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BIOGEOGRAPHY AND ECOLOGY OF AUSTRALIAN ANOSTRACA (CRUSTACEA: BRANCHIOPODA)

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SUMMARY

Three anostracan genera occur in Australia, the native genera *Branchinella* and *Parartemia* and the introduced genus *Artemia*. The nineteen described species of *Branchinella* include some that are widely distributed within Australia, especially *B. australiensis,* and others of local occurrence. Of the eight species of *Parartemia* five occur in south-western Australia, one occurs across southern Australia, another is found in the south-east, and one occurs in the north-east. *Branchinella* species usually occur in ephemeral freshwater pools while *Parartemia* is halobiont, but some species from both genera occur in brackish water. Cladocerans and calanoid copepods generally occur with *Branchinella* and notostracans and conchostracans are often present. *Parartemia* generally occurs with halobiont copepods and ostracods. Some samples contained more than one species of *Branchinella* but there were no co-occurrences of *Parartemia* species. The Australian anostracan fauna is compared with that from other continents and factors influencing the distribution of anostracans are discussed.

Introduction

Three genera of Anostraca occur in Australia, the genera *Branchinella* and *Parartemia* established for Australian material by Sayce (1903) and *Artemia* Leach. *Parartemia,* in the family Branchipodidae, is an endemic genus and is most closely related to the freshwater genus *Branchipodopsis* which is distributed in arid regions of Africa and Asia (Linder, 1941). *Branchinella,* in the family Thamnocephalidae, occurs in Africa, America, Europe and Asia, although most species (19 of 26 described) are Australian (Fig. 1). Other genera in the Thamnocephalidae, *Thamnocephalus* and *Dendrocephalus,* occur in central and South America and Linder (1941) suggests that *Branchinella* may also occur in South America. Australian species of *Branchinella* are endemic. The taxonomy of *Artemia,* family Artemiidae, is presently confused, with what was once considered a single cosmopolitan species now recognised as several sibling species separated on biochemical and chromosomal characters (Bowen *et al.,* 1978). The populations in Australia will, therefore, be referred to as *Artemia* sp.

The taxonomy of the Australian Anostraca is relatively well studied. Linder (1941) revised previous work and described seven new species of *Branchinella* and six new species of *Parartemia,* bringing the number of Australian species in the two genera to nineteen and seven respectively. Since then four new species of *Branchinella* have been described, three others put into synononymy and one declared *nomen dubium* (Geddes, 1981), one new species of *Parartemia* has been described (Geddes, 1973a) and the occurrence of *Artemia* in Australia has been documented (Geddes, 1979). However, other aspects of the biology of the Australian Anostraca are poorly known. This paper aims to show the distributions of the various genera and species in Australia and to discuss their biogeography. Some aspects of anostracan ecology will also be considered.

Distribution

The distribution of the various species of *Branchinella* within Australia is shown in Figure 2. Several species are widely distributed (Fig. 2A): *B. lyrifera* and *B. probiscida* in central Australia, *B. occidentalis* in central and western Australia, *B. frondosa* and *B. affinis* in south-eastern and south-western Australia

