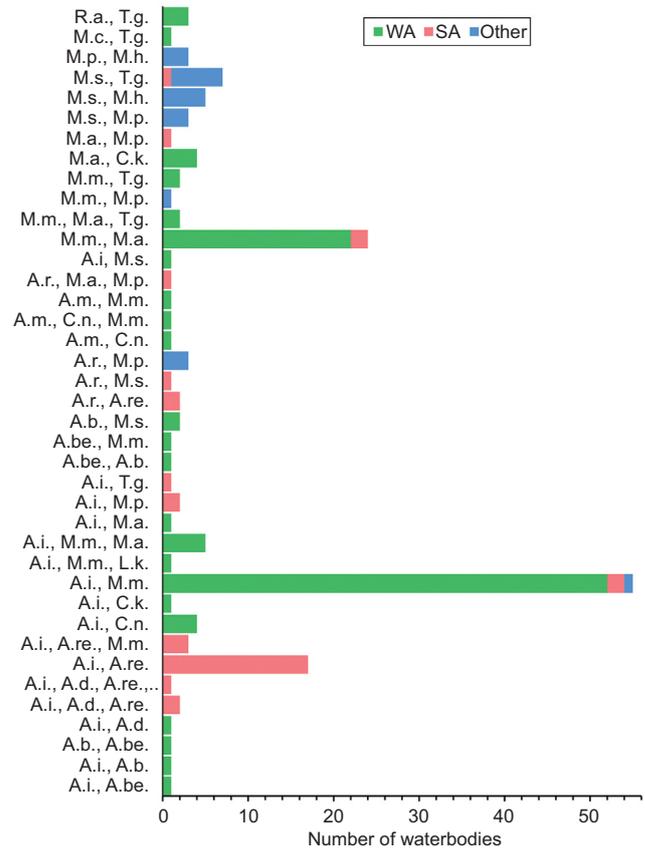


Fig. 7. Number of co-occurrences of giant ostracod species in Western Australia (WA), South Australia (SA) and other Australian states (other). Only described species are included. *Australocypris dispar* has been excluded from this analysis because it may be a misidentified species of *Caboncypris* (see text). Key to species: A.i., *Australocypris insularis*; A.b., *A. beaumonti*; A.be., *A. bennetti*; A.re., *A. rectangularis*; A.r., *A. robusta*; A.m., *A. mongerensis*; M.m., *Mytilocypris mytiloides*; M.a., *M. ambiguosa*; M.s., *M. splendida*; M.p., *M. praenuncia*; M.h., *M. henricae*; M.c., *M. coolcalalaya*; C.n., *Caboncypris nunkeri*; C.k., *C. kondininensis*; L.k., *Lacrimicypris kumbar*; R.a., *Repandocypris austinensis*; T.g., *Trigonoocypris globulosa*.

Smith et al. (2015) indicated that swimming is energetically expensive for ostracods in general; the increased buoyancy from the saline water may reduce the energetic costs of swimming in salt lakes.

Trophic interactions

The diets of giant ostracods have not been well studied and may vary with the stage of life. In a series of laboratory experiments, Campbell (1995) showed that *Australocypris insularis* is an important predator on zooplankton, such as the calanoid copepods *Calamoecia clitellata* and *C. salina*, the small ostracods *Diacypris compacta* and *D. dietzi*, and juvenile ostracods. Large numbers of the copepod *Calamoecia* have been found in the gut and faeces of several *Australocypris* species (De Deckker 1983a). In the laboratory, *A. robusta* has been observed to feed mainly on dead crustaceans (mainly isopods) or filamentous algae if the former is absent (De Deckker 1974) and *A. insularis* has been seen congregating on and consuming living and dead individuals of *Parartemia* brine shrimp (M. Rahman, unpubl. data). Such predatory behaviour, where large numbers of ostracods attack animals much larger than themselves, has also been reported for a small number of marine and non-marine species (e.g. Wilkinson *et al.* 2007). Overall, the available evidence indicates that the diet of *Australocypris* species is broad and opportunistic and that some *Australocypris* species are important predators in salt-lake systems. There is no published information on the diets of other types of giant ostracod.

