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Biogeography of Some Rheophilous Aquatic Insects in the Australian Region

by

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ABSTRACT

Data on the distribution of rheophilous aquatic insects from southeastern Australia (including Tasmania) and New Zealand indicate two unusual features in the Tasmanian fauna: there is a higher level of endemism in Tasmania than would be expected – both from its present geographical location with respect to the Australian mainland, and current knowledge of its geological history – and a number of rheophilous insects groups which could reasonably have been expected to occur in Tasmania are absent. Possible reasons for these apparent zoogeographic anomalies are discussed, but none seem entirely satisfactory.

INTRODUCTION

Although early biogeographic studies were heavily based on the distributions of plants and vertebrates (e.g. Hooker, 1853; Simpson, 1940; Wood, 1950), it has been suggested on numerous occasions that invertebrates, and particularly aquatic invertebrates, may prove even more valuable, (e.g. Brundin, 1966; Illies, 1960). In particular, a number of groups of rheophilous insects display characters which should make them eminently suitable for this purpose.

The Ephemeroptera, Plecoptera, Trichoptera and many of the aquatic Diptera, are all poor fliers or have short adult life histories, which restricts their ability to travel large distances as adults, whilst the immature stages of many species are restricted to flowing water. The principal difficulty with any zoogeographic analysis of these groups in the Australian area has been the paucity of taxonomic and distributional data. This situation has recently been greatly improved, however, by the work of Hynes (Hynes, 1964, 1974a, 1974b, 1976, 1978; Hynes and Hynes, 1975, 1980), Illies (1968, 1969, 1975), Neboiss, (1977) and Zwick, (1975, 1977, 1979).

Although all of these authors have commented on the distributions of the groups on which they worked, there has as yet been no attempt at an overview of the zoogeography of the Australian rheophilous insects. The present paper is a preliminary attempt at such an overview of five groups – the Blephariceridae (Diptera), Plecoptera, Megaloptera, Ephemeroptera and Trichoptera in eastern Australia and New Zealand.

DISTRIBUTIONS OF AUSTRALIAN STREAM INSECTS

An examination of the distribution data for the aquatic insects of Tasmania, mainland Australia and New Zealand reveals two fairly striking phenomena with regard to the Tasmanian fauna. The first is the high degree of endemicity of the Tasmanian aquatic insect fauna, a phenomenon which has also been noted for the Tasmanian freshwater crustacea (Williams, 1974b). The second is the number of groups which show a circumantarctic distribution, and which are represented in South America, New Zealand and mainland Australia but are apparently inexplicably absent from Tasmania.

Endemicity of Tasmanian Stream Insects

A number of authors (e.g. Darlington, 1965; Guiler, 1965) have stated or implied that the Tasmanian fauna is merely a reduced mainland fauna, differing from the mainland fauna mainly through absence of some species. However, the freshwater crustacea of Tasmania display a high degree of endemicity (Bayly and Williams, 1965; Williams, 1974b); and studies on stream insects have also shown that this faunal component is largely endemic and fairly rich compared with the adjacent mainland fauna. This richness should not be too surprising, because MacArthur and Wilson's (1967) hypothesis of the relationship between land area and number of species present is thought to be, to a large extent, a reflection of habitat availability. Tasmania, unlike the rest of Australia, has a high annual rainfall (ranging from just under 50 to 250 cm per annum (Williams, 1974a), and consequently has an abundance of natural permanent freshwater lakes and streams – although the number and extent of these is decreasing at an alarming rate due to the activities of the Tasmanian Hydro-Electric Commission.

In spite of the closeness of Tasmania to the mainland (205 km), with a number of islands between the two, and evidence of connections to the mainland as recently as 13,000 years ago, the greater part of the rheophilous aquatic insect fauna of Tasmania appears to be endemic. Neboiss (1977), for example, points out that 74% of the Trichoptera currently known from Tasmania (116 species) are

Table 1: Number of genera and species in each of the four Australian families of Plecoptera occurring on each side of Bass Strait. (Modified from Hynes, 1979).

