IV. FRESHWATER CRUSTACEA

by

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Introduction

It will be some considerable time before a review even approaching a definitive one of the ecology and biogeography of the Crustacea of Tasmanian inland waters can be produced: it is evident that much remains to be discovered and refined within the taxonomic sphere, that aside from a few exceptions precise ecological information for most species is still lacking, and that many questions of a zoogeographical nature remain unanswered or, indeed, have scarcely been posed. Nevertheless, enough time and material have accumulated since the last review of this sort was attempted (SMITH, 1909a) to make the present chapter a reasonably apposite endeavour. In any event, within the context of this book, omission of such a review would be a major omission, for the Crustacea of Tasmanian inland waters include several forms of significant zoological and biogeographical interest. It may be emphasised that the general arguments of GUILER (1965) concerning the lack of endemicity in the Tasmanian fauna and of DARLINGTON (1960) concerning its low diversity certainly do not apply to the freshwater Crustacea. GUILER's argument has been rebutted in detail elsewhere (BAYLY & WILLIAMS, 1965), but in summary the Tasmanian freshwater Crustacea is noted for its high diversity and endemicity *vis-a-vis* both the Australian mainland fauna and that elsewhere.

Firstly in this account, each of the major crustacean groups is considered in terms of its composition, local distribution and ecology. Broader zoogeographic aspects are considered separately and secondly.

Composition, distribution and ecology

ANOSTRACA

The only published reference to the occurrence of anostracans in Tasmania is a brief note in WILLIAMS (1968a) that 'there is an unpublished report of their presence in Tasmania.' Anostracans were not collected by GEOFFREY SMITH (1909a, 1909c) during his long sojourn in Tasmania, and there is no record of them in GUILER's (1952) list of branchiopods from Tasmania, or in HENRY's (1924) earlier list of Tasmanian phyllopods. They certainly occur, however, and both of the two foremost Australian genera, *Parartemia* and *Branchinella*, have been found (the remaining two,

Table 4.1. Extant Tasmanian freshwater Crustacea

Anostraca
   BRANCHIPODIDAE   *Parartemia zietziana* Sayce
   THAMNOCEPHALIDAE   *Branchinella australiensis* (Richters)
Notostraca
                                  Lepidurus apus viridis Baird
Conchostraca
   LIMNETIDAE   *Lynceus* sp.
   LIMNADIIDAE   *Eulimnadia* sp.
                                    Limnadia sp.
Cladocera
   DAPHNIIDAE   *Daphnia carinata* King
                                    Simocephalus vetula O.F.M.
                                    S. australiensis (Dana)
                                    S. dulvertonensis Smith (? = *S. vetula*)
                                    Ceriodaphnia quadrangula Sars (= *C. hakea* Smith)
                                    C. planifrons Smith (? = *C. quadrangula*)
   BOSMINIDAE   *Eubosmina meridionalis* (Sars) (= *Bosmina rotunda* Smith)
                                    B. sorelli Smith (? = *E. meridionalis*)
                                    B. brevirostris Smith (? = *E. meridionalis*)
   MACROTHRICIDAE   *Macrothrix burstalis* Smith
                                    *M. hirsuticornis Norman and Brady
   CHYDORIDAE   *Alonella nasuta* Smith
                                    A. propinqua Smith
                                    Dunhevedia crassa King
                                    *Alona diaphana King
                                    *A. quadrangularis O.F.M.
                                    *Chydorus poppei-barroisi (group)
Ostracoda
   DARWINULIDAE   *Darwinula* sp.
   CYPRIDIDAE   '*Cyclocypris*' sp.
                                    Bradycypris sp.
                                    Cypridopsis sp.
                                    Newnhamia sp.
                                    *Cypretta sp.
                                    Mytilocypris tasmanica McKenzie
                                    Ilyocypris sp.
                                    Ilyodromus spp.
                                    '*Eucypris*' sp. aff. *thomsoni* Chapman
   CYTHERIDAE   *Gomphocythere* sp.
                                    Lymnocythere conifera Brehm
   ENTOCYTHERIDAE   *Notocythere syssitos* Hart and Hart
                                    N. mirranatwa Hart and Hart
                                    N. tasmanica Hart and Hart
Copepoda
   CYCLOPOIDA   *Macrocyclops albidus* Jur.
                                    Mesocyclops leuckarti Claus (= *Cyclops albicans* Smith)
                                    Mesocyclops dulvertonensis (Smith) (? = *M. leuckarti*)
                                    Ectocyclops phaleratus Koch
                                    Diacyclops crassicaudoides Kief.
                                    Eucyclops nichollsi Brehm
                                    E. speratus Lilljeborg var. *tasmanica* Brehm
                                    Microcyclops sp.
   HARPACTICOIDA   *Attheyella (Chappuisiella) australica* Sars

Table 4.1. (continued)

	A. (Delachauxiella) salvatoris Brehm
	A. (Delachauxiella) incerta Brehm
	A. (Delachauxiella) fimbriata Brehm
CALANOIDA	*Calamoecia tasmanica tasmanica* (Smith)
	C. gibbosa (Brehm)
	C. expansa (Sars) (= *C. australis* (Searle))
	C. ampulla (Searle)
	C. clitellata Bayly
	Boeckella triarticulata (Thomson)
	B. bispinosa Bayly
	B. rubra Smith
	B. symmetrica Sars (= *B. insignis* Smith, = *B. lacuna* Fairbridge)
	B. major Searle
	B. robusta (Sars) (? = *B. major*)
	B. propinqua propinqua Sars
	B. propinqua longisetosa Smith
	B. pseudochelae Searle
	Hemiboeckella searli Sars
	Gladioferens (Gladioferens) spinosus Henry (= *G. henryae* Brehm)
	G. (Gladioferens) pectinatus (Brady)
	*Pseudoboeckella brevicaudata Brady

Branchiura

	Dolops tasmanianus Fryer

Syncarida
  ANASPIDACEA:

ANASPIDIDAE	*Anaspides tasmaniae* (Thomson)
	A. spinulae Williams
	Paranaspides lacustris Smith
	Allanaspides helonomus Swain, Wilson, Hickman and Ong
	A. hickmani Swain, Wilson and Ong
KOONUNGIDAE	*Micraspides calmani* Nicholls
	Koonunga sp.

  BATHYNELLACEA:

BATHYNELLIDAE	'*Bathynella*' spp.
PARABATHYNELLIDAE	*Atopobathynella hospitalis* Schminke

Isopoda
  ONISCOIDEA:

ONISCIDAE	*Haloniscus searlei* Chilton
ASELLOTA:JANIRIDAE	*Pseudasellus nichollsi* Chappuis (? = *Heterias pusilla* (Sayce))
	janirid sp. (? = *Pseudasellus* sp. or *Heterias* sp.)
	** ? janirid sp.

  PHREATOICOIDEA:

AMPHISOPIDAE	*Uramphisopus pearsoni* Nicholls
	Hypsimetopus intrusor Sayce
	Phreatoicoides longicollis Nicholls
PHREATOICIDAE	*Mesacanthotelson setosus* Nicholls
	M. tasmaniae (Thomson) (= *Phreatoicus spinosus* Smith)
	M. decipiens Nicholls
	M. fallax Nicholls
	Onchotelson brevicaudatus (Smith)
	O. spatulatus Nicholls

Table 4.1. (continued)

	Paraphreatoicus relictus Nicholls
	Colubotelson thomsoni Nicholls
	C. evansi Nicholls
	C. campestris Nicholls (? = *C. thomsoni*)
	C. huonensis huonensis Nicholls (? = *C. thomsoni*)
	C. huonensis flynni Nicholls (? = *C. thomsoni*)
	C. gesmithi Nicholls
	C. chiltoni chiltoni (Sheppard)
	C. chiltoni minor Nicholls
	C. chiltoni saycei Nicholls
	C. fontinalis Nicholls
	C. tattersalli tattersalli (Sheppard)
	C. tattersalli dubius Nicholls
	C. intermedius Nicholls
	C. setiferus Nicholls
	Metaphreatoicus magistri Nicholls (? = *C. thomsoni*)
	M. affinis Nicholls

Amphipoda
  CEINIDAE   *Austrochiltonia subtenuis* (Sayce)
                                    A. australis (Sayce)
  EUSIRIDAE   *Paracalliope* sp(p).
  GAMMARIDAE   *Neoniphargus montanus* (Thomson)
                                    N. yuli Smith
                                    N. exiguus Smith
                                    N. tasmanicus Smith
                                    N. wellingtoni Smith
                                    N. alpinus Smith (? = *N. fultoni* (Sayce))
                                    N. niger Smith
                                    N. spenceri (Sayce)
                                    'Gammarus' mortoni (Thomson)
                                    'G.' ripensis Smith
                                    'G.' antipodeus Smith
                                    'G.' australis Sayce

Decapoda
  ATYIDAE   *Paratya tasmaniensis* Riek (? = *P. australiensis* Kemp)
  HYMENOSOMATIDAE   *Halicarcinus lacustris* (Chilton)
  PARASTACIDAE   *Astacopsis franklinii* (Gray)
                                    A. gouldi Clark
                                    A. tricornis Clark
                                    A. fluviatilis Riek
                                    Parastacoides tasmanicus (Erichson) (= *P. setosimerus* Riek)
                                    P. inermis Clark
                                    P. insignis Riek (= *P. inermis*)
                                    P. leptomerus Riek (= *P. tasmanicus*)
                                    P. pulcher Riek (= *P. tasmanicus*)
                                    P. sternalis Riek (= *P. inermis*)
                                    Engaeus fossor (Erichson) (= *E. ignotus* Clark)
                                    E. cunicularius (Erichson)
                                    E. leptorhynchus Clark
                                    Geocherax falcata Clark

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* Macquarie Island only.
** Known only from Deal Island and Macquarie Island.

Artemia and *Streptocephalus*, are only doubtfully known from Australia) (Table 4.1).

Parartemia is represented by *P. zietziana* which occurs in a small area of salt pans near Tunbridge in the Midlands, that is in the driest region of Tasmania. It has been collected there by Dr. M. C. GEDDES (personal communication, 10 November 1972) who records that one of the localities where it occurred in 1971 was temporary, was only 20 cm deep, and had a concentration of total dissolved salts of 86‰, whereas the other was deeper (45 cm), had not dried out for two years prior to sampling, and had a concentration of total salts of 72‰. Other workers have also collected this species from the area (Dr. P. S. LAKE, personal communication, 10 November 1972).

Parartemia zietziana is widespread in south-eastern Australia where it occurs in a variety of inland saline water bodies from small, shallow, impermanent salt pans to larger, deeper and less temporary salt lakes over a range of concentration of total dissolved salts of *ca.* 40 to 300‰ (BAYLY & WILLIAMS, 1973). Its occurrence in similar localities in Tasmania is not the least surprizing.

Branchinella is represented by *B. australiensis*, specimens of which were collected in 1965 by Mr. J. H. WILSON from a small temporary fresh-water pool to the north of Campbelltown in the Midlands. The collection has been examined and identified by Drs. M. C. GEDDES & P. S. LAKE (personal communications, 10 November, 1972). Like *P. zietziana*, *B. australiensis* is widespread in mainland south-eastern Australia so that its occurrence in Tasmania also is not surprizing. Unlike *P. zietziana*, *B. australiensis* is a freshwater species.

NOTOSTRACA

Lepidurus apus viridis (Table 4.1) is widespread throughout the temperate and less arid parts of Australia and, more particularly, in the south-eastern region. It occurs also in New Zealand (HERRIOTT, 1917). Its original description was based on Tasmanian material for which BAIRD (1850) used the name *Lepidurus viridis*. Later, further species of *Lepidurus* were described from Australian mainland material, but these and the Tasmanian form were subsequently assigned in LONGHURST's (1955) review of the Notostraca to subspecific status in the taxon *L. apus*. The nominate subspecies of this, *L. apus apus*, is more or less cosmopolitan in distribution.

The Australian distribution of *L. apus viridis* has been plotted and commented upon by WILLIAMS (1968b) who noted that the only other Australian notostracan, *Triops australiensis australiensis*, a species more characteristic of drier areas, had not been recorded from Tasmania. In WILLIAMS (1968b, fig. 1), nineteen Tasmanian localities for *L. apus viridis* were plotted (including King Island); it is now possible to add several

more (Dr. P. S. LAKE, personal communication, 10 November 1972) so that the species can be regarded as common in Tasmania. Its habitat is small, temporary or semi-permanent freshwater ponds, pools and other still bodies of water, as well as on occasion larger bodies of still water (e.g. Lake Dulverton). Most specimens have been collected in September and October, that is, spring, although rarely specimens have been collected in other months.

CONCHOSTRACA

WILLIAMS (1968a) referred briefly to the presence of conchostracans in Tasmania, and in BISHOP's (1967) key to the Australian genera of Conchostraca there are notes that *Lynceus* (= *Limnetis*) and *Eulimnadia* occur in Tasmania. Although these are the only published references to conchostracans in Tasmania, in neither case were details of species or localities given. Conchostracans were not recorded by SMITH (1909a) or listed by HENRY (1924) or GUILER (1952) whose use of the term 'Conchostraca' to cover his listing of Tasmanian Cladocera was clearly erroneous.

BISHOP's (1967a) records of *Lynceus* and *Eulimnadia* were probably based upon two collections made by Mr. J. H. WILSON: (1) from a temporary pool (area, 0.1 ha; maximum depth, 15 cm; K_{18} = 2,140 μmhos) near Coles Bay in December 1964; and (2) from a temporary pool near Campbelltown in October 1965 (Dr. P. S. LAKE, personal communication, 10 November 1972). One genus occurred in the first collection, both in the second. In addition to these records, Dr. P. S. LAKE collected *Limnadia* sp. from a small temporary pool (area 0.2 ha, maximum depth 20 cm) near Cambridge in September, 1969 (personal communication, 10 November 1972).

It is unfortunate that for none of these collections are species identities available, but considering the degree of taxonomic confusion which presently prevails in the Conchostraca, especially with regard to the distinction of *Eulimnadia* and *Limnadia*, this is perhaps not surprizing. For the moment, it can only be said that three of the more common genera of the mainland occur rarely in Tasmania (Table 4.1), where they occupy similar localities to those most frequently occupied on the mainland.

CLADOCERA

Our knowledge of Tasmanian Cladocera is, to say the least, fragmentary. Little has been published that is at all critical, and the group requires a modern revision. The list of taxa presented in Table 4.1 as cladocerans recorded from the State cannot be regarded, then, as any more than an indication of the extent to which further investigation is required.