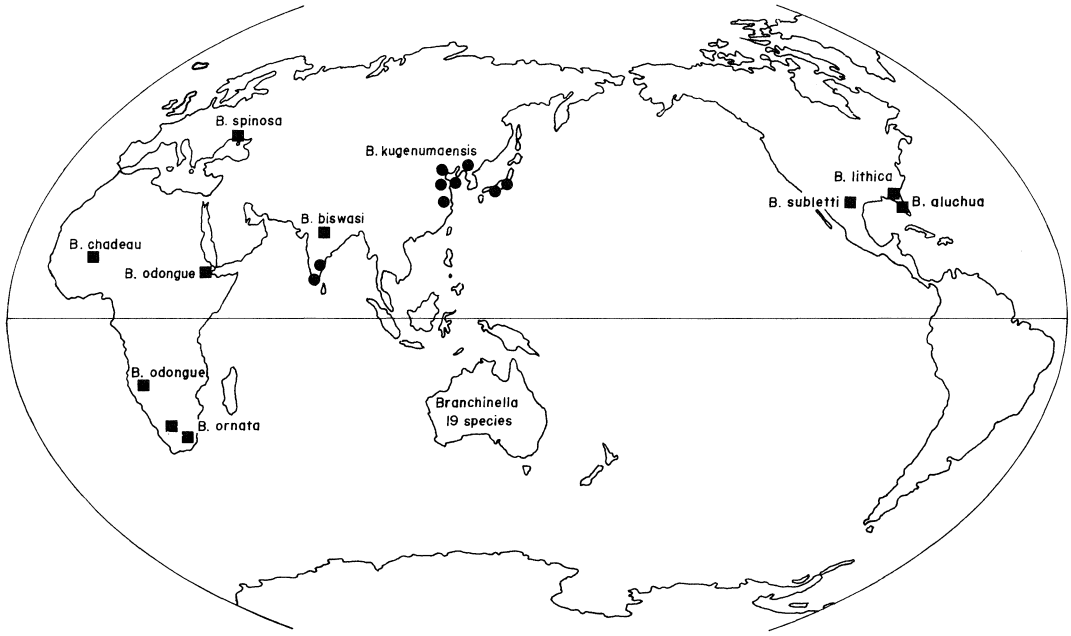

Fig. 1. Distribution of the various species of *Branchinella*.

and *B. australiensis* from most of the continent. Several other species appear to have restricted distributions (Fig. 2B): *B. longirostris* in south western Australia, *B. latzi* in central Australia and *B. compacta* in south eastern Australia. The remaining five species (Fig. 2C) have been collected only once or twice and are probably of local occurrence; all are from Western Australia.

The distribution of *Artemia* and the various species of *Parartemia* is shown in Fig. 3. All *Artemia* collections are from coastal ponds that presently are, or previously were, used for salt production. Two groups of populations are identifiable. Those in the west are parthenogenetic and electrophoretic studies show them to be closely related to parthenogenetic populations in Asia, Europe and Africa (Bowen *et al.*, 1978), while those in Queensland reproduce sexually and are electrophoretically identical to populations from Great Salt Lake, Utah and San Francisco Bay, California (Bowen *et al.*, 1978). The Western Australian populations probably arrived with European man, and those in Queensland certainly represent inoculations of commercial *Artemia* eggs from the U.S.A. (Geddes, 1980). The origin of the single population in South Australia is obscure.

Species of *Parartemia* occur in all of the series of natural salt lakes that have been studied (Fig. 3). In Western Australia there are 6 described species, and two undescribed species also occur (Geddes *et al.*, 1981). Most of these species have fairly restricted distributions and there is little overlap between the three most commonly occurring species, *P. informis* in the north, *P. serventyi* near Kalgoorlie, and *P. longicaudata* in southern coastal areas. One species, *P. cylindrifera,* occurs in south-western Australia and south-eastern South Australia, although it is apparently absent from Victoria and Tasmania. The common species in south-eastern Australia is *P. zietziana* while *P. minuta* is known from one locality, L. Buchanan, in Queensland.

The distribution maps (Figs 2 and 3), when considered together, point to shortcomings in the collecting of Australian anostracans. As might be expected the group is generally restricted to arid and semi-arid regions, with no anostracans known from the tropical north of Australia and only a few collections from the relatively well watered island of Tasmania. However the absence of anostracans from large areas of apparently suitable habitat in central and north-western Australia is a reflection of incomplete sampling. Australia does not appear to have any Anostraca adapted to pools that freeze in winter and are available to aquatic animals in summer, although small areas in which these habitats