Very little is also known about the organisms that feed on giant ostracods. There are reports of *Mytilocypris* in the gut contents of an introduced fish species from salt lakes in Victoria (De Deckker 1977; Khan *et al.* 2002; Khan 2003) and in the gut contents of a native fish species from salt lakes in Western Australia (Halse 1981). Fish could be important predators of giant ostracods except that they are rarely found in giant ostracod habitats (see Halse and McRae 2004). Birds that feed in these habitats are known to consume larger invertebrates such as gastropods (Weston 2007) and brine shrimp (Pedler *et al.* 2018) and probably also feed on giant ostracods; for example, banded stilts have been seen feeding on 'small black ostracods' at Lake King (Bougher 1988), but we are not aware of any published records that specifically mention birds feeding on giant ostracods. Adults and larvae of dytiscid beetles, which have been reported from salinity ranging from 0 to 130 g L⁻¹ in Australia (e.g. Pinder *et al.* 2002), are potential invertebrate predators.

Life history and reproduction

Specific information on the life history and reproduction of giant ostracods is sparse and restricted mainly to *Mytilocypris* species. The life cycle of *M. henricae* in Lake Bathurst comprises nine instars, eight larval stages and the adult (Martens *et al.* 1985), which is typical for ostracods (Smith *et al.* 2015). Giant ostracod populations invariably contain both males and females (De Deckker 1983a; Finston 2000, 2002; Smith *et al.* 2016; M. Rahman, unpubl. data) and

allozyme data have confirmed that five *Mytilocypris* species use sexual reproduction (Finston 2002). Thus, although the Family Cyprididae includes a broad range and high incidence of parthenogenetic lineages, Mytilocypridinae ostracods are likely to be exclusively sexually reproducing. Because is the case with other ostracods, fertilisation in giant ostracods is internal, and males have an elaborate (and taxonomically informative) copulatory apparatus and giant aflagellate sperm (Matzke-Karasz *et al.* 2014; Smith *et al.* 2016). Sperm size has been measured in three species of Mytilocypridinae, namely, *A. robusta*, *M. praenuncia* and *M. mytiloides*, with sizes of ~11 787, 4800 and 4675 µm respectively (Smith *et al.* 2016). The sperm of *A. robusta* is among the longest recorded for any animal (Smith *et al.* 2016).

Giant ostracods are sexually dimorphic, i.e. where structures not directly involved in reproduction show differences in form between the males and females of a species (Cox and Calsbeek 2010). The carapace or body size is larger in females (to accommodate large number of eggs) and has a posterodorsal hump in males (to accommodate the rotation of the hemipenis during copulation). The shape of the carapace also differs between males and females; for example, it is strongly triangular in *T. timmsi* males but subtriangular in females (De Deckker 1978; Halse and McRae 2004). The number and arrangement of claws and setae on the second antennae is also sex specific (De Deckker 1978; Halse and McRae 2004). The first leg is described as strongly sexually dimorphic because it has a prehensile palp in males that is used to clasp the female during copulation (De Deckker 1978; Halse and McRae 2004). Similar patterns in sexual dimorphism are seen in other cypridids (Karanovic 2012; Smith *et al.* 2015). Although sexual dimorphism in animals is often attributed to sexual selection, the basis or bases for sexual dimorphism in giant ostracods is not known and could have a variety of causes (see Punzalan and Hosken 2010).

Female-biased adult sex ratios appear to be common at least in *Mytilocypris* (Finston 2002) and *Australocypris* (J. Chaplin, unpubl. data). Such biases are common in sexually reproducing ostracods in general (reviewed by Chaplin *et al.* 1994; Martins 2019). It is uncertain whether these biases are related to mechanisms of sex determination or subsequent life history or ecological modifications of sex ratio (Ladle and Foster 1992; Martins 2019). Experimental studies using giant ostracods could be used to help resolve these questions.

Growth rate and adult size in *Mytilocypris mytiloides*, a common and widespread species, vary with salinity (Finston 2004, 2007), with individuals tending to grow faster but reaching a smaller size in high-salinity environments and *vice versa*. Finston (2007) suggested that salinity might act as a cue for habitat duration, such that *M. mytiloides* grows faster in ephemeral waterbodies to ensure that eggs can be laid before conditions become unfavourable. De Deckker (1983a) mentioned that adult sizes in *Australocypris* in waterbodies in the Coorong Lagoon system of South Australia

were larger during the winter than in spring and summer when temperatures and salinities were higher and water depth was rapidly receding. He suggested that environmental factors, such as temperature, may have a direct controlling effect on the size, shape and ornamentation of the carapace. These ostracod data fit with suggestions that populations and species from more variable environments show high levels of phenotypic plasticity (Chevin and Hoffmann 2017).

