Odonatologica 13 (1): 147-157 *February 18, 1984*

REGIONS OF TAXONOMIC DISJUNCTION IN AUSTRALIAN ODONATA AND OTHER FRESHWATER INSECTS

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Received October 25, 1983

The montane chain of eastern Australia includes at least four regions where ecological and physiographic boundaries coincide with taxonomic discontinuities in Odonata, Plecoptera and Megaloptera: the gap between the Paluma Range and Eungella (Queensland); the Carnarvon Gorge (Queensland); the southern margin of the northern tablelands of New South Wales; and the northern limit of the southern highlands, near Canberra. The taxonomic disjunctions are, in most cases, at or below the level of closely related species-pairs, and are probably the outcomes of pleistocene climatic fluctuations.

INTRODUCTION

Broad outlines for a zoogeography of Australian Odonata were sketched long ago. TILLYARD (1914, 1917) recognised the basic importance of an old, southern continental fauna among the Australian dragonflies, to which was added a complement of faunal elements from the north. Although the re-establishment of the Gondwana concept has radically altered the interpretation placed on the southern fauna, the concept of two major faunal components has persisted (cf. WATSON, 1981).

LIEFTINCK (1949) documented the importance of the northern elements, which include representatives of many families, particularly the Coenagrionidae and Libellulidae (WATSON, 1981). Although recent studies have greatly increased the number of species known from northern Australia (e.g. WATSON & ABBEY, 1980; WATSON & THEISCHINGER, 1984), they have not disclosed any that conflict with the generalisations that emerged from Lieftinck's

work, or add substantially to them (cf. WATSON, 1981, 1982). In this paper we will, therefore, concentrate on the zoogeography of the old, southern Australian Odonata.

As WATSON (1981) and THEISCHINGER & WATSON (1984) have shown, Odonata that appear to have southern origins, including Gondwanaland, comprise slightly more than 40% of the Australian dragonfly fauna, and include the following groups: Chlorolestidae, Neopetaliinae, Brachytroninae, Petaluridae, Gomphidae (the Ictinogomphinae excepted), Gomphomacromiinae, Synthemistinae, and the genera *Aeshna* and *Pentathemis*. Of these all but *Aeshna, Pentathemis* and the small gomphids (*Hemigomphus* and its allies excepted), which are widespread or occur only in the north, have their headquarters in the montane chain and coastal fringe of eastern mainland Australia, particularly in the south-east, with an outlier in south-western Australia and another, with many fewer species, in the Arnhem Land region of the Northern Territory (WATSON, 1981, 1982). Almost all these species breed in flowing water, or in bogs and seepages, as do those of two other genera, *Argiolestes* (Megapodagrionidae) and *Diphlebia* (Amphipterygidae), whose distributions are also broadly southern and eastern but whose zoogeographic affinities are uncertain (WATSON, 1974, 1977, 1981).

WATSON (1981, 1982) discussed relationships between the ecology, zoogeography and speciation of these Odonata. There is evidence implying ancient geographical isolation of some groups [*Synthemis* and *Argiolestes* in New Guinea and, possibly, New Caledonia; *Archipetalia* and *Synthemiopsis* in Tasmania; "*Hemigomphus*" *armiger* (Till.), *Hesperocordulia* and *Lathrocordulia* in south-western Australia]; the younger separation of others [e.g. *Argiolestes minimus* Till., *Petalura hesperia* Watson, *Austroaeschna anacantha* Till. and *Austrogomphus lateralis* (Selys) in south-western Australia; *Austroaeschna hardyi* Till. and *A. tasmanica* Till. in Tasmania; and *Hemigomphus* sp. "m" and *Austrocordulia territoria* Thei. and Watson in Arnhem Land]; and the more recent separation of several [*Austroagrion cyane* (Selys) (= *coeruleum* auctt; cf. LIEFTINCK, 1982) and *Procordulia affinis* (Selys) in the south-west; *Austrogomphus gordoni* Watson in the north-west of Western Australia]. Further groups appear to have been isolated very recently, particularly the Tasmanian forms of *Ischnura heterosticta* (Burm.) and *Synthemis eustalacta* (Burm.) (cf. TILLYARD, 1913; ALLBROOK, 1979), which probably crossed the low, sandy isthmus that is thought to have connected Tasmania with the Australian mainland until some 12,000 years ago (KEAST, 1981).