Of the eleven families of Cladocera now recognized (that is, accepting, in line with recent reviews (SMIRNOV, 1971), the three recent families of MORDUKHAI-BOLTOVSKOI (1968) and GOULDEN (1968)), four have so far been found in Tasmania: Daphniidae, Bosminidae, Macrothricidae and Chydoridae. The remaining Australian families, Sididae and Moinidae, remain unrecorded.

The number of Daphniidae is uncertain. SMITH (1909a) described three endemic species, but BREHM (1953b) has equated one, *Ceriodaphnia hakea*, to the widespread *C. quadrangula*, and another, *C. planifrons*, was also thought to be probably synonymous with that species. *Simocephalus dulvertonensis*, the other daphniid 'endemic', was thought by BREHM to be synonymous with the widespread *S. vetula*. In any event, both *C. quadrangula* and *S. vetula* have been independently recorded from Tasmania (BREHM, 1953b). *Daphnia carinata* and *S. australiensis*, common mainland forms, also occur, the former being known too from Macquarie Island (EVANS, 1970).

An analogous situation prevails in the Bosminidae. SMITH (1909a) described three endemic forms of which BREHM (1953b) thought one, *Bosmina rotunda*, was almost certainly synonymous with the non-endemic species, *B. hagmanni*, and two, *B. brevirostris* and *B. sorelli*, were thought to be less certainly synonymous. However, as indicated in the recent review of American species of *Eubosmina* by DEEVEY & DEEVEY (1971), *Eubosmina* (= *Bosmina*) *hagmanni* is probably confined to North and South America and, by implication but not direct statement, it is *Eubosmina meridionalis* into which *B. rotunda* and probably SMITH's other two taxa fall. *E. meridionalis* is certainly not endemic to Tasmania and apparently occurs widely on the mainland, at least in the east (e.g. JOLLY, 1966). In this connection, attention may be drawn to the comment by the DEEVEYS (1971: 202) that: 'Because the *Eubosminas* are strongly cyclomorphic, the proportions of carapace, rostrum, and mucro are subject to seasonally differing patterns of allometric growth. Their systematic value is therefore dubious at best . . .'. Yet it was carapace shape that was the first character used by SMITH (1909a) to differentiate his three taxa. The species '*Bosmina geoffreyi* Smith' and '*B. [Bosmina] tasmanica* Smith' noted by HENRY (1922) as recorded from Tasmania are *nomina dubia*.

Only a single macrothricid has been recorded, *Macrothrix burstalis*. It is apparently endemic.

Three chydorids have so far been reported, two of which are apparently endemic, *Alonella nasuta* and *A. propinqua*. *Dunhevedia crassa* also occurs (BREHM, 1953b). For some reason, though *A. nasuta* is mentioned in SMIRNOV's (1971) recent world review of chydorids, reference to *A. propinqua* is omitted.

In addition to *Daphnia carinata*, *Alona diaphona*, *A. quadrangularis*, *Chydorus poppei-barroisi* (group) (all chydorids) and the macrothricid

Macrothrix hirsuticornis have been collected from Macquarie Island (EVANS, 1970).

With regard to the ecological distribution of Tasmania cladocerans, it may be noted that in the zooplankton of the numerous lakes investigated by TYLER (Chapter III), there were one or two cladoceran species of which the commonest were *Daphnia carinata* and *E. meridionalis*. However, a few other zooplanktonic cladocerans have been recorded from Tasmanian lakes: *Ceriodaphnia quadrangula, C. planifrons* (assuming the validity of this species), *Simocephalus vetula*, and, if valid species, *B. brevirostris* and *B. sorelli*. From ponds, dams and smaller bodies of water, the following have been recorded: *Ceriodaphnia quadrangula, Simocephalus australiensis, S. vetula, Daphnia carinata* and *Dunhevedia crassa*. And species that have been collected from amongst weeds in the larger lakes are *Simocephalus dulvertonensis, Macrothrix burstalis, Alonella nasuta* and *A. propinqua*. All cladocerans reported from Macquarie Island by EVANS (1970), with the exception of *Daphnia carinata*, were collected from ponds or lagoons. *D. carinata* occurred in Prion Lake.

The only ecological investigations of the Cladocera that lay any claim to being intensive are the early and uncritical work of POWELL (1946) and the recent comprehensive studies of BURROWS (1968). POWELL investigated the zooplankton of Lake St. Clair over a year and BURROWS that of Lakes Sorell and Crescent over a period of similar length.

In POWELL's study four species were noted as present and these were named *Ceriodaphnia hakea, C. planifrons, Bosmina sorelli* and *B. rotunda*. It is likely, of course, that in fact only two were present, viz. *Ceriodaphnia quadrangula* and *Eusbosmina meridionalis*. All taxa were present in large numbers during the summer months and a distinct cladoceran 'peak' in zooplanktonic numbers was observed in January (which apparently coincided with the occurrence of minimal numbers of other zooplanktonic forms).

BURROWS' (1968) study of lakes Sorell and Crescent showed that in both lakes there were more or less randomly distributed populations of *Eubosmina meridionalis, Daphnia carinata* and *Ceriodaphnia quadrangula*. However, these displayed seasonal differences within each lake and between lakes. Thus, *E. meridionalis* although present in Lake Sorell was not the dominant zooplankter there (that position was occupied by a calanoid copepod, *Boeckella rubra*), whereas it was dominant in Lake Crescent. Concerning seasonal variation in numbers, *E. meridionalis* showed one population peak in both lakes but with apparently greater variation in Lake Crescent. *Daphnia carinata* showed a late winter peak in both lakes whereas *C. quadrangula* apparently had a prolonged winter/early spring population peak in Lake Sorell only. The time of maximal numbers of *D. carinata* agrees in general with the timing elsewhere of the greatest numbers of this species, but elsewhere *C. quadrangula* has a tendency for highest numbers in spring or summer (BAYLY & WILLIAMS, 1973).

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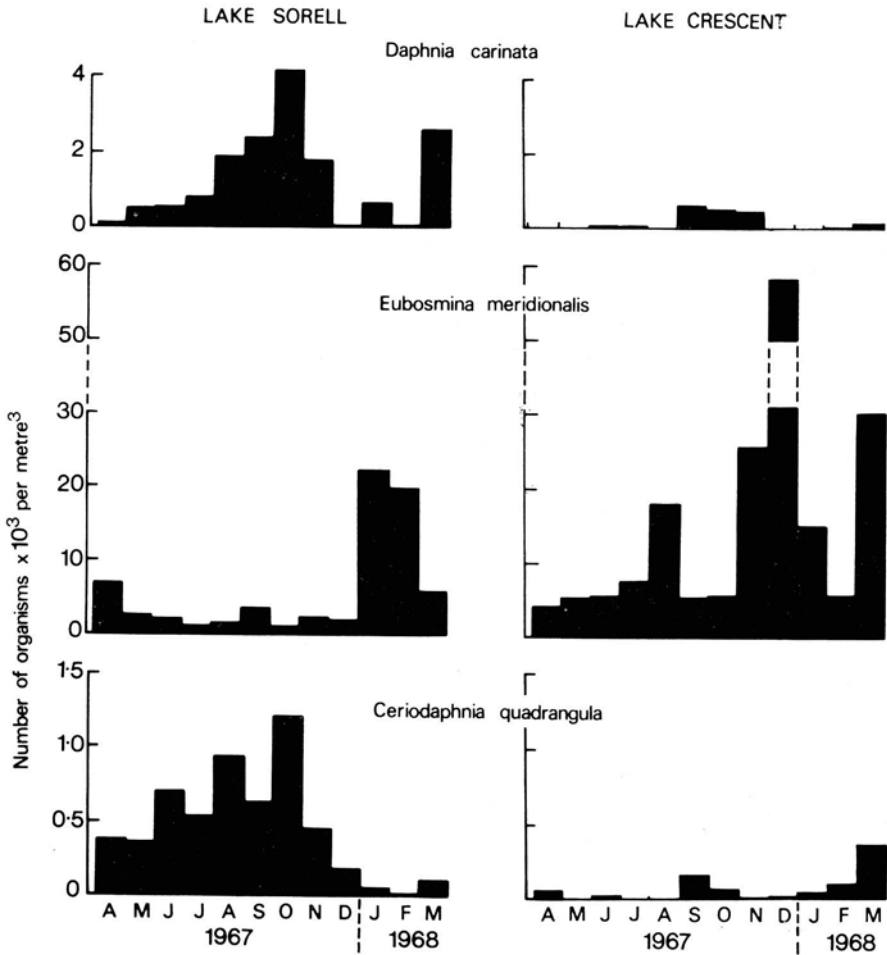
Fig. 4.1. Seasonal variations in numbers of zooplanktonic Cladocera in Lakes Sorell and Crescent (modified from BURROWS, 1968).

Ceriodaphnia quadrangula and *D. carinata* never represented a very large proportion of the total zooplankton population at any season, usually being 10–20 per cent in Lake Sorell and 2–5 per cent in Lake Crescent. Their size, however, made them important food components for secondary consumers. The differences in the cladoceran population of these two lakes is extremely interesting for the lakes are of similar age, origin, morphometry and are adjacent, yet exhibit numerous biological differences of which those between their Cladocera are only a few. BURROWS' (1968) data on seasonal fluctuations in cladoceran population numbers and on the varying composition of the zooplankton of the two lakes are summarized in Figs. 4.1 to 4.3.
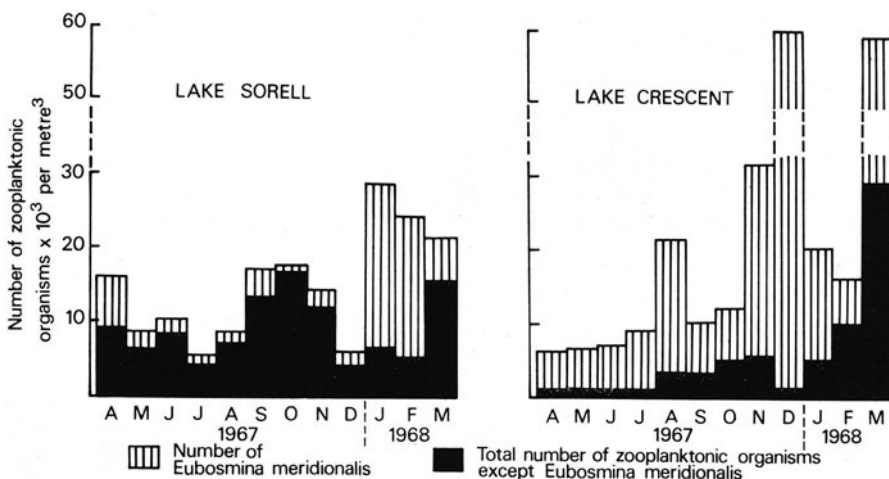
Fig. 4.2. Seasonal variation in total number of zooplanktonic organisms and *Eubosmina meridionalis* in Lakes Sorell and Crescent (modified from BURROWS, 1968).

OSTRACODA

Some idea of the paucity of our knowledge of Tasmanian freshwater ostracods can be gained from noting that neither SMITH (1909a), HENRY (1923) or GUILER (1952) referred to any in their accounts or lists of Tasmanian freshwater Crustacea. Indeed it is only in the last twenty years that investigations of any sort have been pursued on Tasmanian ostracods and even these are sparse, taxonomic in approach, and deal mostly with generic determinations only. This paucity of knowledge is not a reflection of the scarcity of these crustaceans in Tasmania – they are as common and abundant there as are they in mainland Australia and elsewhere – but more a general reflection of the apparent disinterest in Australian freshwater ostracods as a whole by workers in the field (with some honourable exceptions) and, perhaps, a reflection too of the relative difficulty of ostracod systematics. On this account, only the barest of introductions to the composition and ecology of the group can be given here. Only passing reference is made to the fossil ostracods (some extant on mainland) recorded from Cainozoic deposits in north-western Tasmania, namely, *Candona lutea*, *Candonocypris candonoides*, *Darwinula* sp., *Limnicythere mowbrayensis* and *Ilyodromus stanleyanus* (GILL & BANKS, 1956). None of the species recorded has yet been collected alive in Tasmania.

Despite the lack of local study, all four Australian mainland families of freshwater ostracods have been recorded. The Darwinulidae, represented by its only genus *Darwinula*, has been recorded by MCKENZIE (in MCKENZIE, 1971, and WILLIAMS, 1968a), although no species
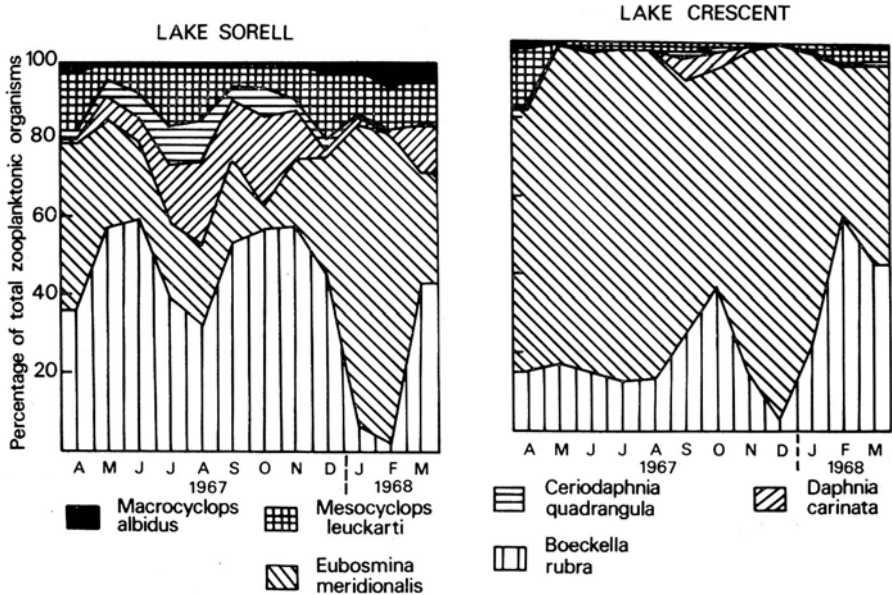
identification is available. The Cyprididae is represented by the genera *Bradyocypris* and *Cypridopsis* from the Furneaux Islands (MCKENZIE & NORMAN, 1968) and by *Newnhamia, Mytilocypris, Ilyocypris, Ilyodromus*, '*Cyclocypris*' and '*Eucypris*' on Tasmania proper (MCKENZIE, 1966, 1971; BAYLY, PETERSON, TYLER & WILLIAMS, 1966). *Cypretta*, another cypridid, was recorded from Macquarie Island by EVANS (1970). With the exception of *Mytilocypris*, for none of these genera is a firm species name available. *Mytilocypris* itself is a genus originally described from Tasmanian material and has a single species so far named, *M. tasmanica*. Two genera of the Cytheridae have been reported: *Gomphocythere* and *Limnocythere*, the latter as *L. conifera* (BREHM, 1953b, MCKENZIE, 1966, 1971). Finally, three species of the Entocytheridae have recently been described from Tasmania by HART & HART (1967), namely *Notocythere syssitos, N. mirranatwa* and *N. tasmanica*.