	Mainland		Tasmania		Both	
	genera	species	genera	species	genera	species
Eustheniidae	3	7	1	4	1	0
Austroperlidae	4	4	3	4	0	0
Gripopterygidae	8	25	8	28	6	4
Notonemouridae	5	8	6	11	5	2

endemic. At least forty-one of the forty-seven species of plecopterans (84%) known from Tasmania, and five out of eighteen genera (Hynes & Hynes, 1980), are endemic (Table 1), as are all six described species of Blephariceridae (Diptera) (Zwick, 1977). Of the Tasmanian Siphlonuridae (Ephemeroptera), the only described species, *Tasmanophlebia lacustris* Tillyard, is endemic; however, nymphs of another species of *Tasmanophlebia* have been collected and this is probably *T. nigrescens*, which is common on the mainland. In addition, nymphs belonging to the genus *Ameletoides* Tillyard have been collected which may belong to a new, and therefore endemic, species. The only megalopteran species known from Tasmania is also endemic.

Distributions of Some Stream Insects in Australia and New Zealand

Apart from the high degree of endemism displayed by rheophilous aquatic insects in Tasmania, there are a number of notable absentees from the fauna. Zwick (1979) has already noted this with regard to the net winged midges of the tribe Apistomyiinae (Blephariceridae, Diptera) and the plecopteran genus, *Stenoperla*, whilst Campbell (1980) noted that siphlonurid mayflies of the genus *Mirawara* are absent from Tasmania. The only Australian oligoneurid genus, *Coloburiscoides*, is also absent from the island, as is the megalopteran family, Corydalidae.

All of the groups mentioned in this connection share similar distributions. In each case, members of the group are widespread on the eastern Australian mainland and have related groups in New Zealand and South America.

Within the Australian Blephariceridae, five species within three genera of the tribe Apistomyiini have so far been described from the Australian mainland, although several undescribed species are also known to occur (Zwick, 1977). All specimens have been collected from the Great Dividing Range in eastern Australia, and the localities range from north of Cairns in the north to within 50 km of Melbourne in the south. Three genera of this tribe occur in New Zealand, two in New Caledonia, two more in the Oriental Region and its sister group occurs in South America (Table 2). It is notable that, within this group, there are not only tropical species but also one species, *Austrocurupira nicholsoni* (Tillyard), which is common in streams near the summit of Mt. Kosciusko, the highest Australian mountain. The apistomyiids have been placed by Zwick (1977) in the subfamily Blepharocerinae, the other subfamily of Blephariceridae, Edwardsininae, is represented on both the mainland of Australia and Tasmania.

Table 2: Distributions of the genera of Apistomyiini (Diptera, Blephariceridae) occurring in Australia, New Zealand and South America.

Tasmania	Australian mainland	New Zealand	Oriental Region and New Caledonia	South America
absent	*Austrocurupira* *Parapistomyia* *Apistomyia**	*Nothohoraia* *Neocurupira* *Peritheates*	*Hammatorrhina* *Horaia* *Apistomyia** *Curupirina* *Nesocurupira*	*Paltostoma* and related genera

* *Apistomyia* occurs in Australia, Asia and Europe.