All species of giant ostracod are likely to produce desiccation-resistant eggs because they all have populations in temporary waterbodies (e.g. see De Deckker 1983a; Halse and McRae 2004). This has been confirmed for *Australocypris insularis* (Williams 1991; Campbell 1995; Campagna 2007), *A. bennetti* (M. Rahman, unpubl. data), *A. beaumonti* (M. Rahman, unpubl. data), *Trigonocypris globulosa* (Timms 1998), *Mytilocypris ambiguosa* (Strachan et al. 2014, 2016; M. Rahman, unpubl. data), *M. mytiloides* (M. Rahman, unpubl. data), and *Cabonocypris kondininensis* (M. Rahman, unpubl. data), which have been raised in the laboratory from sediment samples collected from dry waterbodies. Desiccation-resistant eggs are a general feature of non-marine ostracods (De Deckker 1983a; Rossi et al. 2012). These eggs play a key role in re-establishing populations after unfavourable or dry conditions (De Deckker 1977; De Stasio 1989; Strachan et al. 2014), preventing local extinctions (Rossi et al. 2012), and also in dispersal (Green et al. 2008). Because there are giant ostracod populations in permanent waterbodies, such as, *A. robusta* in Lake Keliambete, it appears that the resting eggs of at least some species do not need to undergo a period of desiccation to hatch (De Deckker 1983a).

The factors that stimulate hatching in eggs after a period of desiccation are largely unknown, but salinity is likely to play a role. De Deckker (1983a) reported that unspecified species of ostracod in athalassic ephemeral lakes in the Coorong Lagoon system tended to hatch, not immediately after rainfall when salinities were still high, but later when salinities were lower. He also mentioned that different species were present in Lake Buchanan in central Queensland in different years when salinity was different, which implies that salinity cues for hatching might be species specific. Finally, he noted that some species, such as *A. robusta*, can hatch at high salinities. Our knowledge of hatching cues in giant ostracods has advanced very little since De Deckker (1983a).

Dispersal

Very little is known about the mechanisms and extent of dispersal in giant ostracods, although it seems likely that the desiccation-resistant eggs are the main dispersal propagules (see De Deckker 1977). These eggs could be transported in a number of ways, such as, being attached to the external surface or in the coeca of water birds (Sandberg and Plusquellec 1974; De Deckker 1977; Figuerola and Green

2002; Green et al. 2008; Sánchez et al. 2012), by egestion from water birds (Proctor 1964; Green et al. 2008), by wind (Brendonck and Riddoch 1999) or by water flow during flooding (Finston 2002). De Deckker (1977) hypothesised that migrating waterfowls are a key dispersal vector for the giant ostracods, largely on the basis that these birds inhabit waterbodies similar to those inhabited by the ostracods. Ultimately, the distribution of ostracod species will depend not only on their capacity for dispersal, but also on the factors that determine the survival and growth of propagules or individuals at the destination waterbody.

Finston (2002) used allozyme data to investigate the population structures of five species of *Mytilocypris*. Conspecific populations were genetically distinguished from each other, suggesting that the amount of gene flow in a species is negligible and populations are self-sustaining (Finston 2002). However, the very common and widespread species, *M. mytiloides*, undergoes more (although still limited) gene flow over larger distances than do the other species (Finston 2002). It is not clear whether this is because this species has a greater dispersal ability per se or because it has broader ecological tolerances (Finston 2002). This begs the question as to whether phenotypic plasticity is generally more pronounced in the more broadly distributed species. Although the amount of gene flow in a giant ostracod species is unlikely to be sufficient to directly affect population dynamics, it will influence a species' chances of colonising new waterbodies and regions, buffer against local extinctions and determine the breakdown of genetic variation within and among populations (Butlin and Menozzi 2000).