The entocytherids, as have been all members of the family, were collected as parasites of freshwater crustaceans, in this case the hosts being the crayfish genera *Astacopsis* and *Parastacoides*. *Darwinula* was obtained from a periglacial tarn in the south-west of the State. *Limnocythere, Mytilocypris, Gomphocythere* and *Ilyocypris* were reported from shallow lagoons near the coast, the last three genera from one which was slightly saline, and *Cypridopsis* and *Bradycypris* from pools also coastal in location. Two species of *Ilyodromus* and a species of '*Eucypris*' occurred in the psam-

mon of Lake Pedder's quartzite beach and 'Cyclocypris' occurred in the
benthos community of this lake. The species of Cypretta recorded from
Macquarie Island was collected from ponds and a lagoon.

COPEPODA

There are no published records of freshwater parasitic copepods in
Tasmania: all published material relates to free-living species in the
orders Cyclopoida, Harpacticoida and Calanoida. Only three workers
have attempted to deal at all seriously with the taxonomy of these,
namely SMITH (1909a) in his early survey of Tasmanian freshwater
crustaceans, BREHM (1950, 1953a) in his restricted treatment of Tas-
manian Copepoda, and BAYLY (1961, 1963, 1964b, 1967) as part of his
revision of Australian calanoids. Additionally there exist a few incidental
references to the group, and two lake zooplankton studies which included
ecological considerations of cyclopoid and calanoid copepods (POWELL,
1946; BURROWS, 1968). For present purposes, each of the three orders
is best considered separately.

Within the Cyclopoida, two taxa were recognized by SMITH (1909a)
and these he regarded as new species, 'Cyclops albicans' and 'C. dulvertonensis'.
Both of SMITH's taxa were subsequently transferred to the genus Meso-
cyclops, and the first synonymized with the cosmopolitan species, Meso-
cyclops leuckarti. SMITH's other taxon, according to BREHM (1953a), is also
likely to be synonymous with M. leuckarti. BREHM (1953) himself rec-
ognized six cyclopoid taxa – including M. leuckarti but not Mesocyclops
dulvertonensis – of which three were cosmopolitan (Macrocyclops albidus,
Mesocyclops leuckarti and Ectocyclops phaleratus), one was Australasian
(Diacyclops crassicaudoides), and two were Tasmanian endemics (Eucyclops
nichollsi*, E. speratus var. tasmanica) but thought likely to occur also on
the mainland. In addition to these initial records, Macrocyclops albidus
was reported from Lake Pedder by BAYLY, PETERSON, TYLER & WIL-
LIAMS (1966), and this species and M. leuckarti from King Island by
BRAND (1967) who further reported the presence there of Microcyclops
a genus otherwise previously unrecorded from Tasmania. Mesocyclops
leuckarti (erroneously reported as Microcyclops leuckarti) and M. albidus
have been reported too by BURROWS (1968), and M. leuckarti (as Cyclops
albicans) by POWELL (1946).

Ecological data for these various cyclopoid occurrences are in general
rather imprecise, but localities to which they refer range in type from
pools in the beds of rivers to roadside ponds and large lakes. Unidentified
cyclopoids were present too in several of the collections of interstitial

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* A brief description of this species appeared first in 1950 (BREHM, 1950) thus predating
by three years the description that BREHM (1953a) apparently intended as the original
one.
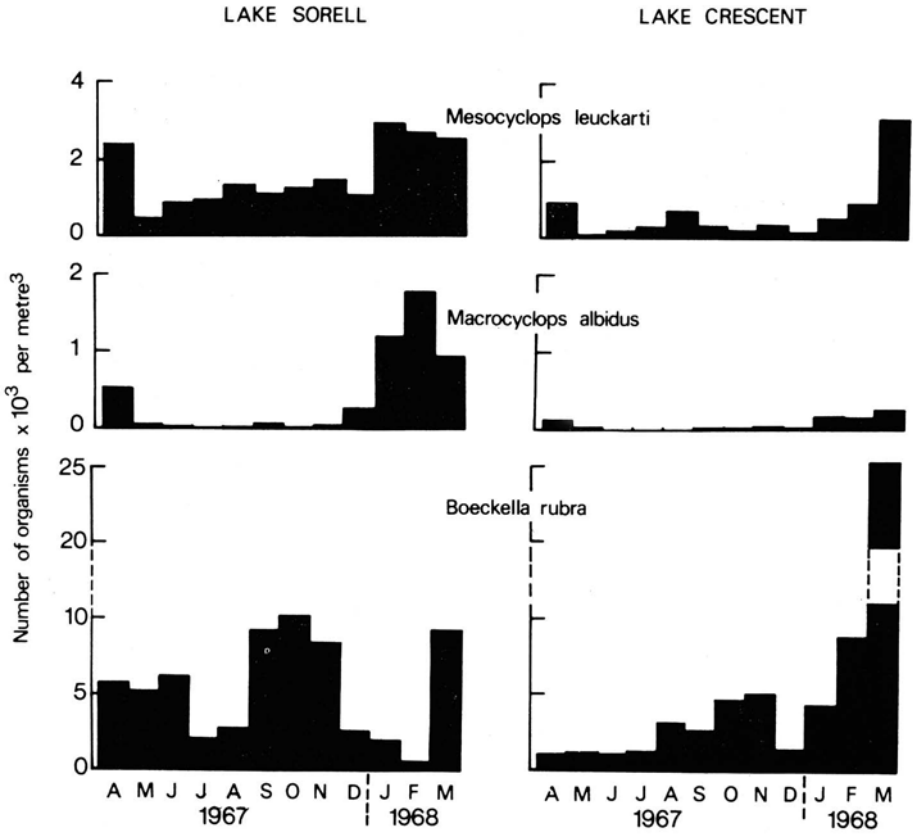
Fig. 4.4. Seasonal variation in numbers of zooplanktonic Copepoda in Lakes Sorell and Crescent (modified from BURROWS, 1968).

fauna made by SCHMINKE (1971) in the course of his investigations of Tasmanian syncarids (see below). Perhaps in lakes most species *typically* occur in peripheral littoral regions as cyclopoids usually do elsewhere. Nevertheless, some species certainly are truly planktonic; although not usually dominant in the zooplankton of the numerous Tasmanian lakes studied by TYLER (Chapter III), both *Macrocyclops albidus* and *Mesocyclops leuckarti* are common cyclopoids in these, and, for example, both species occur in the zooplankton of Lakes Sorell and Crescent (BURROWS, 1968). *Mesocyclops leuckarti* (as *Cyclops albicans*) and 'a large [cyclopoid] species' occur in the zooplankton of Lake St. Clair (POWELL, 1946: 86). *Mesocyclops leuckarti* was noted by BREHM (1953a: 57) as present in all the samples investigated by him and as 'obviously the most frequent Cyclops of the island'.

Concerning the ecological investigations by POWELL (1946) and

BURROWS (1968), it may be noted that in Lake St. Clair cyclopoids represented about 5 per cent of total zooplanktonic Crustacea (POWELL, 1946) and never more than about 10 per cent of the zooplankton of Lakes Sorell and Crescent BURROWS (1968) (see Fig. 4.3). Exact quantitative data on total numbers are available only for Lakes Sorell and Crescent; in these lakes, total numbers never exceeded 4,000 individuals per cubic metre for *M. leuckarti* and 2,000 for *M. albidus* (Fig. 4.4). In both lakes, *M. leuckarti* was perennially present but displayed, as did *M. albidus*, a single population peak which seemed to coincide with an autumnal primary production peak (BURROWS, 1968). Both species appeared to be univoltine.

The freshwater harpacticoids have been investigated by BREHM (1950, 1953a) who recorded at least five species but named only four: one previously known from the Australian mainland, *viz. Attheyella (Chappuisiella) australica*, and three new ones, viz. *A. (Delachauxiella) salvatoris*, *A. (Delachauxiella) incerta*, and *A. (Delachauxiella) fimbriata*. The latter species was definitely named in BREHM's paper published in 1950, yet left unnamed in his second (!) description of Tasmanian harpacticoids published in 1953. BREHM regarded the subgenera into which these species are placed here as genera.

The only ecological information available for all these species is that the samples studied by BREHM came from pools in the bed of the Jordan River and from Big Lake Waterhouse. That harpacticoids also occur in Tasmania in interstitial waters associated with rivers is indicated by SCHMINKE's (1971) work noted above; he recorded harpacticoids in association with the cyclopoids also present.

Brief reference may be made here to the possibility of *Tigriopus californicus* occurring in Tasmanian fresh waters. This harpacticoid was recorded in the estuary of the Brown River by LANG (1934) but outside Tasmania has been collected additionally from fresh waters; for example, it has been recorded by BREHM (1935) from a lake in the Andes located at 3,000 m above sea-level. LANG (1948: 342) noted that 'Diese Art kommt sowohl in Brack- als in Süsswasser vor, bisweilen weit vom Meere entfernt'.

All the calanoids recorded belong to the family Centropagidae, by far the most important, but not the only Australian family. Four genera occur in Tasmania *sensu stricto*, *Calamoecia*, *Boeckella*, *Hemiboeckella* and *Gladioferens*. In addition, *Pseudoboeckella* occurs on Macquarie Island. Due mainly to the recent Australia-wide systematic studies of BAYLY (1961, 1963, 1964b, 1967) perhaps more is known concerning the taxonomy of this group of Tasmanian crustaceans than any other. However, it is inappropriate here, and unnecessary, to consider the detailed systematic history; the following summary is sufficient for present purposes.

SMITH (1909a) recorded only one species of *Calamoecia*, *C. tasmanica*,

as also did BREHM (1950, 1953a), *C. gibbosa*. Both were described first from Tasmanian material as species of *Brunella* and remain valid species, but have subsequently been found to occur in one or more mainland States (BAYLY, 1961, 1964a; BAYLY & WILLIAMS, 1964). There is thus no longer any species of this genus endemic to Tasmania. The current total list of species of *Calamoecia* now known to occur in Tasmania, and including both previously published records (BAYLY, 1961) and several unpublished ones (BAYLY, personal communication, 28 November 1972) is: *C. tasmanica tasmanica, C. gibbosa, C. expansa, C. ampulla* and *C. clitellata*. None of these occurs in New Zealand and, perhaps surprizingly, the widespread Australasian species, *C. lucasi*, has not yet been recorded from Tasmania.

With regard to *Boeckella*, SMITH (1909a) identified four species from Tasmanian material of which three were regarded as new. The fourth, *B. robusta*, had previously been described from the mainland and in any event, according to BAYLY (1964b), may have been a misidentification of *B. major* also known from the mainland. Of SMITH's proposed new species, one, *B. rubra*, remains valid and endemic, one has been synonymized with the non-endemic species *B. symmetrica*, and one has been given subspecific status in another non-endemic species, *B. propinqua*. BREHM (1950, 1953a) recorded three additional species of which one was thought to be new, but was later synonymized by BAYLY (1964b) with a known species. Finally, BAYLY (1964b) has dealt intensively with material from Tasmania and recorded several new taxa additional to those seen by SMITH and BREHM. The present position then is that there are definitely seven species present and perhaps eight, one of which is represented by both of its recognized subspecies. Of these taxa, one species and one subspecies are endemic to Tasmania (respectively, *B. rubra* and *B. propinqua longisetosa*), three or four occur on the Australian mainland as well as in Tasmania (*B. pseudochelae, B. major, B. bispinosa*, and perhaps *B. robusta*), and three also occur on the mainland and in New Zealand (*B. propinqua propinqua, B. symmetrica*, and *B. triarticulata*). No species of *Boeckella* is restricted to Tasmania *and* New Zealand (although it may be noted that *B. propinqua propinqua* has not been recorded in Victoria since 1910, and as some doubt attaches to this record it is possible that this species is restricted to Tasmania and New Zealand).

The remaining Tasmanian calanoid genera are much less diverse. One, *Hemiboeckella*, has a single Tasmanian species, *H. searli*, which is also recorded from Victoria. The other, *Gladioferens*, is represented by two species, *G. (Gladioferens) spinosus* and *G. (Gladioferens) pectinatus*, of which the first also occurs on the Australian mainland and includes the nomen *G. henryae* described as a Tasmanian endemic by BREHM (1950, 1953a), while the second occurs on the Australian mainland and in New Zealand.

Finally, the only definite record of a copepod from Macquarie Island by EVANS (1970) is that of *Pseudoboeckella brevicaudata*.

Table 4.2. Calanoid copepod associations recorded in five Tasmanian localities (extracted from BAYLY & WILLIAMS, 1973)

Locality	Large species	Small species
1	*B. symmetrica*	*B. rubra*
2	*B. triarticulata*	*B. rubra*
3	*B. symmetrica*	*C. gibbosa*
4	*B. propinqua*	*C. gibbosa*
5	*B. major*	*B. pseudochelae*

Several of the calanoid species enumerated above occur together in associations which suggest that HUTCHINSON's (1951) ideas about size differentiation and competition in copepods are in operation. BAYLY (1964b) has already drawn attention to the fact that two differently-sized calanoids quite commonly occur in Australian lakes. Such associations have been noted in several Tasmanian localities and those that have been recorded in BAYLY & WILLIAMS (1973, table 6:3) are shown in Table 4.2. Occasionally, more than two calanoids coexist, and in one Tasmanian locality a total of five have been found together, namely *Boeckella major*, *B. pseudochelae*, *B. bispinosa*, *B. triarticulata* and *Calamoecia gibbosa*. This association was found in a small pool near Campbelltown (BAYLY, 1967).

The sorts of habitat from which Tasmanian calanoids have been collected are extremely varied. They range from pools in the beds of rivers to roadside pools and ponds, man-made impoundments of all sizes, small and large lowland and highland lakes, coastal lagoons, inland saline water bodies and the lower reaches of the large rivers. Predictably, however, calanoids were not amongst the copepods collected by SCHMINKE (1971) from interstitial waters associated with Tasmanian rivers. Some species occur in a variety of habitat, others are much more restricted; some are local in distribution, others are widespread throughout the island.