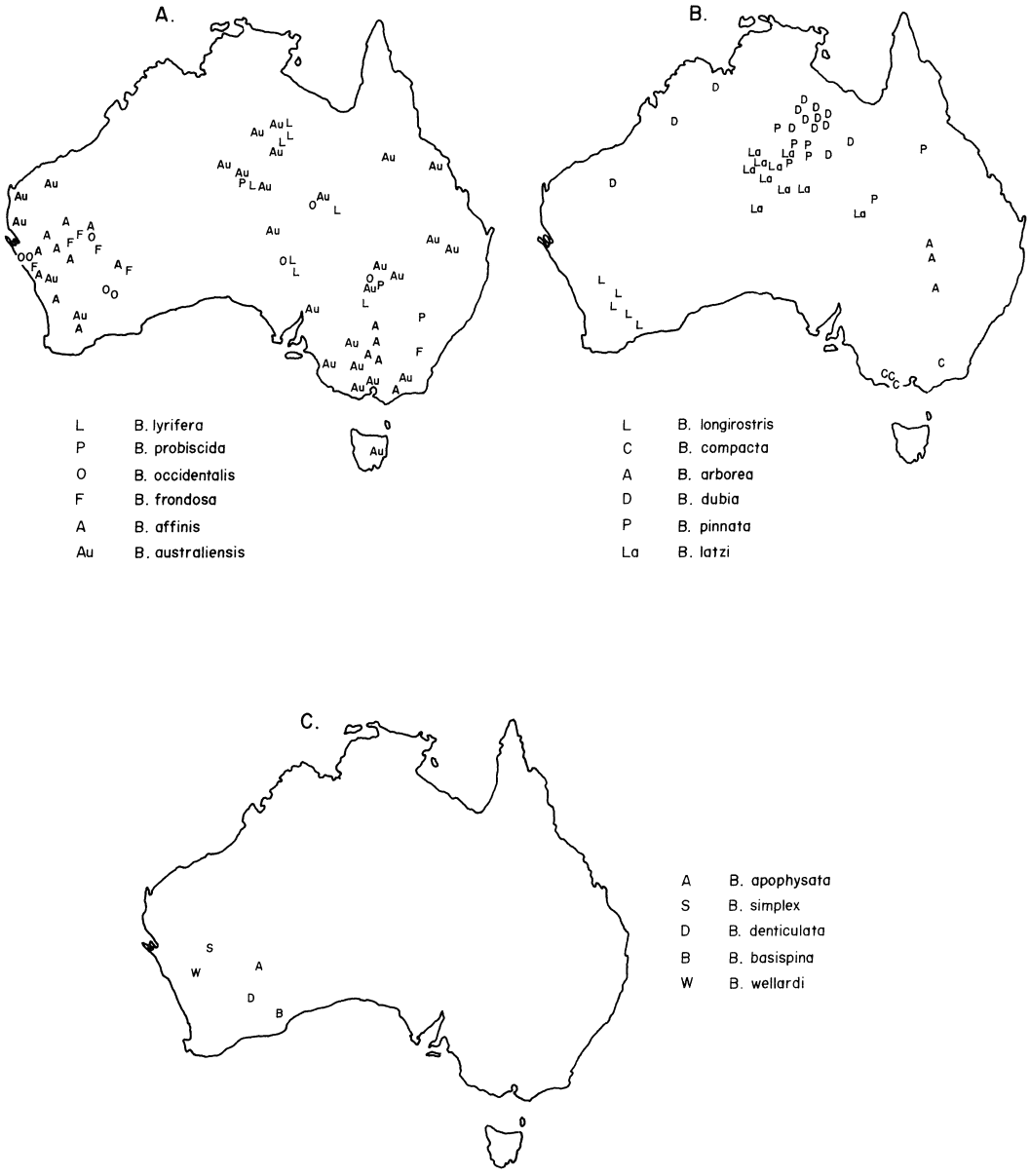

Fig. 2. Distribution of the Australian species of *Branchinella*.

occur do exist in the Australian Alps and in Tasmania. In the northern hemisphere many species and some genera occur in, and are restricted to, such environments (Pennak, 1978).