The distribution of the Eustheniidae (Plecoptera) has a number of striking similarities to that of the Blephariceridae. Two subfamilies are recognised within the eustheniids (Zwick, 1979) – the Eustheniinae, containing three genera: *Neuroperlopsis* Illies, *Eusthenia* Gray and *Thaumatoperla* Tillyard; and the Stenoperlinae, containing the two genera: *Stenoperla* McLachlan and *Neuroperla* Illies. One genus from each subfamily (*Neuroperlopsis* Illies and *Neuroperla* Illies) occur only in South America, whilst the other genera are all restricted to Australia and New Zealand. Their distributions are shown on Figure 1. It can be seen from the figure that, although the species of the Eustheniinae have fairly restricted distributions, with one genus (*Thaumatoperla* Tillyard) restricted to a few localities in Victoria and the other (*Eusthenia* Gray) to the cool south eastern part of Australia plus Tasmania, the genus *Stenoperla* has a very wide distribution. *Stenoperla prasina* (Newman), one of the two species occurring in New Zealand, is described by Zwick (1979) as being present "all over both islands and has been taken at sea level as well as at great altitudes". Similarly, the Australian species *Stenoperla australis* Tillyard is recorded from the Atherton Tableland, near Cairns in northern Queensland, to the Otway Ranges, at the southern tip of

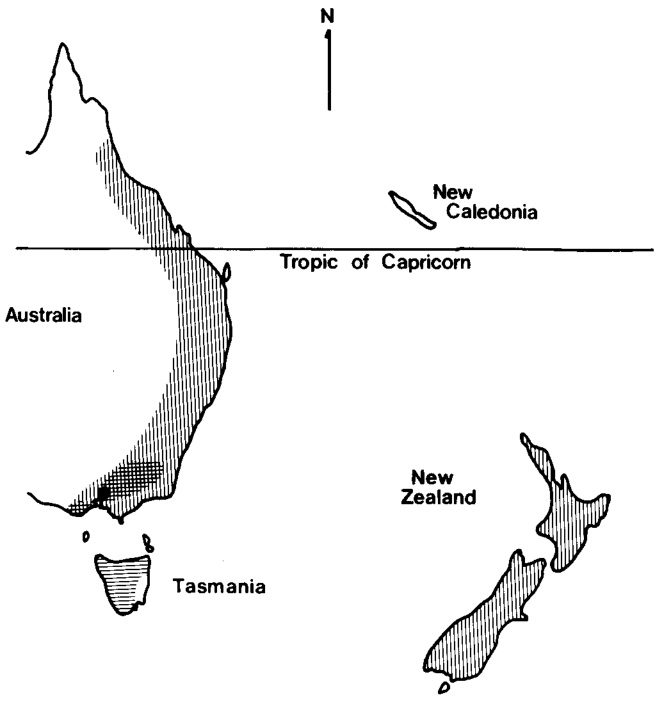

Figure 1. Distributions of the Australian genera of Eustheniidae (Plecoptera). The distribution of *Stenoperla* is represented by the vertical shading, *Eusthenia* by the horizontal shading and *Thaumatoperla* by the black dot.

Victoria. It also occurs over a wide altitudinal range, being recorded from an altitude of only a few metres in the Otway Ranges of Victoria and from Lake Albina, at an altitude of 1900 metres, on Mt. Kosciusko. In view of this, the absence of *Stenoperla* from Tasmania is a puzzle.

Two megalopteran families are recorded from the Australian region (Riek, 1970). Of these, one, the Sialidae, is represented by the Australian endemic genus, *Austrosialis*, which occurs from Queensland to Victoria on the eastern coast with one species present in Tasmania. The other family, the Corydalidae, is represented by two genera from the subfamily Chauliodinae. One genus, *Austrochauliodes* Riek, contains the single species *Austrochauliodes dubitatus* (Walker), which is restricted to Queensland and northern New South Wales; but the other genus, *Archichauliodes* Weele, has three mainland Australian species, which occur down the east coast from north Queensland to Victoria with one species apparently restricted to the Snowy Mountains. Another species, *A. diversus* (Walker), is recorded from New Zealand (Wise, 1977); the genus is also recorded from Chile (Riek, 1970) but no corydalids occur in Tasmania.

Within the Ephemeroptera, one of three siphlonurid genera and the only oligoneurid genus show similar distributions to those of the three previous groups. The distributions by land mass of the genera of the oligoneurid and the three subfamilies of siphlonurids which occur in Australia are indicated in Table 3. The only oligoneurid, *Coloburiscoides* Lestage, has a somewhat similar distribution; however, *Coloburiscoides* is far more restricted in its Australian distribution (Fig. 2b). There is no record of *Coloburiscoides* occurring north of 35° South, although the nymphs are large and distinctive and have been sought by numerous collectors.