There is little need to document for all species distributional range and habitat preferences, but mention of some of the more interesting occurrences needs no excuse. *Calamoecia clitellata*, as on the mainland, is found only in highly saline inland lakes where salinities it is able to tolerate may exceed 100‰. It is known in Tasmania from a small salt lake near Tunbridge. *C. expansa* dominates the zooplankton of Lake Pedder and Lake Edgar which are therefore two of only three known localities in which this species occurs in large populations (the other is Wartook Reservoir in Victoria) (BAYLY in JOHNSON, 1972). *C. tasmanica tasmanica* is restricted to waters of low salinity and calcium content and the presence of humic acids seems to provide optimal environments (BRAND, 1967). Unlike mainland populations of this species which are almost entirely restricted to coastal situations, in Tasmania it has been collected well

inland, for example in the Maria Lake complex at Lake Pedder (BAYLY, PETERSON, TYLER & WILLIAMS, 1966) and from moorland pools at considerable altitude.

Three species of *Boeckella*, viz *B. major*, *B. pseudochelae* and *B. bispinosa*, are probably restricted to small bodies of fresh water where they occur during late autumn to early spring (BAYLY, 1967). The others, except *B. robusta*, occur in water bodies of various sizes but inclusive of many large lakes throughout the island. Species of *Gladioferens* and *Hemiboeckella* are only recorded from coastal localities.

In determining these distributions, factors related to altitude, such as temperature, probably play some role, but perhaps less than was suggested by BAYLY (1964b) who gave a table (table 2) relating all records of *Calamoecia* and *Boeckella* to altitude. Subsequent records indicate that the altitudinal stratification is somewhat less precise than BAYLY seemed to have thought; for example, both *B. pseudochelae* and *B. major*, formerly thought to be confined to low altitudes, are now known to occur at altitudes in excess of 1,000 metre above sea-level. It remains true, nonetheless, that some taxa are clearly highland forms *(B. rubra, B. propinqua longisetosa)*, and others lowland (e.g. *B. propinqua propinqua*, various coastal species). The highland distribution of *B. rubra* was a feature commented on by SMITH (1909a) in his description of the species.

Seasonal data exist for two calanoids populating the limnetic regions of Tasmanian lakes. POWELL (1946) studied, *inter alia*, a population of *B. propinqua longisetosa* (as *B. longisetosa*) in Lake St. Clair. And BURROWS (1968) studied populations of *B. rubra* in Lakes Sorell and Crescent. Briefly, in Lake St. Clair, *B. propinqua longisetosa* constituted about 57 per cent of total zooplankton, was perennially present, and showed indistinct spring and autumn maxima in numbers. Two similar numerical maxima were displayed by *B. rubra* in Lakes Sorell and Crescent; these occurred in spring and late autumn (Fig. 4.4), and appeared to coincide approximately with two peaks in primary production. This species likewise was perennially present and accounted for a significant proportion of the zooplankton throughout most of the year in both lakes (Fig. 4.3), though was less important in Lake Crescent than in Lake Sorell (about 45 per cent in Lake Sorell, and usually 20 per cent in Lake Crescent).

Full discussion of the intensive ecological study of *Pseudoboeckella brevicaudata* on Macquarie Island is beyond the scope of this chapter. It need be noted only that this calanoid dominated the zooplankton there, occurred widely throughout the island and in nearly all types of water body except very shallow ponds lacking vegetation. There were certain differences in life-cycle and associated phenomena according to the type of water body inhabited, but eggs hatched throughout the year in all populations although hatching rates varied seasonally. Adults were perennially present and maximum numbers of copepodids occurred in late spring/early summer.
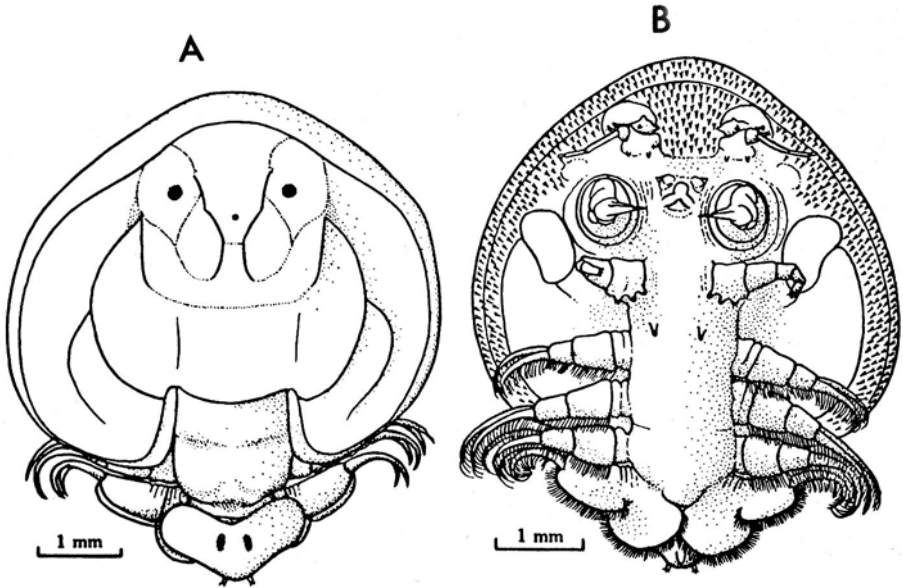
Fig. 4.5. Dolops tasmanianus, adult female. A, dorsal aspect; B, ventral aspect (from FRYER, 1969).

BRANCHIURA

Four extant genera of Branchiura are known, and one of these, *Dolops*, has recently been recorded from Tasmania (FRYER, 1969). The species in question, *D. tasmanianus* (Fig. 4.5), is endemic to the island. It is one of eleven known species of *Dolops*, nine of the other ten of which occur in South America, and one in Africa. *Dolops tasmanianus* was obtained as an ectoparasite of a galaxiid fish (? *Galaxias affinis*) living in Lake Surprize, a small circular lake at about 650 metre altitude in the Frankland Ranges some 2.5 km south of Lake Pedder. Apart from this record, there are no other firmly published records of freshwater branchiurans in Australia, though RIEK (1959) does mention the possibility of an endemic species of *Argulus* occurring as an ectoparasite on freshwater fish in Queensland.

SYNCARIDA

Syncarid crustaceans have provided a strong focal point for the interest of carcinologists in Tasmania since the beginning of this century. However, it is only recently that the full extent of the Tasmanian syncarid fauna has begun to be elucidated; for many years interest revolved around three species of Anaspidacea, namely *Anaspides tasmaniae*, *Paranaspides lacustris* and, later, *Micraspides calmani*, but a further three new species

80

in the Anaspididae (including a new genus, *Allanspides*) have recently been described in addition to the recent discovery and description of at least five new species in both families (Bathynellidae, Parabathynellidae) of the Bathynellacea, an order hitherto unknown from Tasmania – or, indeed, Australasia. No Tasmanian representatives of the remaining extant order of the Syncarida, the Stygocaridacea, have yet come to light, but since this order, formerly thought to be restricted to South America, has now been discovered in New Zealand (SCHMINKE & NOODT, 1968) and mainland Australia (SCHMINKE, 1971) it seems more than likely that sooner or later it will be found in Tasmania also. Clearly much remains to be discovered concerning Tasmanian syncarids.

Anaspides tasmaniae (Fig. 4.6) was the first Tasmanian syncarid described. It was recorded first as *Anaspis tasmaniae* (THOMSON, 1893) but described a year later (THOMSON, 1894a) with the generic name corrected to *Anaspides*. Several authors have discussed its anatomical and structural features (though a detailed study of the external morphology other than of the mouthparts has yet to be made) including SMITH (1908, 1909b), CANNON & MANTON (1927, 1929), MANTON (1931), NICHOLLS & SPARGO (1932), HANSTRÖM (1934, 1936) and SIEWING (1956). In addition, HICKMAN (1937) has studied the embryology of the species in detail. Fewer authors, predictably, have been concerned with ecological observations, but HICKMAN's (1937) paper does have a short account of the life-cycle and some notes on distribution and food have been given by SMITH (1909c), FLYNN (1918), THOMSON (1926), MANTON (1929, 1930) and NICHOLLS (1929, 1947). These ecological observations have been summarized and added to recently by WILLIAMS (1965a) in a review of the ecology of Tasmanian Syncarida known to 1965. It is largely upon this account that the following one is based.

The geographical distribution of *A. tasmaniae* was plotted in map form in WILLIAMS (1965a, fig. 2). From the map it was suggested that the area of distribution of the species included the Central Plateau and the southern highlands, but not the northern and eastern regions of the island. Additional records have come to hand since the publication of that statement, but in general they do not alter its validity; none of these records relates to far northern or eastern localities. At the same time, it may be added that the species is more common in the south-west than was previously indicated, it occurs further north than was thought (there are unpublished records of its occurrence on the edge of the Western Tiers and at Black Bluff), and it has been found as far west as Frenchman's Cap and the Eldon Range (Dr. P. S. LAKE, personal communication, February 1973).

With regard to the ecological distribution of *A. tasmaniae*, WILLIAMS (1965a) on the basis of original samples and a reexamination of materials and records by others concluded that the typical habitat was small upland streams and moorland pools, and that lakes were only doubtfully inhabited. Some correction to that statement is now necessary for several
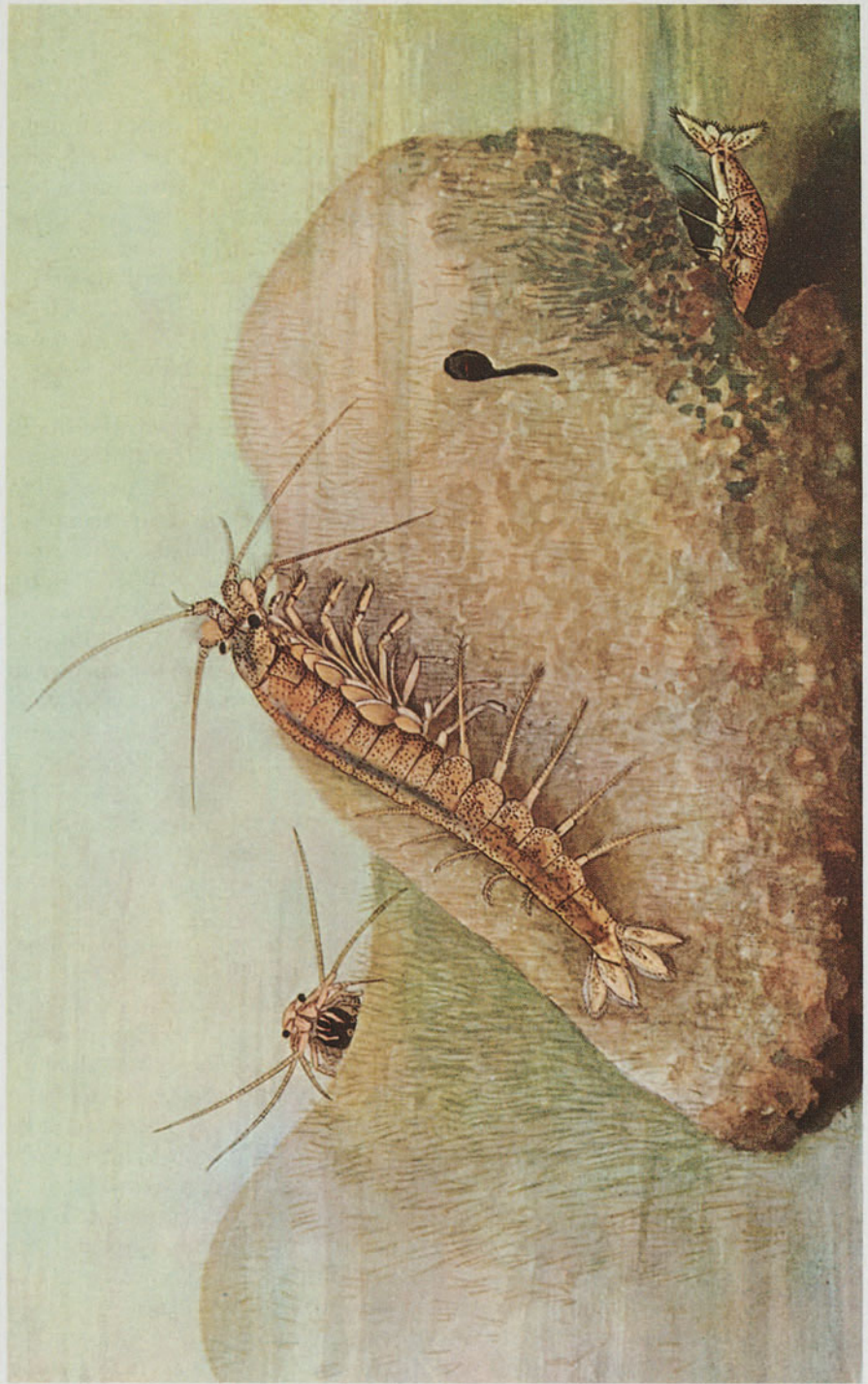
Fig. 4.6. Light variety of *Anaspides tasmaniae* from the slopes of Mount Wellington below about 2000 ft. From the original engraving first published in Proceedings of the Zoological Society of London, 1930, plate iv; reproduced by courtesy of the ZOOLOGICAL SOCIETY OF LONDON and Dr. S. M. MANTON, F.R.S.

collections have recently been made of *A. tasmaniae* from lakes; specimens have been collected, for example, from Lake Osborne in the Hartz National Park (August 1965), from No. 1 Tarn Mount Sarah Jane (June 1966), and from Lake Skinner in the Snowy Range (November 1971, coll. M. FENTON). Additionally, SWAIN (1972) has noted that the species 'is common in mountain tarns and lakes in the south-west, less common in creeks and has even been found in buttongrass pools.' As previously suggested (WILLIAMS, 1970b) in general terms, one explanation for the greater abundance in lakes in the south-west may be that since many of these are remote, they do not (yet?) contain the introduced trout, *Salmo trutta*, a known predator of *A. tasmaniae*, and it is the absence of this fish which allows continued survival of the syncarid in habitats which were previously perhaps more typical for it over the whole of the island. The implication is that *A. tasmaniae* survives only in those places where predation by trout is not unduly heavy or which are inaccessible to trout.