Ecology

Branchinella species typically occur in small (<2 ha), shallow (<1 m) temporary pools that persist from two to ten months, although some records are from permanent but very astatic pools. In northern

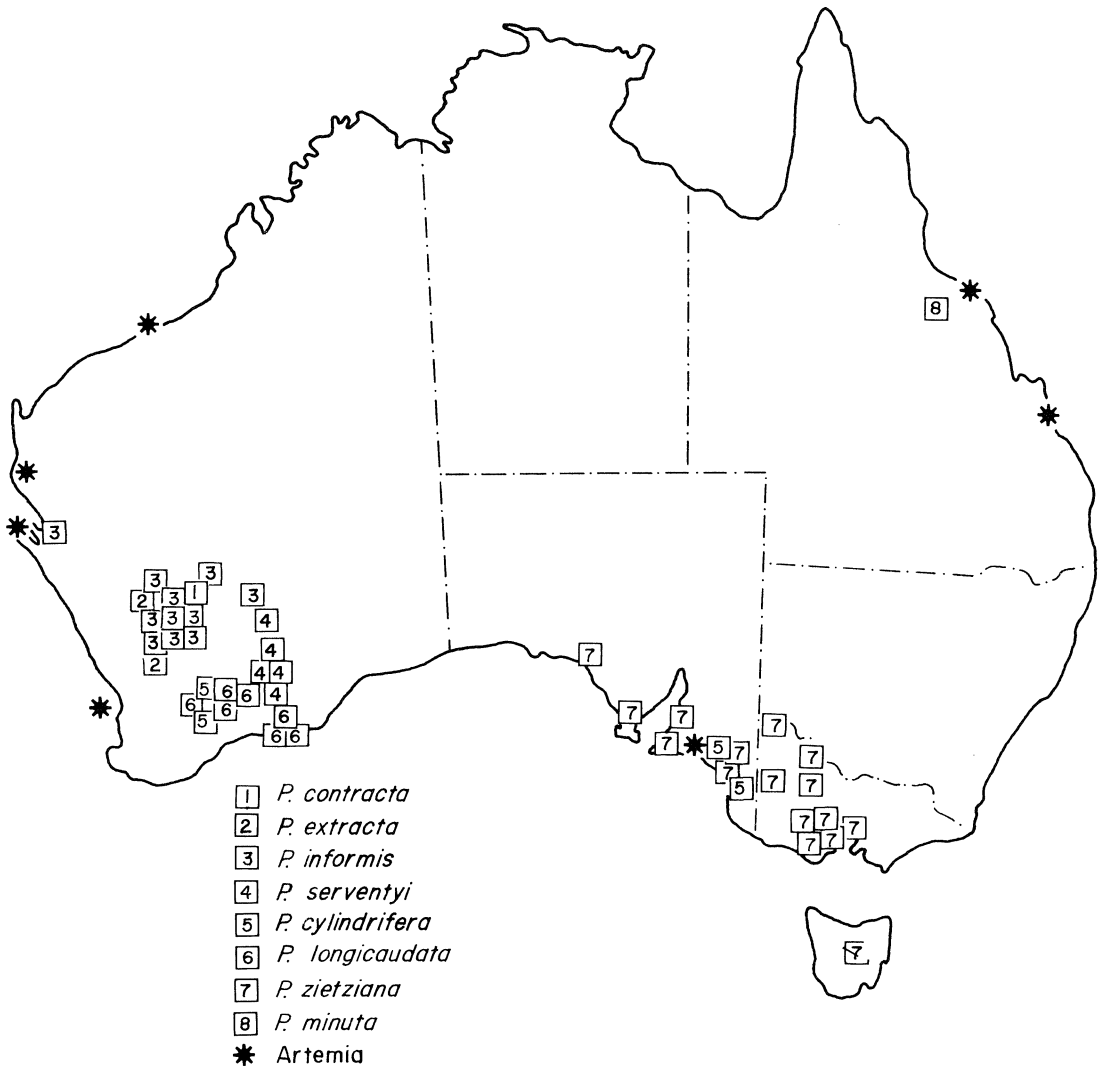

Fig. 3. Distribution of *Artemia* sp.(*) and the various species of *Parartemia* (□) in Australia.