All these cases clearly involve populations that are, in effect, insular, isolated from congeners elsewhere in Australia by extensive regions lacking suitable fresh waters. However, it is becoming apparent that there are other, much less evident regions of taxonomic disjunction in the Australian Odonata, specifically in the

Great Dividing Range, a mountain chain that parallels the eastern Australian coast, generally not far inland. Other freshwater insects that are also likely Gondwana relics, e.g., various Plecoptera and Megaloptera (ZWICK, 1981; THEISCHINGER, 1983a, 1983b) show similar taxonomic disjunction in some of these regions. Our knowledge of the disjunctions involved is still fragmentary, but four areas are clear enough that their significance can be documented (Fig. 1). These are:

(1) the gap between the Paluma Range (ca 19° S) (Fig. 1.1) and Eungella (ca 21° S) (Fig. 1.2), Queensland;
(2) the Carnarvon Gorge (ca 25° S, 148° E) (Fig. 1.3), Queensland;
(3) the southern margin of the northern tablelands of New South Wales, at approximately 32° S (Fig. 1.4);
(4) the northern margin of the southern highlands (the Australian Alps and the mountains of the Australian Capital Territory), between 35° and 36° S (Fig. 1.6).

We now examine each of these areas in turn.

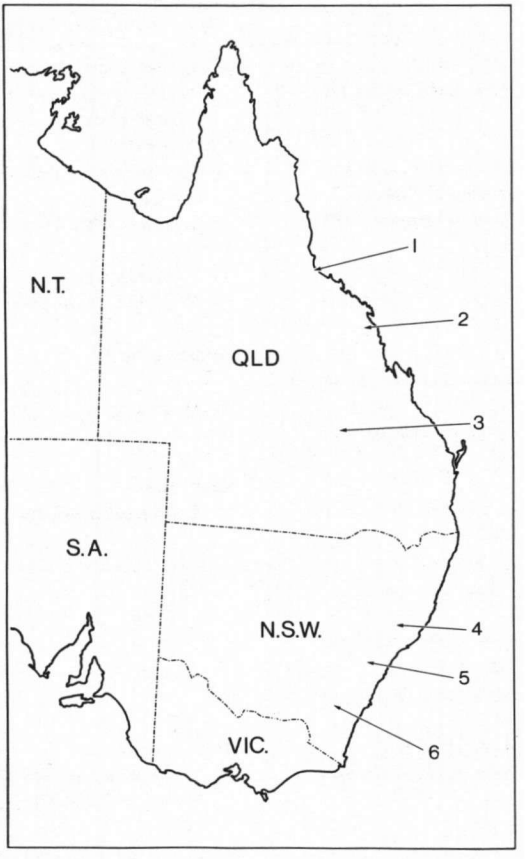

Fig. 1. Map of eastern Australia, showing relevant localities. N.S.W. = New South Wales; N.T. = Northern Territory; QLD = Queensland; S.A. = South Australia; VIC. = Victoria. 1 = Paluma Range; 2 = Eungella; 3 = Carnarvon Gorge; 4 = Barrington Tops; 5 = Blue Mountains; 6 = Canberra.

THE PALUMA RANGE AND EUNGELLA

The Paluma Range (Fig. 1.1) and Eungella (Fig. 1.2) are approximately 350 km apart. Paluma marks the southern boundary of the major block of northern Queensland rainforest that extends north almost to Cooktown (ca 15° 50'S). Eungella lies in the northernmost of a series of

Table 1

Odonata, Plecoptera and Megaloptera with limits of distribution at the gap, Paluma Range--Eungella; "vs" indicates species-pairs