Perhaps the occurrence of *A. tasmaniae* in caves, a further habitat for the species not noted in WILLIAMS (1965a), may also be explained, at least for some, on the basis of refugial populations from trout predation. In any event, it is of interest to record here that some cave specimens whilst undoubtedly conspecific with *A. tasmaniae* do exhibit certain differences from surface forms; the smaller amounts of pigment in specimens from a cave in north-central Tasmania were recorded by WILLIAMS (1965b), and in specimens from a cave in southern Tasmania a progressive reduction in the pigment of the eyes has been noted (unpublished data).

Irrespective of the general nature of the habitats of *A. tasmaniae*, they are usually in the highlands, although the total altitudinal range is from *ca.* 15 to > 1,200 m above sea level. Most collections have been taken at altitudes in excess of 750 m. Concomitantly, most localities are subject to near-freezing temperatures in winter, although it is doubtful if any freeze solid. THOMSON (1894a) observed, nevertheless, that specimens occurred in pools which had a thick ice cover, and MANTON (1930) noted the presence of specimens in an area under snow for two to three months each year. The upper limit for temperature tolerance appears to be between 15 and 20 °C.

The life-cycle has been studied by HICKMAN (1937) and his data have been slightly added to and reexamined by WILLIAMS (1965a). SWAIN (1972) has further commented on this aspect of the ecology of *A. tasmaniae*. In summary, the overall schedule is as follows. The usual length of life is three years but some specimens may persist for four years. For about the first year and a half of life, growth is not seasonally restricted. Breeding probably occurs after approximately 15 months, that is when males and females are around 18 mm long. Eggs are about 1 mm in diameter and occur singly on submerged vegetation. Most are laid in spring and hatch between June and October. Thus most eggs take about eight months to

develop, though those laid in autumn and winter may require up to fourteen months. Most individuals have a two-year interval between the time they are laid as eggs and the time they first breed, and most breed twice.

Finally a brief note may be made that the diet of *A. tasmaniae* is omnivorous: submerged mosses and liverworts, periphytic algae, small invertebrates, and detritus have all been recorded as part of the diet.

The only other species of *Anaspides* known, *A. spinulae*, occurs at shallow depths in Lake St. Clair (WILLIAMS, 1965a). To date it has not been collected elsewhere despite specific searches for it. Thus, it was not collected in Lakes Sorell and Crescent when these lakes were sampled in 1966 using the same apparatus as was used to collect specimens from Lake St. Clair, and it was not present in any benthic samples obtained recently by Dr. B. V. TIMMS (personal communication, 15 November 1972) from Lakes Leake, Tooms, Dobson, Sorell, Crescent or Dove. It should be noted, however, that Dr. TIMMS was unable to recollect the species from Lake St. Clair (northern and southern ends), and prior to its initial collection from that lake, both SMITH (1909c) and NICHOLLS (1947), too, had failed to collect it there despite dredgings.

In Lake St. Clair, WILLIAMS (1965a) collected the species from depths of 3.0 to 4.5 m on a sandy bottom at least partly covered by flocculent algae. He did not obtain any specimens from the adjacent shore. A further collection of this species (in collections of the Tasmanian Museum) is labelled as having been dredged from Lake St. Clair in 1937.

The presence where it is of a benthic species of *Anaspides* distinct from the species of streams, pools and the littoral margins of lakes raises several interesting questions, for it is now quite clear that during the Pleistocene glacial period Lake St. Clair was occupied by a large glacier (DERBY-SHIRE, 1972) the presence of which would obviously have precluded the concurrent presence of *A. spinulae*. One explanation that has been offered (WILLIAMS, 1965a) is that *A. spinulae* survived the Pleistocene glaciation is unglaciated lakes near to Lake St. Clair that had conditions then similar to those in which *A. spinulae* now lives. The presence of such lakes was thought to be not unlikely by E. DERBYSHIRE (personal communica-tion in WILLIAMS, 1965a), and his map of the retreat stages of the Lake St. Clair glacier published subsequently (DERBYSHIRE, 1971, fig. 9) indicates that temporary lakes resulting from the ponding of meltwater were probably not uncommon. DAVIES (Chapter II), also, has suggested that such lakes would have provided refuges for lacustrine biota during the time of the Pleistocene glacials. An alternative explanation, and one subject to investigation, is that *A. spinulae* is no more than a phenotype or a geographical race (subspecies) of *A. tasmaniae* which occurs in lakes. At the time *A. spinulae* was described, *A. tasmaniae* was thought not to inhabit either the littoral or benthic regions of lakes; now that it is known that it does occur at least in lake littoral regions, the degree of genetic

separation between the two taxa is clearly less than previously presumed, and this raises the possibility that there may, after all, exist an intergradation of morphological characters. This has not been studied.

Paranaspides lacustris, the other anaspidid found in lake benthic communities, is, like *A. spinulae*, also rather restricted in distribution, and, despite odd comments to the contrary (e.g. RIEK, 1959) and some specific but unsuccessful searches for benthic syncarids (see above), it has actually been recorded from only the Great Lake, Shannon Lagoon and Penstock Lagoon (WILLIAMS, 1965a). The latter two localities are relatively small artificial impoundments that lie not far to the south of the Great Lake and connected to it by the Shannon River. The species was first reported by SMITH (1908) and described a year later (SMITH, 1909b). Some information of an ecological tenor – albeit rather restricted in extent and relating mainly to temporal fluctuations and feeding mechanisms – was contributed later by CANNON & MANTON (1929), MANTON (1929, 1930), NICHOLLS (1929, 1947), TILLYARD (1933), EVANS (1942) and GORDON (1961). This information was summarised, reviewed and expanded by WILLIAMS (1965a).

In brief, the species has a depth range of apparently about 1 to 8 m and occurs throughout the lake in suitable situations (it is definitely not 'limnetic', at least in the usual sense of that word, as HUTCHINSON (1967: 94) suggested). There are equal numbers of males and females. The life-cycle may be similar to that of *A. tasmaniae* but the total life-span is perhaps less. Food appears to consist mainly of fine detritus and plant (mostly algal) material. And the introduced brown trout, *Salmo trutta*, is a confirmed predator. With regard to the variation in time of population numbers, there is fairly good evidence that fluctuations of this sort have taken place. They have been explained as due to the introduction of trout or, with greater conviction, the artificial elevation of the water level of the lake for purposes of increased water storage. At the time of SMITH's collection of the species, it was apparently abundant despite the fact that trout had been in the lake some forty years. In the 1920s and 1930s, however, it became almost extinct according to MANTON (1929) and TILLYARD (1933), but had recovered by the 1940s (EVANS, 1942; PLOMLEY, 1946; NICHOLLS, 1947). It was clearly common in 1963 (WILLIAMS, 1965a) and in 1966 when in February of that year 144 specimens were easily collected from the middle of Christmas Bay in the south-west corner of the lake and when 40 specimens were collected from near the adjacent shore using a standardized dredge method. With the same method, however, no further specimens were obtained in November 1969, February 1971 and November 1972. Both periods of apparently reduced population numbers (i.e. 1920s and 1930s, and *post* 1966) follow artificial elevations of the water level of the lake, namely 7.5 m in 1922 and about 4.0 m in 1967, a relationship which, if true, seems unlikely to be entirely coincidental. At all events, the present situation

is that no collections of *P. lacustris* have been obtained since 1966 from the Great Lake. The species is still common, however, in Shannon Lagoon.

The surprize expressed by HUTCHINSON (1957: 68) that *P. lacustris* should occur at all in the Great Lake was based on the adherence by this author to the superceded views of LEWIS (1933) and VOISEY (1949a, 1949b) that the Great Lake was of glacial origin. It is now known that although the Great Lake may well have experienced periglacial conditions during the Pleistocene, it was not glaciated and is certainly not of glacial origin (e.g. DAVIES, 1962).

The members of the Anaspididae not yet discussed are those recently discovered in the south-west and for which a new genus, *Allanaspides*, was erected (SWAIN, WILSON, HICKMAN & ONG, 1970). They are *A. helonomus* and *A. hickmani* (a heading '*A. bickmani*' in the original description of the latter is obviously a printer's error*). The genus is apparently very restricted in distribution: *A. helonomus* (Fig. 4.7) is known only from the Lake Pedder area and from an area about 6.5 km to the north; *A. hickmani* is known only from the latter locality where it occasionally occurs sympatrically with *A. helonomus*. Both species occur in areas referred to locally as buttongrass plains where they live in the burrows of the land crayfish *Parastacoides tasmanicus* (see below) and in surface pools (SWAIN, WILSON & ONG, 1971). Of considerable interest is the presence in this genus of an organ on the cephalo-thoracic tergite which has been termed the fenestra dorsalis. This structure appears to be unique within the Crustacea (SWAIN, 1972)**. Recent work (LAKE, SWAIN & ONG, in preparation) on the ultrastructure of the fenestra dorsalis has revealed that the organ appears to be a region of active ion transport. The epithelial cells of the fenestra dorsalis have both regions of well-developed apical infoldings and basal folds.

There are published reports of only a single representative of the Koonungidae in Tasmania, namely *Micraspides calmani*. This was collected by NICHOLLS (1931, 1947) in a few localities on the west coast near Queenstown. More recently it has also apparently been collected in a region north of Lake Pedder and north of the region inhabited by *Allanaspides* species ('unpublished observations' referred to in SWAIN, WILSON & ONG, 1971). NICHOLLS found the species in muddy water beneath moss and in the burrows of land crayfish; in the region north of Lake Pedder it apparently occurs in the same sort of habitat as is occupied by *Allanaspides*. Nothing else is known of the ecology of the species. In addition to the published records of Koonungidae, there also exist some unpublished reports of the occurrence of *Koonunga* sp. in the

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* But there is no question as to the validity of the species-group name *hickmani* (*Internat. Code Zool. Nomen.* Art. 32(a)(ii)).
** Although apparently comparable structures occur in some harpacticoids (Dr. H. K. SCHMINKE, personal communication, 12 March 1973).
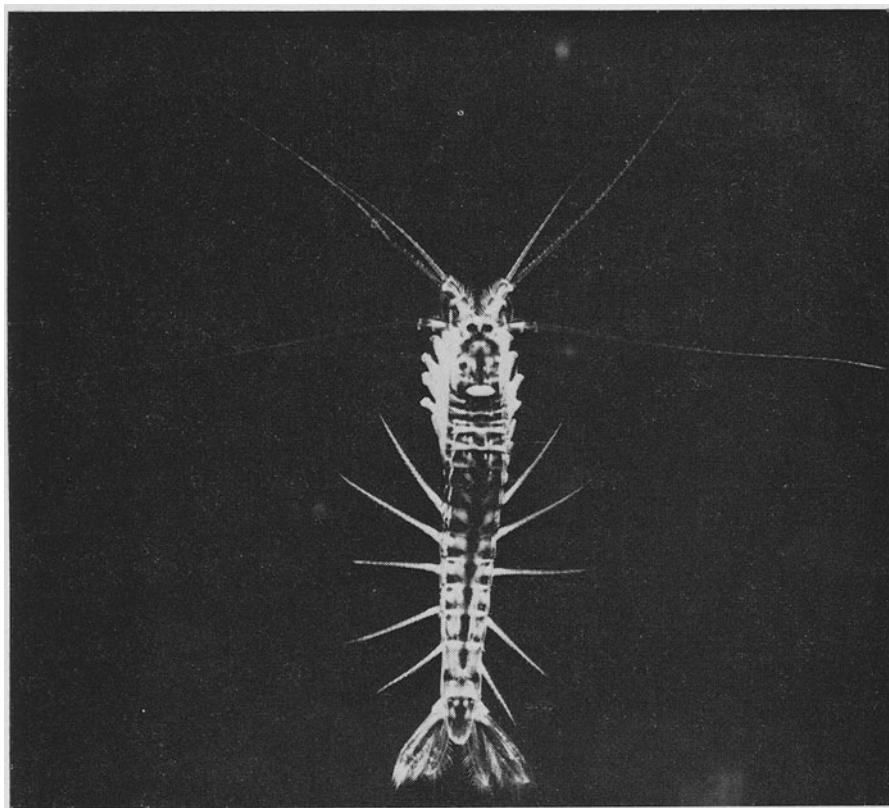
Fig. 4.7. A mature male specimen of *Allanaspides helonomus*. Photography by courtesy of Dr. R. SWAIN.

north-west and on King Island (Drs. J. L. HICKMAN and P. S. LAKE, personal communications, February 1973).

The Bathynellacea, the other Tasmanian order of Syncarida, remains for discussion. At least five new species, as noted, occur and have been described (SCHMINKE, 1971, 1973). One of these belongs in the Parabathynellidae, *Atopobathynella hospitalis;* the others belong in the Bathynellidae and have been provisionally placed in the genus *Bathynella*. At the time of preparation of this chapter no formal publication of the bathynellid species names had been made, and in order not to prejudice such publication they are not referred to here by name.

All these bathynellaceans were discovered by Dr. H. K. SCHMINKE during a visit to Tasmania in June 1968, and were collected by digging holes in gravel on the banks of rivers. From the water which subsequently filled a hole, the various species were removed by fine net. Clearly, therefore, these syncarids like most bathynellaceans are interstitial forms.

Their presence is not entirely unexpected for it had been predicted some twenty years earlier by NICHOLLS (1946) in a general account of syncarids in interstitial habitats. Specimens were obtained in the western and northern parts of the State from the North Esk River (bathynellid), St. Patrick's River (bathynellid and *Atopobathynella hospitalis*), Nelson River (bathynellid) and Stirling River (bathynellid). They were collected together with a variety of nematodes, oligochaetes, and cyclopoid and harpacticoid copepods. Since each locality investigated yielded a different (and new) species, there is every reason to expect that further investigation in other parts of the State, too, will yield additional taxa.

<center>ISOPODA</center>

There are representatives of three isopodan suborders: Asellota, Oniscoidea and Phreatoicidea. All have several features of interest.

The Asellota is represented by at least one species of the Janiridae, *Pseudasellus nichollsi* (CHAPPUIS, 1951), a family that is otherwise mainly marine. However, whether this is truly the generic name that should be used is somewhat doubtful. In a chapter like this it is inappropriate to give details of the reasons underlying this doubt, but a brief resumé is appropriate. CHAPPUIS (1951) described fully a collection of small, blind isopods collected from the Guide River in northern Tasmania. This material he regarded as representing a new species and new genus. It is clear, however, that CHAPPUIS overlooked an earlier description by SAYCE (1900) of similar blind janirid isopods ('*Janirella pusilla*') from Victoria. Unfortunately comparison of CHAPPUIS' and SAYCE's descriptions does not settle the question of whether the same genus or species is involved, for SAYCE's description is inadequate and he did not, for example, describe the male second pleopod, a most critical appendage taxonomically. Victorian material, from Lake Wendouree, that agrees well with SAYCE's description (and indeed that had been independently identified as *J. pusilla* by Dr. E. F. RIEK, personal communication) also agrees well with CHAPPUIS's description of *P. nichollsi*. Agreement is particularly marked in the conformation of the male first and second pleopods. Thus, there is suggestive evidence that *P. nichollsi* is congeneric if not conspecific with the Victorian taxon described by SAYCE. A final solution to this problem will need to await formal redescription of the Victorian species.