Australia, where temperatures and evaporation rates are particularly high, *Branchinella* spp. were collected from considerably deeper (to 4 m) and larger (to several hundred ha) pools. In fact, in the north anostracans were generally absent from small shallow pools possibly as they were too short-lived. *Branchinella* habitats are usually turbid and have considerable diurnal fluctuations in temperature. Fish are usually absent but may be present in habitats that are formed by river flooding. Some examples of environments from which *Branchinella* has been collected are roadside ditches, claypans, natural depressions on volcanic or clay soils, temporary farm dams, temporary lagoons beside streams, and pools in the channels of intermittent streams (especially in northern and central Australia).

Parartemia typically occurs in ephemeral saline lakes which are less than 1.5 m deep when full and covered by a salt crust when dry. Some localities (e.g. Pink L., western Victoria) do not dry out every year but do have wide fluctuations in salinity and occasional desiccation. However, *Parartemia* does not occur in the more eustatic salt lakes in western Victoria (Geddes, 1976). *Parartemia* localities vary greatly in surface area from less than 1 ha to very large playa lakes like L. Monger and L. Moore in Western Australia.

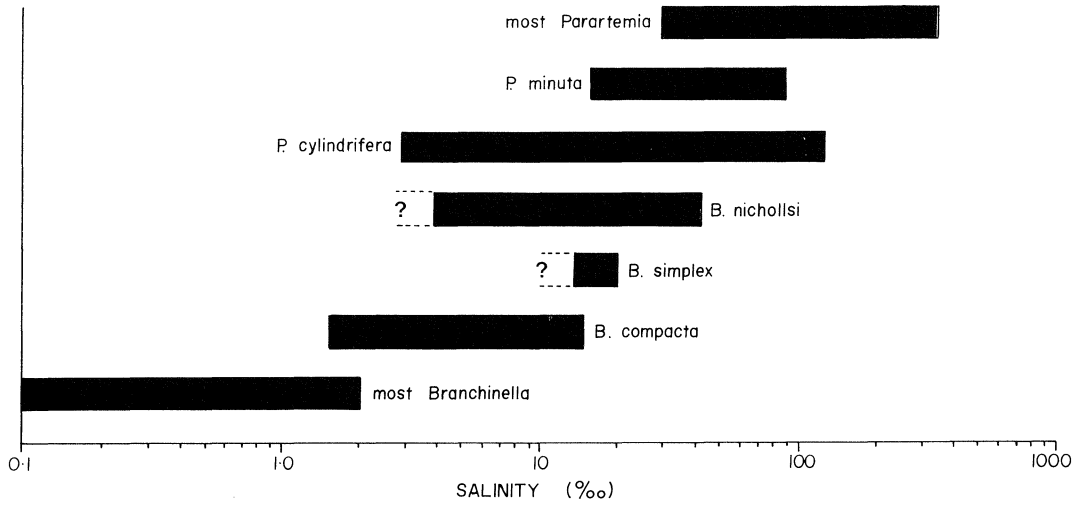

Fig. 4. Field salinity ranges for various species of Australian Anostraca.