Conservation status

The Mytilocypridinae ostracods warrant attention in conservation plans in view of their unique evolutionary history and ecology and ongoing threats to their habitats, which are outlined in the introduction. Species that are rare and geographically restricted (Category 6 in Table 2) are seemingly most in need of consideration. These include *R. gleneagles*, which has been collected only from Lake Eyre South, South Australia (Halse and McRae 2004), and *T. timmsi*, which is known only from Pine Tree Lagoon, Queensland, and has not been found since its original description (De Deckker 1976). Although recent sampling has increased the number of known populations, both *Australocypris mongerensis* and *A. beaumonti* are still known only from a few sites in the northern edge of the Wheatbelt and Esperance regions in Western Australia respectively (see Fig. 4, Table S2). Species that are restricted to low-salinity habitats (see Table 3, Fig. 5) may be particularly vulnerable to a drying climate because waterbodies fill less often, hold water for shorter periods of time and contain higher-salinity water (Lawrie et al. 2021). Many giant ostracod

populations occur in nature reserves, which is important because habitat protection is the only way to conserve giant ostracod species (see Halse and McRae 2004). However, although nature reserves offer some degree of protection, they can still be affected by increasing aridity, secondary salinisation by a regional rise in groundwater, and other disturbances within their catchment (Williams 2002; Atkinson *et al.* 2021).

We do not know of any confirmed loss of a giant ostracod population from a waterbody. Populations in some of the very large salt lakes in Western Australia that were once more or less seasonal but now rarely fill may be particularly susceptible to extirpation. For example, despite repeated attempts, we have been unable to find *Australocypris* sp. in Lake De Courcy since ~2011 (J. Chaplin, unpubl. data). The desiccation-resistant eggs of giant ostracods should help prevent extirpation, but the details will depend on the factors that influence the viability and hatching of these eggs, which are currently unknown.

Conclusions and directions for future research

Approximately 8% of the ~1000 species of non-marine cypridid ostracods are 'giant'. Giant species are found in at least seven subfamilies and in all zoogeographic regions, except Antarctica. Most species are unstudied, except for taxonomy and accompanying notes on distribution and habitat. The giant ostracods occur mainly in small standing-water ecosystems and are potentially an important component of the fauna of these systems. The subfamily Mytilocypridinae, which is endemic to Australia, is relatively well studied. A few mytilocypridinids occur in freshwater or low-salinity water, but most occur in salt lakes, sometimes in extreme conditions. Approximately one-third of known Mytilocypridinae species have been discovered in the past 20 years. The highest levels of diversity occur in south-western Australia. Most species have broad and often overlapping physicochemical tolerances. Nevertheless, there is considerable variation in the ubiquity and abundance of species and congeners rarely co-occur in the same waterbody.

Studies that generate basic information about the biology of non-Mytilocypridinae giant ostracods are urgently required. Future studies of Mytilocypridinae ostracods should prioritise the following:

- incorporating molecular data into taxonomic research to test for the presence of cryptic species and plastic morphological characters;
- conducting phylogeographic analyses to help understand critical events in the evolution of these ostracods and how these relate to the past and present Australian 'landscape';

- ascertaining species' tolerances to salinity and other environmental stresses across all stages of their life cycles;
- determining the mechanism that species use to survive in acid lakes;
- clarifying the abiotic and biotic factors that determine species' distributions, including why congeneric species rarely co-occur;
- elucidating the long-term viability and hatching stimuli for desiccation-resistant eggs and whether this varies among species;
- comparing patterns and mechanisms of dispersal and gene flow in broadly distributed and geographically restricted species;
- documenting the trophic roles of giant ostracods in their communities;
- using laboratory experiments to test ecological (e.g. about species co-existence) and evolutionary (e.g. about sex ratios) predictions;
- assessing the levels of anthropogenic impacts, including secondary salinisation and mining activities, on giant ostracods;
- identifying any critical habitats, such as sites that may serve as refugia during unfavourable conditions.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data that support the findings of this study are available from the references identified in figures and tables, Supplementary Table S2 and a database held by the Department of Biodiversity, Conservation and Attractions of Western Australia. The DBCA dataset may be obtained from the authority upon reasonable request.

Conflicts of interest. The authors declare that they have no conflicts of interest.

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