The situation is a little further complicated by the fact that the genus-group name chosen by SAYCE (1900) was unavailable because BONNIER (1896) had used it a few years earlier. RICHARDSON (1904) recognised this and proposed *Heterias* as a replacement. At present, then, it is suggested that CHAPPUIS' nomen be left standing, but that it be noted that the taxon involved may be congeneric or conspecific with *Heterias pusilla*.

No definite records of *P. nichollsi* have been published since the original

description. There is, nevertheless, a small (< 5 mm long) freshwater asellote known from many localities in Tasmania, and, whilst a description of this awaits publication, it may be noted here that it is similar but not identical with CHAPPUIS' taxon. The structure of the male first and second pleopods are especially similar to those of *P. nichollsi*. It does, on the other hand, have eyes, although this is a character to which not a great deal of taxonomic significance must necessarily be attached (cf. WOLFF, 1962). This asellote is known from many lentic localities including the Great Lake, Shannon Lagoon, Lake Sorell, Lake Crescent, Woods Lake, Clarence Lagoon, Lake Augusta, Lake Ada and the Maria complex of lakes near Lake Pedder. In these it occurs mainly littorally and particularly amongst gravel and stones.

Small (< 2 mm long) janirid-like asellotes (paraselloids) have also been collected from freshwater streams on Macquarie Islands (EVANS, 1970; original data) and Deal Island in the Bass Strait. Those from Macquarie Island are blind. Several differences from *Pseudasellus* are displayed by specimens from both islands.

Haloniscus searlei (Oniscidae) represents the Oniscoidea. Unlike almost all other members of the suborder, this species is truly aquatic, and it occurs in inland salt lakes. Such an occurrence is unique if the somewhat doubtful record of *Desertoniscus birsteini* from Lake Delili in Turkmenia (BORUTSKII, 1945) is ignored, and even so the occurrence of aquatic oniscoids is certainly unusual. The species has a geographical range extending from south-western Western Australia to Tasmania and Victoria, but is unknown outside Australia. Its only congener, *H. stepheni*, is found in Western Australia. The taxon has been fully redescribed recently (WILLIAMS, 1970a) and much ecological information on it has been given by ELLIS & WILLIAMS (1970). BAYLY & ELLIS (1969) have studied its osmoregulatory abilities.

In Tasmania, *H. searlei* has been recorded (ELLIS & WILLIAMS, 1970) from a small salt lake near Tunbridge where, at the time of collection, the salinity (based on conductivity readings) was 74.8‰. This value falls well inside the documented range of salinity within which the species has been found elsewhere, *viz.* 8 to 159‰. At all events, *H. searlei* is well capable of hypo-osmotic regulation in relation to the external medium at that salinity, and the haemolymph salinity – extrapolating from the experimental results of BAYLY & ELLIS (1969) – would then have been less than half that of the external medium. The species is also capable of powerful hyper-osmoregulation. It should be emphasised that when collected, all specimens were found totally submerged; none was taken from above the water level, a finding in direct accord with all previous experience of this species on the mainland. Brief reference to *H. searlei* is made also in chapter IX.

By far the most important isopods in Tasmania, both in terms of diversity and abundance, are those representing the Phreatoicoidea.

Indeed it is Tasmania above anywhere else that this suborder displays maximum species numbers and where these isopods are numerically commonest and most widespread. They have restricted distributions in India, South Africa and New Zealand, and though occurring in all mainland States of Australia (and the Northern Territory) are not nearly as important a component of the freshwater fauna there as are they in Tasmania.

The two most important families both occur in Tasmania (the third extant one, the Nichollsidae, is restricted to India), namely the Amphisopidae with three genera and three species, and the Phreatoicidae with five genera and nineteen species (Table 4.1). Two genera of the Amphisopidae (*Uramphisopus* and *Hypsimetopus*) are monotopic and endemic to Tasmania; the third is known also from Victoria. Three genera of the Phreatoicidae (*Mesacanthotelson*, *Onchotelson* and the monotypic *Paraphreatoicus*) are endemic; the other two occur also in New South Wales or Victoria. All *species* of phreatoicids known from Tasmania are endemic.

THOMSON (1893) was the first to record a phreatoicid from Tasmania when he noted, almost by accident, a single immature specimen amongst a collection of amphipods from Mount Wellington. He regarded this specimen as conspecific with '*Phreatoicus australis*', a species described by CHILTON (1891) from Mount Kosciusko, New South Wales, only eight years after the very first phreatoicid (from New Zealand) had been discovered. A further Tasmanian species, '*Phreatoicus tasmaniae*', was described by THOMSON (1894b) from the Great Lake. Subsequently, SAYCE (1902) described a single new species from the west coast, and SMITH (1909a) recorded three taxa, of which two were considered new species. Some thirty-odd years later NICHOLLS (1943, 1944, 1946) began his intensive taxonomic survey of the entire suborder, and it was only then that the extent of diversity in Tasmanian phreatoicids became appreciated. In this regard, however, the study by KNOTT (1971) should be given attention; whilst not primarily concerned with a taxonomic survey, he arrived at some rather significant conclusions concerning the degree of phenotypic morphological variation amongst certain populations. In brief, he found on the basis of a careful study of a large number of meristic characters backed up by statistical analyses that four of NICHOLLS' species (in two genera!) fell easily within the phenotypic variation displayed by a single one of the species. The taxa involved were *Colubotelson thomsoni*, *C. campestris*, *C. huonensis* and *Metaphreatoicus magistri*, and these, according to KNOTT, should all be regarded as a single species *(C. thomsoni)*. Clearly the implications of this study are far-going and necessitate considerable reevaluation of the systematic status of all Tasmanian phreatoicids. For the present, however, and certainly until KNOTT's work is formally published, the situation must rest upon the basis provided by NICHOLLS (1943, 1944).

Within Tasmania, and in terms of gross geographical distribution, the

90

family Phreatoicidae is more or less restricted to regions that have been subject at various geologically recent times to climatic, glacial or orogenic disturbance. The Amphisopidae, on the other hand, is more or less restricted to the geologically very old, stable and essentially Precarboniferous western region. In terms of more local distribution, a variety of freshwater habitats support phreatoicids, but in general they do not occur in the more swiftly-flowing reaches of streams, a reflection no doubt of their slow-moving benthic habits. Special note may be made of the occurrence of certain species in association with crayfish burrows and in the psammon that occurred in the quartzite beach of Lake Pedder (BAYLY, PETERSON, TYLER & WILLIAMS, 1966).

The phreatoicid fauna of the Great Lake is of particular interest for from this single locality have been recognized no less than nine species. Almost all are restricted to the lake, and two of the genera, *Mesacanthotelson* and *Onchotelson*, have certainly not been recorded elsewhere. None of the species was amongst those studied by KNOTT (1971), and the question arises then as to what extent a study of them on similar lines to that undertaken by KNOTT on *Colubotelson* spp. and *Metaphreatoicus* would reveal synonymies. But even assuming some specific synonymies we are still left with three coexisting genera. This apparently high diversity could perhaps be regarded as an indication of considerable geological longevity of the lake. Further biological evidence that could be used in support is the degree of apparent endemism (within the lake) in some other crustacean and non-crustacean groups. This line of argument seems very tenuous to the present author and pending a thorough revision of the fauna of the Great Lake should not be overweighted. It may be noted that in many freshwater localities, including some relatively impermanent ones, there may be considerable diversity within restricted crustacean groups (cf. remarks above on calanoid copepod associations).

Whilst isolated remarks bearing upon the ecology of Tasmanian phreatoicids lie scattered in the systematic literature, only two accounts, both theses, deal at all intensively with this subject: those of ENGEMANN (1963) and KNOTT (1971) which are concerned with *Colubotelson thomsoni (sensu lato)*. The latter account is the most comprehensive. The salient findings may be summarised as follows. Within creeks there appears to be a noticeable degree of aggregation ('clumping'). Food and feeding have not yet been described accurately, but ENGEMANN (1963) reported a mainly vegetarian diet, and KNOTT (1971) an indeterminate one involving extensive mud-swallowing. ENGEMANN delimited three population size-classes, the implication being that the life-cycle lasts three years, but KNOTT found only two and regarded the life-cycle as lasting only two years. KNOTT's proposals for the entire life-cycle are that the young are released from the marsupium in late spring to late summer; that juveniles released early grow until winter when growth of both juveniles and adults ceases; that growth for juveniles is rapid in their

second summer at which time they achieve sexual maturity; and that pairing is from mid-February to July for highland populations and April/ May to September for lowland ones. Egg numbers (from < 10 to 38 per female) varied, predictably, with the size of the mother, and the sex-ratio was about 1:1.

KNOTT also undertook investigation of certain additional aspects of the biology of *C. thomsoni* some of which have ecological relevance. In particular he found there was a limited ability to osmoregulate in environments of low and moderate salinity, but the ability was insufficient to cope with marine or semi-marine salinities. Nor surprizingly, therefore, *C. thomsoni* was found to tolerate (in the laboratory) a fairly broad range of salinities – and even broader at lower temperatures – but could not survive long in salinities approaching that of the sea. Animals could not survive being frozen solid, but temperatures between *ca.* 0 and 28 °C were tolerated. Little ability to survive desiccation was noted, but there is apparently enough to enable limited migration through damp vegetation between water bodies in winter. Parasites recorded by KNOTT were an acantho-cephalan (? *Polymorphus*) and a nematomorph.

Finally, it may be noted that the introduced trout is a major predator on phreatoicids. Thus, the early work of EVANS (1942) showed that be-tween 1936 and 1941 phreatoicids were present in 48 per cent of all trout stomachs examined from the Great Lake (total 272 stomachs), and 76 per cent of those from Shannon Lagoon (98). Comparable results were obtained by WILSON (unpubl.) who found that in the season 1960–61 phreatoicids were present in 36 per cent of all trout from the Great Lake and 39 per cent of those from other waters.

AMPHIPODA

Several writers have stressed the need for a taxonomic revision of Austral-ian freshwater amphipods. Some attempt is being made to provide this revision (WILLIAMS, 1962; unpublished) but in a chapter such as the present it is inappropriate to provide details. Taxonomically the group is best dealt with here mainly on the basis of published material.

Prior to the recent and ongoing comprehensive gammaridean revisions of BARNARD (1964, 1969, 1970a, 1970b, 1972, in press), the known fresh-water amphipods of Tasmania were *apparently* easily grouped into three families (cf. WILLIAMS, 1968a, table 4): the Gammaridae inclusive of the genera *Neoniphargus* and '*Gammarus*' (THOMSON, 1893; SMITH, 1909a; STRASKRABA, 1964), the Hyalellidae with *Austrochiltonia* (SAYCE, 1901; SMITH, 1909a; WILLIAMS, 1962), and the Calliopiidae with *Paracalliope* (B. KNOTT, personal communication, 29 November 1972). The situation now at both the familial and generic level is somewhat less straightforward, though to be welcomed nonetheless for it undoubtedly reflects the trend towards a more rational treatment and management of the taxa involved.

At the familial level (BARNARD, 1972), it appears at present that *Austrochiltonia* is best regarded as part of a new family, the Ceinidae (subfamily Chiltoniinae), and *Paracalliope*, whose status 'cannot be explored until some order has been restored to the pontogeneiid genera' (p. 183), is best treated, provisionally at least, as a member of an expanded Eusiridae. No suggested changes of family are recorded for genera in the Gammaridae, in which, however, the status of '*Gammarus*' remains as indeterminate as ever. Even NICHOLLS (1929), who was quite willing to accept the occurrence in Australia of the 'European' genus *Niphargus* (Gammaridae), was quite careful some forty years ago not to give support (but nor directly deny) the proposal that *Gammarus sensu stricto* occurred in Australia. More recently, WILLIAMS (1967, 1968a) expressed similar doubts as did BARNARD (1972: 6) when he referred generally to such freshwater species in the southern hemisphere as 'so-called gammaruses'. The status of *Neoniphargus*, on the other hand, seems clearer now; STRASKRABA (1964) has rediagnosed this genus and with the removal from it of two Asiatic species it is now reasonably well-defined and endemic to Australia.

The present arrangement then is as in Table 4.1. There are two species of *Austrochiltonia* (Ceinidae), neither endemic to Tasmania and both widespread on the mainland; there are four species of '*Gammarus*' (Gammaridae) three of which are endemic to Tasmania with one known also from Victoria; there are eight species of *Neoniphargus* (Gammaridae) of which six or seven are endemic, with one or two in Victoria also; and there is at least one undetermined species of *Paracalliope* (Eusiridae) which may or may not be endemic. With this number of species, Tasmania has the greatest species diversity of freshwater amphipods in Australia.

Little is known about the ecology of any member of the group, and remarks upon this aspect must in the main be confined to general notes upon habitats. The commonest and apparently most widespread species are those of *Austrochiltonia*, a fact first noted by SMITH (1909a) and supported by more recent evidence (WILLIAMS, 1962; unpublished data). No obvious differences of habitat are displayed by the two species involved, and both are known from the littoral and benthic regions of lakes, a variety of other types of standing water bodies, and streams and rivers. *Austrochiltonia*, however, is not characteristic of the more highland and mountainous regions (though it occurs abundantly on the Central Plateau) where it is displaced by various species of the Gammaridae some of which, nevertheless, are known outside such regions. *Paracalliope* is found mainly in brackish waters (B. KNOTT, personal communication, 23 November 1972), but has been recorded from well within the freshwater region of several creeks.

Like the phreatoicids (see above), Tasmanian amphipods are predated by the introduced trout. Such predation, however, seems to be less intensive, and EVANS (1942) noted the presence of amphipods in only one

per cent of trout stomachs from the Great Lake during the period 1936–41 (cf. 48 per cent for phreatoicids). Likewise WILSON (unpubl.) in a more recent study of trout food in Tasmania commented that amphipods 'do not appear to be of as much importance for trout food' [as phreatoicids].

<center>DECAPODA</center>

Three of the five Australian families of decapods occur in Tasmanian fresh waters: the Atyidae (freshwater shrimps), Hymenosomatidae (crabs), and Parastacidae (freshwater crayfish).