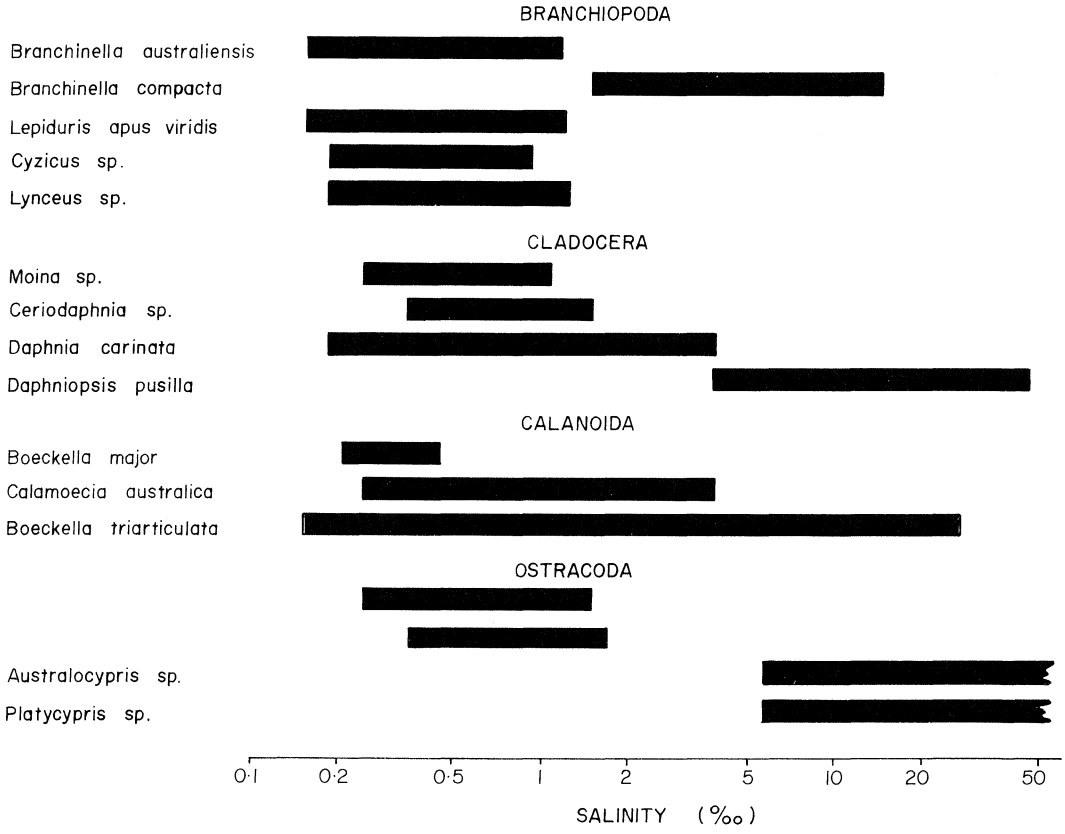

Fig. 5. Field salinity ranges for various crustaceans in temporary pools in western Victoria.

The field salinity ranges for the various species of Anostraca in Australia are shown in Fig. 4. Basically, *Branchinella* is a freshwater genus and *Parartemia* is halobiont. However at least three species of *Branchinella, B. compacta, B. simplex* and *B. nichollsi,* show tolerance to intermediate salinities and *P. minuta* and *P. cylindrifera* penetrate to slightly saline water. In L. Buchanan, Queensland, *B. nichollsi* occurred with *P. minuta* at salinities of 15.7 and 42.6°/oo (Geddes, 1973a). A similar mixture of stenohaline freshwater and euryhaline species of anostracans was reported by Hartland-Rowe (1966) in the temporary waters of western Canada.

Tables 1 and 2 show the fauna collected in association with several anostracans and so provide descriptions of the communities of ephemeral waters. Several studies have been made on the fauna of ephemeral saline lakes (Geddes, 1976; De Deckker and Geddes, 1980; Geddes *et al.,* 1981) and so the communities associated with *Parartemia* are well known. However little work has been done on ephemeral freshwaters and the only published record of communities containing *Branchinella* is by Morton and Bayly (1977).

Table 1 shows the fauna collected with several species of *Branchinella* in western Queensland and the Northern Territory, with *B. australiensis* in three areas in south-eastern Australia and with *B. compacta* in western Victoria. In all cases the communities were dominated by crustaceans, especially cladocerans and calanoid copepods. *Daphnia* (generally *D. carinata* s.l.) and *Boeckella* (generally *B. triarticulata*) almost always occurred with species of *Branchinella.* Notostraca and Conchostraca often occurred but they were not always present, and were usually absent in the larger, deeper *Branchinella* habitats in Queensland and the Northern Territory. A restricted fauna occurs in the slightly saline pools inhabited by *B. compacta* and presence of particular species appears to depend on salinity. The salinity range of *B. australiensis* and *B. compacta* and their associated faunas in western Victoria is shown in Figure 5. *Daphniopsis pusilla, Boeckella triarticulata* and ostracods make up the halophilic community associated with *B. compacta.*