Within the Siphlonuridae, the distribution of the Ameletopsinae is quite similar to the Stenoperlinae in the Plecoptera. The range of *Mirawara* Harker coincides well with the range of *Stenoperla australis* on the mainland (Fig. 2a) and *Ameletopsis* Phillips occurs on both islands of new Zealand and is described by Phillips (1933) as being "moderately distributed". In both of the other subfamilies of Siphlonuridae on mainland Australia (the Siphlonuridae and the Oniscigastrinae), the distributions are apparently readily explicable. *Ameletoides* Tillyard (subfamily Siphlonuridae) occurs both on the mainland of Australia and I have now also collected it from Tasmania. On the mainland it occurs only in lakes and stony streams at high altitudes, and has only been collected from sites near Mt.

Table 3: The distributions of the genera of three sub-families of Siphlonuridae and the Oligoneuridae (Ephemeroptera) present in Australia, South America and New Zealand.

Family	Sub-family	South America	New Zealand	Australia	Tasmania
Oligoneuridae	Coloburiscinae	*Murphyella*	*Coloburiscus*	*Coloburiscoides*	—
Siphlonuridae	Oniscigastrinae	*Siphlonella*	*Oniscigaster*	*Tasmanophlebia*	*Tasmanophlebia*
Siphlonuridae	Siphlonurinae	*Metamonius*	*Nesameletus*	*Ameletoides*	*Ameletoides*
Siphlonuridae	Ameletopsinae	*Chaquihua* *Chiloporter*	*Ameletopsis*	*Mirawara*	—

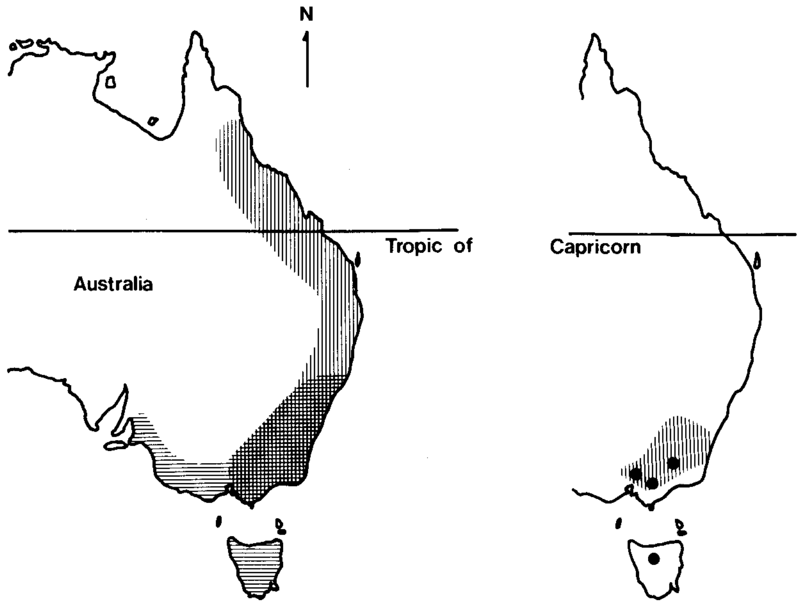

Figure 2. The distributions of the genera of Australian Siphlonuridae and Oligoneuridae (Ephemeroptera). The distributions of *Mirawara* (vertical shading) and *Tasmanophlebia* (horizontal shading) are indicated on the left and *Coloburiscoides* (shading) and *Ameletoides* (dots) on the right.