The Atyidae has a single species, *Paratya tasmaniensis*, regarded originally as conspecific with the wide-ranging mainland form, *P. australiensis* (but recorded as *Xiphocaris compressa* by SMITH, 1909a, and EVANS, 1942). RIEK (1953), however, on the basis of material from the south-east considered Tasmanian atyid populations as belonging to a distinct and endemic species. More recent work (T. WALKER, personal communication, 8 December 1972; WILLIAMS, unpublished) suggests that the degree of phenotypic variation displayed by mainland populations of *P. australiensis* and by Tasmanian populations of *P. tasmaniensis* is sufficient for both sorts of population to be regarded as belonging to a single species, viz. *P. australiensis*. The work of WALKER on Tasmanian populations is particularly revealing; after a careful study of material from six different localities extending from the north-east to the south-east he concluded that there was no significant morphological difference between Tasmanian material and *P. australiensis* as originally described and as redescribed by RIEK (1953), but that some clinal variation existed in the Tasmanian material. However, until formal publication of the detailed investigation by WALKER, the taxon is best regarded here as *P. tasmaniensis*.

SMITH (1909a) noted that *P. tasmaniensis* was very abundant in streams discoloured by flowing over sandstones, and in similarly turbid lakes such as Sorell, Crescent and Tiberias. RIEK (1959: 252), on the other hand, referring to atyid prawns generally, noted that 'in Tasmania they are restricted to the coastal streams.' Recent collecting (P. S. LAKE, T. WALKER, personal communications, 10 November and 8 December 1972; WILLIAMS, unpublished data) shows that, on the contrary, they occur very widely throughout Tasmania in lowland creeks and rivers to the north, east and south of the Central Plateau, and in several of the larger lakes (including Lakes Sorell and Crescent on the edge of the Central Plateau). In this distribution, Tasmanian atyids parallel that of *P. australiensis* which is known from such localities over a very wide area of south-eastern mainland Australia (BISHOP, 1967b; WILLIAMS, 1968a).

The Hymenosomatidae is represented by *Halicarcinus lacustris*, a species known also from Victoria, South Australia, New Zealand and Lord Howe and Norfolk Islands (see WALKER, 1969, for details). The species was recorded from Tasmania by CHILTON (1919) and the only subsequent

published record appears to be that of GUILER (1952). CHILTON's material came from a small creek near Flowerdale in north-western Tasmania where the specimens were found nestling in the crevices of rotting wood. GUILER's record relates to material in Launceston Museum from Smithton, a small coastal town also in the north-west. In addition to these records, there are many unpublished ones (Dr. P. S. LAKE, personal communication, February, 1973); they relate to King Island, and coastal streams in the south-east, on the east coast (near Bicheno), and in the north-eastern and north-western plains.

Although no ecological information is available directly for Tasmanian material, it seems unlikely that the results of WALKER's (1969) ecological investigations of this species in Victoria do not apply. Thus, we may expect that this crab occurs in Tasmanian inland waters between *ca.* 0.1 and 10‰ salinity, and probably at no great distance from the coast.

The Parastacidae, in contrast to the Atyidae and Hymenosomatidae, is represented by numerous species, all but one of which are endemic. Two of the four Tasmanian genera are endemic, *viz. Astacopsis* and *Parastacoides;* the other two, *Engaeus* and *Geocherax*, occur also in the south-eastern region of the mainland.* For comprehensiveness, *Engaeus* and *Parastacoides* are considered here as freshwater crustaceans although their species are certainly less dependent upon fresh water than other crayfish, and often construct burrows some considerable distance from permanent surface water. Nonetheless, the burrows contain water in a large central chamber so that the vernacular names 'land crayfish' and 'land crabs' are not as truly descriptive of their habits as might at first be suggested. The most recent taxonomic survey of Australian freshwater crayfish is that by RIEK (1969, and unpublished appendix). Other information of interest in the present connection includes especially that given by SMITH (1912), SMITH & SCHUSTER (1913), CLARK (1939), RIEK (1951, 1967), NEWCOMBE (1970) and SUMNER (1971).

Currently, four species of *Astacopsis* are recognized. The first described, *A. franklinii*, is known only from the Launceston area; the others occur in the western half of the north coast *(A. gouldi)*, the Lake St. Clair area of the Central Plateau *(A. tricornis)*, and an area in the south embracing the Hartz Mountains and Hobart environs *(A. fluviatilis)*. There is also a tentative record of *A. gouldi* from the north-east (Dr. J. L. HICKMAN, personal communication, 8 February 1973). Body size of adult specimens varies from 6 to almost 40 cm. The largest specimens are of *A. gouldi*, reputedly the largest known freshwater crayfish in the world (FRANCOIS, 1960). LYNCH (1969) noted that individuals of this species weighing 3 kg are common; even heavier ones are known.

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* The Tasmanian record of *Cherax bicarrinatus (sic)* by GUILER (1952) from west coast material in Launceston Museum is evidently a misidentification or is incorrectly labelled. *C. bicarinatus* is a northern Australian species.

All species of *Parastacoides* are confined to the western half of the island, mainly the south-west but extending northwards almost as far as the coast. Body length in this genus is usually less than 6 cm. Six species names are currently valid (Table 4.1). However, an extremely meticulous study of the genus involving the use of thin layer chromatography and electrophoresis techniques as well as more conventional morphological criteria but on a strict statistical basis has indicated that only two species occur, *P. tasmanicus* and *P. inermis*, though there are also some hybrid populations and geographical races (SUMNER, 1971). SUMNER's study remains unpublished, and no formal synonymy is intended in this chapter.

Published distribution records for the three Tasmanian species of *Engaeus*, all of which are endemic, relate to the northern edge of the island. The genus has also been found, however, on the east coast (Zeehan) and on King Island (Dr. J. L. HICKMAN, personal communication, 8 February 1972). Like the other twenty species of *Engaeus*, a genus otherwise almost entirely restricted to Victoria (only two species are recorded from south-eastern New South Wales), they seem to occur in relatively small and discrete areas, although some recent unpublished work suggests the distributions are not as discrete as was formerly thought to be so. *E. fossor* occurs in the north-western corner and the north-east, *E. cunicularius* in the environs of Launceston and apparently on King Island, and *E. leptorhynchus* in the north-eastern corner.

The only Tasmanian species of *Geocherax*, *G. falcata*, is also the only species of freshwater crayfish shared with the mainland. It is known from south-western Victoria, King Island and the tip of north-western Tasmania. The one other described species occurs in south-western Victoria also, and there is apparently an undescribed species on Kangaroo Island (RIEK, 1969).

Apart from an unpublished but detailed ecological study of *Parastacoides* by NEWCOMBE (1970), and an earlier and much less detailed account of the life-cycle of *Euastacus kershawi*, the Gippsland (Victoria) crayfish, by CLARK (1937), our ecological knowledge of south-east Australian freshwater crayfish remains distressingly sparse despite their diversity, the relatively large size of most species, and the broadly-based zoological interest of the group as a whole. Mostly, as with the majority of Australian freshwater crustaceans, our ecological knowledge is more or less confined to habitat data and information of a basically anecdotal type.

NEWCOMBE's study was of *Parastacoides tasmanicus (sensu* SUMNER, 1971), which was investigated in an area of button grass *(Gymnoschoenus sphaerocephalus)* plain, or moor podzol peat, some 90 km west of Hobart. The results of his study may be summarized as follows. The species lives in an extensive series of burrows located in marshy areas where adults show clear preference to remain in or near free water. The burrows may be very complex with a number of openings and, always, a retreat chamber. The latter is located at the lowest level of permanent water and in well-

drained areas may be as far as 1.5 metre from the ground surface; when permanent water lies nearer ground level, the chamber may be only about 20 cm deep. Mostly, burrows contain only one mature animal, but there may also be present several juveniles. Although thermal tolerance is low, tolerance to near anoxic conditions, extreme pH values, and, in adults, to low humidities (desiccation) is well-developed. Soil and atmospheric moisture levels are apparently critical factors governing distribution. Most activity occurs between dusk and dawn. Rather less exoskeletal calcium appears to be present than in other freshwater decapods, but at least the same amount of calcium occurs in the gastroliths before ecdysis. Calcium is conserved by consumption of the exuviae, and there may possibly be some uptake through the pleopods. Probably, adults moult once per summer. Sexual maturity is not reached until the carapace is about 2.5 cm long. The main breeding season is April to November or December, and incubation of eggs takes about six months. Maximum egg numbers are of the order of eighty. Adults, of which more are female than male, may survive for eight years. Food consists largely, it seems, of plant material, but oligochaetes, various sorts of terrestrial insects, and freshwater amphipods also figure in the diet. Symbiotic temnocephalan worms are common associates, as are endoparasitic nematodes (HART & HART (1967) have also recorded entocytherid ostracods as commensals on *Parastacoides* spp. – and *Astacopsis* spp.).

Less is known about *Engaeus* which, as previously noted, has similar habits to *Parastacoides*. It is known that deep burrows may be constructed in which there are several branches each with a terminal chamber containing liquid mud and the crayfish (SMITH, 1909c). Often the burrows extend to and beyond 1.5 metre deep, the depth being related to the level of the water table. Activity appears to be mainly nocturnal, and the diet is said to consist of animal material (SMITH & SCHUSTER, 1913).

A little is known, too, about the ecology of *Astacopsis gouldi* – no doubt largely a reflection of the sheer size of individuals. The species prefers deep still river pools where some cover is available, but may be found in small swiftly-flowing streams. Berried females occur in late spring (LYNCH, 1969). Food seems to be predominently plant material (GOULD, 1871). Some attempt is being made to extend further our knowledge of this crayfish and for this purpose a 'crayfish reserve' was recently established on Caroline Creek by the Tasmanian Inland Fisheries Commission (LYNCH, 1969).

Zoogeographical relationships

Unlike most animal groups, the freshwater Crustacea display a wide range in dispersal abilities and hence pose zoogeographical problems of varied complexity. On the one hand, certain crustaceans have small

resistant eggs which are easily transported; on the other, some have no stage in their life-cycle resistant to desiccation and are themselves little able to undertake active dispersal either by virtue of their own character or the character of the habitat they occupy. It is surprizing therefore that comparatively little attention has been accorded freshwater Crustacea within a zoogeographical context, although their value in this respect has long been recognized. It had even been recognized by earlier workers on the Tasmanian freshwater Crustacea: thus SMITH (1909c: 135) was able to write early this century that 'although the freshwater Crustacea are not very commonly employed to illustrate an argument on zoogeographical distribution it so happens that they are very instructive in regard to this particular problem.' Instructive or not, they are still paid relatively scant attention by influential zoogeographers, a fact recently noted by FRYER (1969) as applicable indeed to invertebrates as a whole. It is only in the past few years that the zoogeographical value of the group has been widely recognized, and in particular the value of those members which display significant taxonomic diversity, have had a long evolutionary history, have poor powers of dispersal and tolerance to environmental stress, and which inhabit discrete habitats.

The occurrence in Tasmania of many of the forms with easily transported eggs resistant to desiccation no doubt happened very soon after the origin of suitable environmental conditions. Direct aerial transport across the Bass Strait and/or access via the intermittent land bridges of the Cainozoic would have permitted such occurrence so that the presence of the Anostraca, Notostraca and Conchostraca in particular probably bears little direct relationship to historical factors in the way the presence of many other crustacean groups does. Some of these branchiopods may have persisted in Tasmania in favourable areas from a time well before that of the Pleistocene land bridge, which structure, in any event, would certainly have permitted their ingress then (see chapters I, XI and XIV for details, and JENNINGS (1971) for a modern synthesis of data relating to the extent in time and space of the Pleistocene link). In all cases, of course, the genera involved are either widespread on the mainland though endemic to Australia *(Parartemia)*, cosmopolitan, or widespread in and outside Australia. The species involved that have so far been recognized (Table 4.1) are also widespread on the mainland, and whilst information on the identity of the conchostracan species is lacking, it would be surprizing indeed if these too were not common mainland species. The total situation is probably that for these groups Tasmania is or has been insufficiently isolated geographically for genetic divergences to occur, and that Tasmanian populations and those at least in south-eastern mainland Australia effectively form a single gene pool.

A similar situation probably prevails for at least some members of the other entomostracan orders too. It almost certainly prevails for many if not all of the cladocerans and cyclopoid and calanoid copepods, of which

the most abundant and widespread Tasmanian species are all widespread in mainland Australia or indeed are widespread or cosmopolitan forms. It may also apply to many free-living ostracods, but because species identifications are mostly lacking for this order, no firm statement on applicability can be made here.

Those cladocerans and copepods to which the situation does not apparently apply are those, of course, which are endemic to Tasmania. No doubt some of these, particularly those occurring in lakes at low or moderate altitude, on closer systematic scrutiny will be shown to be conspecific with mainland forms. The endemicity of some of the remainder can be partly explained as resulting from a long occupancy of Tasmanian localities not widely parallelled ecologically on the mainland. Such an explanation would seem to apply to *Boeckella rubra* which is restricted in Tasmania to highland lakes: on the mainland there is a distinct paucity of this sort of lake and only five natural and distinctly fresh ones occur in the highest parts of the Great Dividing Range (the Kosciusko area), all of which are of comparatively recent (Pleistocene) origin (WILLIAMS, WALKER & BRAND, 1970). The endemicity of others in this category, e.g. the two chydorid species, probably reflects in part *relatively* poor dispersal powers and a general tendency therefore for the formation of species with restricted distributions (cf. FREY, 1972).

Although all entomostracan genera known from Tasmania occur else-where as well, some show sufficient restriction in their total geographical distribution to be of interest in regard to broader zoogeographical questions than those concerned with Australian mainland/Tasmanian relationships. Considerable attention of this sort (e.g. by BREHM, 1936; SEWELL, 1956; McKENZIE, 1971) has been given especially to the distributions of the genera *Newnhamia*, *Attheyella*, *Calamoecia*, *Boeckella* and *Gladioferens*, and the patterns displayed have been variously used in discussions of southern hemisphere zoogeography. BREHM (1936) and SEWELL (1956), in particular, used the distributional patterns of some of these genera in support of WEGENER's theory of continental drift *prior* to the advent of the much firmer geophysical support now available (e.g. see TARLING & TARLING, 1971). However, their arguments can at best be regarded as no more than circumstantial support. A more complete treatment of the genera considered by them (and above all of the centropagids), especially along the lines followed by BRUNDIN (1966) and outlined first by HENNIG (1950 *et seq.*), would be of great interest in this connection. (General readers should note that considerable dissension exists amongst systematists and zoogeographers on the applicability and significance of HENNIG's ideas. Some claim little relevancy for them (e.g. COLLESS, 1967, 1969; DARLINGTON, 1970); others are strong protagonists (e.g. BRUNDIN, 1966; ILLIES, 1961). Whatever viewpoint is held, there can be no doubt that attempts to apply HENNIG's ideas have strongly stimulated and renewed interest in southern hemisphere zoogeography, and

led to significant systematic work on several invertebrate groups.)