Species occurring: *North from Paluma*	*At or south from Eungella*	References
ODONATA:	Megapodagrionidae	
Argiolestes aureus Till.	*Argiolestes* sp. near *A. calcaris* Fraser	O'Farrell & Theischinger, in prep.
	Chlorolestidae	
Episynlestes cristatus Watson & Moulds	vs *Episynlestes* sp. near *E. cristatus*	Theischinger & Watson, in prep.
Synlestes tropicus Till.	vs *Synlestes selysi* Till.	Theischinger & Watson, in prep.
	Amphipterygidae	
Diphlebia euphaeoides Till.	vs *Diphlebia coerulescens* Till.	STEWART, 1980; Watson, unpubl.
	Gomphidae	
Austrogomphus doddi Till.		Watson, in prep.
	Petaluridae	
Petalura ingentissima Till.		Watson, unpubl.
	Aeshnidae	
Austroaeschna forcipata Till.	*Austroaeschna sigma* Thei.	THEISCHINGER, 1982a, unpubl.
Austroaeschna weiskei (Förster)	*Austroaeschna pulchra* Till.	
	Corduliidae	
Archaeophya magnifica Thei. & Watson		THEISCHINGER & WATSON, 1978
Pseudocordulia elliptica Till.		THEISCHINGER & WATSON, 1978
PLECOPTERA:	Gripopterygidae	
Dinotoperla cardaleae Thei.	*Dinotoperla eungella* Thei.	THEISCHINGER, 1982b
	Dinotoperla parabrevipennis Thei.	THEISCHINGER, 1982b
Illiesoperla sp. "b"	vs *Illiesoperla mayi* (Perk.)	Theischinger, unpubl.
Illiesoperla cerberus Thei.	*Illiesoperla franzeni* (Perk.)	THEISCHINGER, 1982b
MEGALOPTERA:	Corydalidae	
Archichauliodes phaeoscius Riek	*Archichauliodes deceptor* Kimmins	THEISCHINGER, 1983a
Protochauliodes kirramae Thei.	vs *Protochauliodes* sp. near *P. kirramae*	THEISCHINGER, 1983a, unpubl.

substantial, isolated patches of rainforest that extend southwards into New South Wales. The region between Paluma and Eungella is relatively arid, and supports sclerophyl woodland dominated by species of *Eucalyptus*.

Species of Odonata, Plecoptera and Megaloptera with known distributional

limits lying on one side or the other of this gap are listed in Table I. Three species--pairs of Odonata and one of Megaloptera stand astride the gap. There are, however, more species that, if related at all, have only remote affinities with congeners on the other side of it. Some northern species (e.g. *Petalura ingentissima* and *Pseudocordulia elliptica*) have close relatives only in the northern rainforests (*P. pulcherrima* Till. and *P. circularis* Till. respectively); others (e.g. *Argiolestes aureus, Austrogomphus doddi* and *Archaeophya magnifica*) are closely related to species from south-eastern Queensland or north--eastern New South Wales [*A. chrysoides* Till., *Austrogomphus* sp. "c" (cf. WATSON, 1974) and *A. adamsi* Fraser respectively]; and a few (e.g. *Austroaeschna forcipata* and *A. weiskei*) appear to have no close relatives (Watson & Theischinger, unpubl. data).

CARNARVON GORGE

THEISCHINGER & WATSON (1979) discussed the Odonata of Carnarvon Gorge (Fig. 1.3), which contains permanent streams. It harbours an outlier of the odonate fauna characteristic of the better-watered, montane region of south--eastern Queensland (cf. WATSON, 1974), the inland margin of which lies some 130 km east of the gorge (THEISCHINGER & WATSON, 1979). The permanent waters at Carnarvon Gorge are an oasis in an area where the rainfall is low, and seasonal; at Injune (25° 51'S, 148° 34'E), between Carnarvon Gorge and the coastal ranges, the annual rainfall averages approximately 580 mm, and

Table II

Odonata, Plecoptera and Megaloptera endemic to Carnarvon Gorge, and their closest coastal congeners