Kosciusco, N.S.W. and Mt. Buller, Mt. Stirling and Mt. Baw Baw in Victoria. I have recently collected it from the Pencil Pine River near Cradle Mt. in Tasmania. Evidently the distribution is relictual. *Tasmanophlebia* Tillyard is widespread, with one endemic and probably one other species in Tasmania, and two other species described from the mainland. Nymphs have been collected from as far north as 32° South and from as far west as the Adelaide Hills in South Australia. Members of the genus occur in streams and lakes at all altitudes down to sea level.

Factors Determining Distributions

The absence of the Apistomyiinae, Stenoperlinae, Ameletopsinae, Coloburiscinae and Chauliodinae from Tasmania presents somewhat of a zoogeographic problem. In each case, apparently suitable habitat is abundantly present in Tasmania, and in each case related groups are also present. There are two plausible explanations for the distributions of these groups:

1. They arrived in Australia via a northerly route, and were unable to reach Tasmania either across Bass Strait or via a land bridge.
2. They were present in Australia before Tasmania was separated from the mainland, but died out in Tasmania and have failed to re-invade.

Zwick (1977, 1979) has suggested the first of these possibilities to explain the distributions of the Apistomyiinae and the Stenoperlinae. He believes that the Apistomyiinae must have reached the Australian region via a land link, and suggests that the most likely route was via the West Antarctica to New Zealand, after Australia had separated from the rest of Gondwanaland sometime in the mid-Cretaceous. This route, initially suggested by King and Downard (1964), may have persisted until the Miocene according to Harrington (1965). Northward land links from New Zealand to New Caledonia were probably disrupted in the late Cretaceous (Fleming, 1962), and links between New Caledonia and New Guinea by the end of the Mesozoic (Thorne, 1963). These links would have enabled the apistomyiids to enter Australia from the north via the land connections with New Guinea, which it is now suggested (Mackerras, 1970) occurred during the Pliocene. Land bridges between the mainland and Tasmania which have occurred since that time would not have provided, Zwick argues, suitable habitats for Blephariceridae. The same migrational path could also have been followed by the other groups mentioned above, although none of these three groups has been recorded from New Caledonia, as the apistomyiids have. However, although a migrational path passing through the tropics may be perfectly acceptable for organisms which presently extend into the tropics in Australia, one of these groups, the Coloburiscinae, is represented in Australia only by a decidedly cool adapted genus – *Coloburiscoides*. It is difficult to reconcile such an origin with our knowledge of the present day requirements of this genus.

An additional difficulty with this route comes from the suggestion by Davies (1974) and others that New Zealand split from Gondwanaland in the late Mesozoic, before Australia. Hayes and Ringis (1973) present data indicating that the Tasman Sea formed in the late Cretaceous, about 60-80 million years ago; whereas Australia seems to have separated from Antarctica somewhat later than this, probably in the Eocence about 56 million years ago (Glomar Challenger, 1973). This sequence of events is not compatible with the route proposed by Zwick.

The second possible explanation proffered above is also difficult to accept. This explanation requires some factor which could eliminate all of these groups from Tasmania. The factors most usually postulated in such cases are major climatic changes and, whilst there is evidence for at least two glaciations in Tasmania (Davies, 1974), there a number of reasons for doubting that they caused such an extinction. The first of these is the present day distributions of the groups concerned. All of them have representatives occurring near the summit of Mt. Kosciusko at an altitude of about 2000 m; this region is snow covered for at least four months of the year. In addition, all but Coloburiscoides extend well into sub-tropical or even tropical climates. It seems hard to reconcile such distributions with extermination due to climatic change.

The second reason for doubting that climatic change caused extinction of these groups in Tasmania is the presence of their related groups on the island. Particularly striking is the presence of *Ameletoides* in Tasmania in the absence of *Coloburiscoides*. On the mainland, *Ameletoides* occurs both in lakes and running waters. In all but one of the streams in which it occurs I have also collected *Coloburiscoides*. However, *Coloburiscoides* is also found at altitudes well below those at which *Ameletoides* occurs, that is, it seems far more tolerant of environmental conditions than *Ameletoides*. One would expect, therefore, that *Ameletoides* would be eliminated under conditions of climatic change before *Coloburiscoides*, but that both genera would be more greatly affected by warmer climates than by glacial periods. In the other cases the argument applies equally – why should *Archichauliodes* be eliminated by climatic change and *Austrosialis* not?