The only group of Tasmanian – indeed Australian – freshwater crustaceans which have been considered in this manner, that is to say using HENNIG's ideas of phylogenetic systematics, is the syncarid bathynellaceans (SCHMINKE, 1971, 1973). SCHMINKE's results, especially those concerning the Parabathynellidae, though of limited use in terms of local, Tasmanian, zoogeographical problems, are very pertinent in terms of southern hemisphere zoogeography for the group is restricted to interstitial waters and clearly has very limited powers of epigean dispersal. Using HENNIG's ideas, SCHMINKE proposed an origin for the family in eastern Asia. From there, two evolutionary lines led to South America, one, the 'Chilibathynella-Gruppe', via Australia and Antarctica, the other, the 'Cteniobathynella-Gruppe', via Africa. Within the former group are genera and even species common to Australia and New Zealand *(Atopobathynella, Notobathynella*; A. compagna)* and genera common to Australia and South America *(Chilibathynella, Atopobathynella)*. The phylogenetic relationships (sister group relationships *sensu* HENNIG) displayed suggest close zoogeographical affinities for these land masses. The genus *Atopobathynella* illustrates this well (brackets indicate sister group relationships according to SCHMINKE, 1971):

A. *hospitalis* (Tasmania)
A. *compagna* (New Zealand, Australian mainland)
A. *valdiviana* (South America)
A. *chelifera* (Australian mainland)

The sister group to *Atopobathynella* is *Chilibathynella*, and within this genus one species, *C. clandestina*, is confined to South America (NOODT, 1963), and the other, *C. australiensis*, to Australia. All in all, therefore, although the presumed evolutionary history of the Parabathynellidae is quite different to that of the chironomid groups investigated by BRUNDIN (1966), which are said to display *primary* trans-antarctic relationships, the results of SCHMINKE's investigation, like those of BRUNDIN's, provide a significant contribution to the literature on southern hemisphere zoogeography. The amphitropical Bathynellidae, also investigated by SCHMINKE (1971), are at present less useful in this respect. Relationships have not yet been fully worked out for this family, but there is increasing evidence that the distribution of the Bathynellidae may have paralleled that of the Parabathynellidae, i.e. South America has been colonised by two separate lines, one coming from Australia via Antarctica, the other from Africa (SCHMINKE & WELLS, in press).

Extant representatives of the other syncarid order known from Tasmania, the Anaspidacea, are so far unrecorded outside Australia, so that our present knowledge of this order can scarcely contribute to any general discussion of southern hemisphere relationships. On a world

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* Also *Hexabathynella*, a coastal genus of less significance in the present connection.

basis, NOODT (1964: 88) regarded it as clearly relictual: 'Heute bieten die Anaspidacea das typische Bild einer echten Reliktgruppe. Sie haben sich in nur wenigen Arten im geographischen Refugium des Südkontinentes Australien–Tasmanien erhalten, wo sie außerdem auf konkurrenzarme Extrembiotope im Sinne von ökologischen Refugien beschränkt sind.' Since the only truly freshwater fossil anaspidacean known, *Anaspidites*, is recorded from Triassic strata of New South Wales (BROOKS, 1962) and is closely related to extant anaspidaceans, it is likely that the order has long existed in south-east Australian fresh waters. Its present diversity and abundance in Tasmania *vis-a-vis* mainland Australia has been suggested in part as the result of the (present) relative scarcity of suitable habitats on the mainland and of previous and present climatic differences between the two regions (WILLIAMS, 1965a). It is certainly interesting to note that both mainland representatives (*Koonunga cursor* in the Koonungidae and a new species in a new family related to the Anaspididae recently discovered in New South Wales by SCHMINKE (1971; personal communication, 12 March 1973)) occur in subsurface aquatic situations, that is to say in habitats in which these regional differences presumably have been and are minimized.

Completely satisfactory explanations for the variously restricted distributions of the Anaspidacea *within* Tasmania cannot yet be offered. Of course, the distribution of suitable habitats is involved, but the absence of some species from apparently suitable habitats requires explanation. The restriction of *Paranaspides lacustris*, to the Great Lake (and two artificial impoundments), for example, remains unexplained. The apparent absence of *Anaspides tasmaniae* from the north-eastern highland region is also noteworthy. In this latter case, WILLIAMS (1965a) has suggested the possibility that the midland graben of Tertiary age separating this area from the west provided a barrier to dispersal after the elimination of the species from the north-east at some time in the Tertiary when the species survived only in limited western refuges.

No other group of Tasmanian freshwater Crustacea are relictual in the sense the Anaspidacea appear to be. Of those remaining for discussion, some are apparently regional invaders of inland waters from marine or terrestrial sources, others are representatives of groups limited to certain southern hemisphere (or former Gondwanaland) land masses, and there is one group that probably immigrated from Asia. Of perhaps greatest interest in the light of the previous discussion of southern hemisphere zoogeography are the Phreatoicoidea (occurring in Australia, New Zealand, India and South Africa), the Parastacidae (Australia, New Guinea, New Zealand, South America and Madagascar), and the branchiuran genus *Dolops* (Tasmania, Africa, South America). Unfortunately their evolution and systematic relationships have not yet been fully analysed so that present ideas concerning their zoogeography must remain imprecise and speculative.

The most recent comment on the evolution and zoogeography of the Phreatoicoidea is that by KNOTT (1971). Briefly, he noted that the centre of origin for the suborder cannot yet be ascertained but suggested three possibilities: 1. an origin in Gondwanaland; 2. an origin in Atlantica (i.e. the Palaeozoic and early Mesozoic continent comprising eastern North America and Europe); and 3. an origin in both Gondwanaland and Atlantica from a widely dispersed gene pool as a phenotypic response to Palaeozoic glacial perturbations. If the first possibility is correct, subsequent spread to Atlantica is presumed to have taken place via land bridges; if the second one is, then a similar spread is presumed in the opposite direction. In any event, eventual extinction of northern hemisphere forms occurred for there is clear fossil evidence of the former and early presence there of phreatoicids (e.g. SCHRAM, 1970). In Australasia, however, if not in India and South Africa, a phreatoicid radiation took place which, KNOTT (1971) has suggested, was a response either to Tertiary orogenic movements or Pleistocene glaciations or both. If this is true, then members of the Phreatoicidae, at least, form a comparatively recent group probably still speciating, a situation, it may be emphasised, quite contrary to that envisaged by NICHOLLS (1944). The linkage by KNOTT of speciation to glacial-climatic events may also explain of course the greater diversity of the group in Tasmania *vis-a-vis* the Australian mainland, where certainly Pleistocene glaciation was much less extensive. The absence of phreatoicids from South America is explained by KNOTT as due to either their non-arrival or Pleistocene extinction (resulting from the extensive glaciation that occurred). Alternatively, the suborder may occur in South America and remain undiscovered.

Views on the evolution and zoogeography of the family Parastacidae as a group are equally speculative. Early opinion generally seemed to favour an evolution on a southern continent which connected Australia, New Zealand and South America (e.g. SMITH, 1909a; HARRISON, 1926). Later, opinions became less firm, and some quite different. Thus RIEK (1959) was generally in favour of independent regional origins from marine ancestors and his view in summary was that present distributions (p. 257) 'could have been attained without the necessity of land connections between the southern continents.' An even more recent opinion, on the other hand, is that the 'distribution has never been satisfactorily explained' (BISHOP, 1967b: 112). An alternative speculation to those involving a single or several independent southern origins, of course, is that present distributions are merely relictual and the parastacids were formerly more widespread, but have been eliminated from previously occupied areas by competition. According to BANARESCU (1971), competition of this sort (from freshwater crabs) eliminated parastacids from Africa and tropical South America.

Whatever the primary origins of the family, it is quite clear that Australia, particularly the south-eastern region, represents a centre of

parastacid radiation, and that Tasmania has shared adequately in the results of speciation. The genera endemic to Tasmania, *Astacopsis* and *Parastacoides*, may easily be envisaged as having evolved from a widely dispersed eastern 'euastacoid' group as a response to local environmental conditions – especially *Parastacoides* which inhabits the coldest and wettest area in the south-west. The Tasmanian species of *Engaeus* and *Geocherax*, as easily, may be envisaged as the results of localized isolation of fragments of ancestral populations which inhabited southern Victoria, northern Tasmania, and an exposed area between now submerged by the Bass Strait. In the case of *Geocherax*, with one species common to Victoria, Tasmania and King Island *(G. falcata)*, the ancestral population probably inhabited the Pleistocene land bridge(s); in the case of *Engaeus*, with no such common species, the ancestral population may have inhabited an earlier, Tertiary (Pliocene?) land bridge (see chapter I).

The distribution of *Dolops*, the remaining Tasmanian freshwater crustacean showing an unequivocally disjunct distribution inclusive of the major southern hemisphere land masses, has recently been discussed at length by FRYER (1969). No firm conclusion was arrived at, but on balance less difficulties of explanation were envisaged if the presence of a former Antarctic continent linking Tasmania, Africa and South America were accepted than if not.

Those crustaceans of Tasmania inland waters that appear to be regional invaders from marine sources are the amphipods, the Janiridae and the Hymenosomatidae, though by enumerating these groups together there are no implications that the invasions are of similar age. In regarding the amphipods as being of marine derivation, credence is given here to J. L. BARNARD's (1972) recent and undoubtedly authoritative views on this matter. These may be interpreted as being that 1. the gammarus-like amphipods of South Africa (see K. H. BARNARD, 1927), South America and Australia are probably derived from marine ancestors that were based in or passed through the tropics, and 2. marine ceinids were the basic stock to the freshwater 'chiltonias' of Africa, Australia and New Zealand. It does not follow, of course, that the immigration into southern fresh waters of these two families was a geologically recent event – in the way that the immigration of *Paracalliope* probably is, and nor does the suggested evolution preclude the involvement of a common southern hemisphere continent (Gondwanaland) in dispersal. However, until the relationships of southern hemisphere freshwater amphipods have been investigated more fully it seems best not to regard their distribution uncritically as parallelling that of the Parastacidae and Phreatoicoidea and thereby implying closer relationships between the Ceinidae of South Africa, Australia and New Zealand, and for the Gammaridae between these regions and South America, than may actually be the case. With the removal of the Chiltoniinae (that is, South African and Australasian chiltonias) from the Hyalellidae, now

mainly an American and circumtropical taxon (BARNARD, 1972), and the acceptance of direct southern derivation for the Gammaridae (cf. SMITH's (1909a) idea of an Andean migration from the northern hemisphere), former connections with South America certainly seem to be less important than were previously thought. In any event, the simplistic approach of SMITH (1909a) and BREHM (1936) to the southern distribution of freshwater gammarids and 'chiltonias' can bear considerable examination and extension.

Considering now the distribution of freshwater amphipods in Tasmania at a less general level, it is evident that no real problems are posed by the occurrence there of the two species of *Austrochiltonia* and of the *Paracalliope* species. The former taxa are widespread in south-eastern mainland Australia at low or moderate altitudes, and easy access (or genetic confluence) can be assumed to have occurred via the low-level Pleistocene or earlier land bridges across Bass Strait. *Paracalliope* is known to occur in Victorian coastal streams (unpublished data) so that a similar explanation probably applies to this taxon too – at least at the generic level pending investigation of species identities. The diversity and abundance of the Gammaridae, on the other hand, is less easy to explain. Present and previous climatic differences between Tasmania and the mainland of Australia, and reflecting these the probably greater permanence, stability and abundance of fresh waters in Tasmania, are no doubt involved, but a simple recession to Tasmania (*sensu* RIEK, 1959) of mainland gammarids following climatic change seems unlikely to be the whole explanation. The presence of some species common to the mainland and Tasmania does indicate, it is true, the former close connections of the Tasmanian and mainland gammarid fauna, but some sort of local radiation appears to have occurred.

Of the remaining invaders from marine sources, the Janiridae seems to provide a somewhat analogous general case to that provided, superficially at least, by the Gammaridae. Thus, this group too is represented in South African and South American (Brazil) fresh waters. HUTCHINSON (1967) has suggested that the co-occurrence in Africa and Australia may represent an old Austral invasion by the family which, apart from these occurrences and a few others in isolated northern hemisphere and mainly coastal fresh waters, is marine. At present, and until relationships between South African, South American and Australian freshwater janirids are better clarified, the Tasmanian janirids, however, are best regarded as regional invaders. More certainty attaches to the regional restriction of the invasion by *Halicarcinus lacustris*, an invasion, moreover, which is probably of fairly recent occurrence (WALKER, 1969). The presence of this species on the mainland, King Island, and Tasmania has been attributed in a straightforward manner to the existence of Pleistocene land bridges (WALKER, 1969). CHILTON's (1915) view that its occurrence in New Zealand as well as in Australia indicated former land

connections between these countries, is, however, quite untenable.

Finally, there remains for discussion the origins and distribution of *Haloniscus searlei* (Oniscoidea) and *Paratya tasmaniensis* (Atyidae). Their occurrence in Tasmania provides no great explanatory difficulties. The most likely picture with regard to *H. searlei* is that this taxon, having arisen in a large mainland endorheic area from terrestrial ancestors (CHILTON, 1920; BAYLY & WILLIAMS, 1966), gained access to Tasmania via the Pleistocene land bridge when conditions, according to the recent evidence of BOWLER & HAMADA (1971), were more arid than are they now in this region and therefore more likely to have extended the present distribution of *H. searlei* in Victoria both eastwards and southwards. *Paratya* also, it would seem likely, gained access to Tasmania via a Pleistocene (or perhaps an older) land bridge. The occurrence of clinal morphological variation from the north-east to the south-east (see systematic discussion above) clearly suggests that primary access was gained in the east rather than in the west. Whatever the situation, this genus is clearly of Asiatic origin and has invaded Australia from the north (BISHOP, 1967b); Tasmania represents its southernmost extension. If the Tasmanian species is indeed endemic, then perhaps an older connection across Bass Strait provided an access which was then followed by specific divergence from mainland populations.

Acknowledgements

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* Not seen.

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