The fauna collected with various species of *Parartemia* is shown in Table 2. *Parartemia zietziana* in south-eastern Australia and the halobiont species of *Parartemia* in Western Australia occur with halobiont copepods and ostracods. *P. cylindrifera* in South Australia occurs in pools with a much wider range of species including the cladoceran *Daphniopsis pusilla,* the amphipod *Austrochiltonia australis,* the isopod *Haloniscus searlei,* the gastropod *Coxiella* sp., and a polychaete worm. These pools generally have rich beds of the aquatic grasses *Ruppia* and *Lepilaena.*

Many of the localities sampled contained more than one species of *Branchinella.* Some co-occurrences are listed in Table 3. Most co-occurrences are of a large species, *B. australiensis* or *B. occidentalis,* with a smaller species, and it may be this size difference that makes co-existence possible. No co-occurrences of *Parartemia* species are known, although the distributions of several species in Western Australia overlap. A *Parartemia* species does co-occur with a species of *Branchinella* in at least one locality.

Discussion

Perhaps the most notable features of the Australian anostracan fauna are the low diversity at the generic level and the high degree of endemism. Whereas only two anostracan genera occur naturally in Australia, ten are known in North America (Belk, 1975), ten in Europe (Daday, 1910) and five in South Africa (Barnard, 1929). No Australian anostracan species occur outside Australia, and the otherwise cosmopolitan genus *Artemia* was apparently absent from the continent before the arrival of European man. Low diversity of higher taxonomic categories and high endemism are well known phenomena in Australia, but are somewhat surprising in a group of the age and supposedly high dispersal ability of the Anostraca. It should be recognised that the Australian anostracan fauna is isolated by climatic barriers as well as geographic ones, as no suitable environments exist in tropical northern Australia or in New Guinea and south-east Asia to allow movement of anostracans into Australia from Asia. Several authors (e.g. Bishop, 1967; Belk and Cole, 1975) have suggested that the dispersal ability of phyllopods may not be universally high. The world-wide distribution of *Branchinella* suggests that it is a very old genus which may have dispersed when geographic and climatic conditions were more favourable.

It is interesting to contrast the high degree of speciation in the Australian brine shrimp *Parartemia,* with the situation in *Artemia* where populations throughout the world are morphologically alike, although genetically somewhat different. *Artemia* is unusual among anostracans in that its resistant eggs generally float and are blown to the edge of lakes from where they are easily dispersed by wind and/or birds. The eggs of *Parartemia,* like those of most anostracans, sink and are bound up in the sediments of the lake, thus limiting their chances of dispersal.

Table 1. Zooplankton with species of *Branchinella* in various parts of Australia. (M) present in many localities; (F) few localities; (S) single locality; (X) only one or two localities investigated, and so no estimate of frequency of occurrence.

Taxa	*Branchinella* Qld. & N.T.	*B. australiensis* Carrieton, S.A.	*B. australiensis* western Victoria	*B. australiensis* Gippsland, Vic.	*B. compacta* western Victoria
BRANCHIOPODA					
Cyzicus	F	X	M		
Eulimnadia	S				
Lynceus	F		M	X	
Triops	F				
Lepidurus		X	F	X	
CLADOCERA					
Daphnia	M	X	M	X	F
Moina	M		F		
Diaphonosoma	F	X			
Ceriodaphnia			F		F
Daphniopsis					M
Saycia				X	
Neothrix	S				
Alona				X	
Biapertura				X	
chydorids	F		M		F
COPEPODA					
Boeckella	M	X	M	X	M
Diaptomus	M				
Hemiboeckella				X	
Calamoecia	M	X	F		S
Mesocyclops	M	X	M	X	
Microcyclops			F	X	
Attheyella				X	
OTHER				the following	
rotifers	F		M	ostracods:	
ostracods	F		M	*Newnhamia*	M
notonectids	M	X	M	*Cypretta*	F
corixids			F	*Cypris*	F
dytiscids	M	X	M		

In Australia anostracans occur more commonly in warm, arid and semi-arid areas than in cooler well-watered ones. Thus of 53 temporary freshwater pools in coastal eastern Victoria only three contained anostracans (Morton and Bayly, 1977), while they were present in most temporary pools investigated in the Northern Territory and western Queensland.