Rawlinson (1975) and Davies (1975) have discussed the biological effects of the most recent glaciation, which occurred between 25,000 and 15,000 years ago and which, it is suggested, resulted in significant areas of permanent ice in Tasmania and a lowering of the treeline to about 450 m above sea level. However, while this may have reduced the area of habitat available for stream insects, the groups discussed here are amongst those least likely to be affected by glacial activity for the reasons already outlined. In addition it would be reasonable to expect that a glaciation severe enough to eliminate species so capable of surviving the cool conditions in which those above are found, would result in an extremely depauperate biota, even today; but this is certainly not the case in Tasmania, either in respect of the freshwater fauna or of most other faunal elements.

Both of the proposed explanations listed above require an effective barrier between Tasmania and the mainland. The high level of endemicity of the Tasmanian freshwater fauna indicates that this has been the case – probably both when there was a land connection between the two as well as periods when they were isolated by sea. The most recent land connection between Tasmania and the Australian mainland probably occurred during the Pleistocene glaciation, when the sea level was some 150 m lower than at present. This would have exposed an extensive area of fairly low relief between the two present day land masses, generally referred to as the Bassian Isthmus. In view of the physical nature of the isthmus, the streams flowing across it must have been quite sluggish. Such streams are not suitable for Blephariceridae or *Coloburiscoides*. Another critical factor determining suitability of the habitat is water temperature. It had been generally believed that the climate during the Pleistocene glaciation was cool and pluvial, with ambient temperatures 5-10°C lower than at present (Davies, 1974). If this were the case, one would expect the isthmus streams would have been quite suitable for organisms such as *Stenoperla australis* and *Archichauliodes*. However, Hynes (1976) notes that, of the six plecoptera which occur on both sides of Bass Strait, five occur in warm streams in Victoria. It would seem strange that only these organisms could cross the isthmus if the climate during the Pleistocene was significant cooler than at present.

More recent authors (e.g. Bowler, 1975; Galloway, 1965, 1971) have disputed the accepted Pleistocene climate for Southeastern Australia. They suggest that the climate was, in fact, drier than at present, with cooler winters but warmer summers. If this were the case, there may not have been many streams on the Bassian Isthmus, and the high summer water temperatures would have restricted the number of species capable of surviving in those there were. In particular, species with life histories requiring more than a year may not have been able to survive. *Stenoperla australis* and at least one species of *Coloburiscoides* are known to have two-year life histories (Hynes and Hynes, 1975; Duncan, 1972).

CONCLUSIONS

The insect fauna of Tasmanian streams is highly endemic; however, a number of insect groups one would expect to find in Tasmania are absent. Such insects include the Apistomyiinae (Diptera, Blephariceridae), Stenoperlinae (Plecoptera, Eustheniidae), Coloburiscinae and Ameletopsinae (Ephemeroptera, Siphlonuridae) and the Chauliodinae (Megaloptera, Corydalidae). All of these groups show an Austral distribution, having representatives in South America, New Zealand and Australia; and all have at least one species on the mainland of Australia which can withstand cold conditions. Most also have species in tropical or subtropical habitats in Australia. The two possible origins of this type of distribution are:

1. The groups involved entered Australia via a northern route, and were unable to cross to Tasmania because of the sea barrier or lack of suitable habitats in Bassian Isthmus.
2. The groups involved were formerly widespread in Australia and Tasmania, but have become extinct in Tasmania at some time for some reason and have been unable to re-invade.

For various reasons both of these explanations are unsatisfactory. It is concluded, however, that both the present Bass Strait and the Pleistocene Bassian Isthmus were effective barriers to many stream insects.

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