The distribution of anostracan species appears to be related to temperature and water chemistry (Belk, 1977; Hartland-Rowe, 1966), and also to other factors such as chance and food availability (Daborn, 1978). The effect of salinity on the distribution of Australian species is clearly shown in Figure 4. The restriction of some species of *Branchinella (B. dubia, B. latzi, B. pinnata)* to northern Australia where rainfall coincides with high temperature, and others *(B. compacta, B. longirostris)* to winter rainfall areas in southern Australia may be the result of temperature-dependent egg development as shown by Belk (1977).

The diversity of anostracans in any one area has been related to the chemical heterogeneity among habitats, especially in relation to salinity, and thermal variation resulting from ponds refilling in different seasons and from distribution of ponds along altitudinal and latitudinal gradients (Belk, 1977). In Australia the effect of variation in salinity on species diversity is clearly seen. In western Victoria three species of anostracan occur, with *B. australiensis* in fresh pools (<1°/00), *B. compacta* in adjacent slightly saline pools (2-15°/00) and *P. zietziana* in highly saline pools (Geddes, 1973b, 1975). In the

Table 2. Zooplankton with species of *Parartemia* in various parts of Australia. (M) present in many localities; (F) few localities; (S) single locality; (X) only one locality investigated.

Taxa	*P. zietziana* western Victoria	*P. zietziana* South Australia	*Parartemia* spp. Western Australia	*P. cylindrifera* South Australia Qld.	*P. minuta* L. Buchanan,
CLADOCERA					
Daphniopsis				M	
COPEPODA					
Calamoecia	M	M	F	M	
Boeckella				S	
Microcyclops	M	M	M	M	
Apocyclops					X
Mesochra	M	M		M	
Schizopera				S	
OSTRACODA					
Platycypris	M	M	M	M	
Diacypris	M	M	M	M	
Australocypris	M	M	M	M	
Reticypris		M	M	M	
Mytilocypris				F	
Limnocythere				S	
OTHER					
	Ephydrella S chironomid S		*Coxiella* F	*Austrochiltonia* M *Haloniscus* F *Coxiella* M polychaete F	*Branchinella*

Table 3. Co-occurrences of species of *Branchinella*.

locality	species present
Brunette Downs, N.T.	*B. lyrifera, B. dubia, B.* sp., *B. australiensis*
Hatches Ck Mine, N.T.	*B. pinnata, B.* sp., *B. australiensis*
Napperby Station, N.T.	*B. latzi, B.* sp., *B. australiensis*
Alice Springs, N.T.	*B. pinnata, B. australiensis*
Mt Doreen Station, N.T.	*B. latzi, B. australiensis*
Tenant Creek, N.T.	*B. dubia, B. australiensis*
nr Prairie, Qld.	*B. dubia, B. australiensis*
nth Barringun, Qld.	*B. arborea, B. australiensis*
L. Buchanan, Qld.	*Parartemia minuta, B. nichollsi*
nr Stratford, Vic.	*B. affinis, B. australiensis*
claypan nr L. Eyre, S.A.	*B. lyrifera, B. occidentalis*

Coorong region of South Australia a similar pattern occurs except that *P. cylindrifera* occupies the pools of intermediate salinity (De Deckker and Geddes, in press). The greatest diversity of Anostraca in Australia is found in Western Australia with 11 species of *Branchinella* and 6 species of *Parartemia* recorded. At least three factors appear to be operating to produce this diversity: (1) there is considerable variation in the salinity of the waters, (2) the semi-arid region extends over a considerable latitudinal gradient and is affected by both winter rain from the south-west and summer rain from the north, resulting in ponds filling under various thermal conditions, (3) the area is one of long continued geological stability and aridity (van de Graaff *et al.*, 1977). The first two factors provide habitat heterogeneity, while the third provides the time necessary for speciation to proceed within the area.

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