Endemic species	Allied coastal species	References
ODONATA:	Aeshnidae	
Austroaeschna muelleri Thei.	*Austroaeschna pulchra* Till.	THEISCHINGER, 1982a
Telephlebia sp."u"	*Telephlebia tryoni* Till.	Theischinger, unpubl.
	Corduliidae	
Eusynthemis deniseae Thei.	?*Eusynthemis virgula* (Selys)	THEISCHINGER, 1977
PLECOPTERA:	Gripopterygidae	
Dinotoperla carnarvonensis Thei.		THEISCHINGER, 1982b
Illiesoperla sp. "c"	*Illiesoperla mayi* (Perk.), *I. franzeni* (Perk.)	Theischinger, unpubl.
MEGALOPTERA:	Corydalidae	
Archichauliodes rieki Thei.	*Archichauliodes neoguttiferus* Thei.	THEISCHINGER, 1983a

at Tambo (24° 53'S, 146° 15'E), inland of Carnarvon Gorge, it averages approximately 490 mm. Bundaberg (24° 52'S, 152° 21'E), east on the coast, has an average annual rainfall of almost 1,100 mm.

The occurrence of apparently endemic taxa, all distinct at the species-group level, in Odonata, Plecoptera and Megaloptera is documented in Table II. Four species of Odonata not mentioned in the Table, *Argiolestes icteromelas* Selys, *Episynlestes albicauda* (Till.), *Synlestes tillyardi* Fraser and *Eusynthemis nigra* (Till.), show differences in size or pigmentation between coastal populations and those from Carnarvon Gorge. Some other insect groups show similar endemism. For example, the area surrounding Carnarvon Gorge harbours an endemic species of termite, *Nasutitermes carnarvonensis* (Hill), a close relative of the widely-distributed southern Australian species *N. exitiosus* (Hill), which ranges from south-western Australia to extreme south-eastern Queensland (HILL, 1942).

THE NORTHERN TABLELANDS OF NEW SOUTH WALES

The northern tablelands of New South Wales are the northernmost of three main mountain regions in the southern half of the Great Dividing Range, the others being the Blue Mountains (Fig. 1.5) and associated ranges, inland to south-west of Sydney, and the southern highlands (see next section). The southern margin of the northern tablelands lies close to the northern side of the Hunter River Valley, and the fauna characteristic of the northern tablelands commonly extends south to the high country of the Barrington Tops (ca 32° S) (Fig. 1.4). Several northern tablelands species (some of which occur farther north, in Queensland, with a few ranging to Eungella or beyond) have related southern counterparts that range north to the Blue Mountains, some reaching the southern side of the Hunter Valley. The levels of relationship between these and the northern tablelands species vary, from that of closely allied species-pairs to consistently distinguishable forms, differing as larvae or adults, that have not been accorded nomenclatorial recognition.

The taxa showing distributional limits at or about the Hunter Valley are listed in Table III. Members of one species-pair, *Austroaeschna sigma* and *A. obscura,* are known to occur together, at Watagan, near Morisset (ca 33° S), on the coastal plain contiguous with the Hunter Valley.

Among the Plecoptera there is a tendency for the nearest counterparts of northern tablelands species to be found south of the Blue Mountains, in the southern highlands; the intervening region, which is some 375 km wide, is evidently inhospitable for them. These species-pairs are documented in the next section.

Table III

Odonata, Plecoptera and Megaloptera with limits of distribution at or near the Hunter Valley; "vs" indicates closely related forms

Species occurring: *North from Hunter Valley*	*South from Blue Mts*	References
ODONATA:	Megapodagrionidae	
Argiolestes sp. near *A. alpinus* Till.	*Argiolestes* sp. "i"	O'Farrell & Theischinger, unpubl.
Argiolestes sp. near *A. calcaris* Fraser	vs *Argiolestes calcaris*	O'Farrell & Theischinger, unpubl.
	Chlorolestidae	
Synlestes tillyardi Fraser (hornless larvae)	vs *Synlestes tillyardi* (horned larvae)	Theischinger & Watson, unpubl.
	Amphipterygidae	
Diphlebia lestoides tillyardi Fraser	vs *Diphlebia l. lestoides* (Selys)	STEWART, 1980
	Aeshnidae	
Austroaeschna sigma Thei.	vs *Austroaeschna obscura* Thei.	THEISCHINGER, 1982a
Austroaeschna subapicalis Thei. (northern form)	vs *Austroaeschna subapicalis* (southern form)	THEISCHINGER, 1982a
Notoaeschna geminata Thei.	vs *Notoaeschna sagittata* (Martin)	THEISCHINGER, 1982a
	Corduliidae	
Eusynthemis guttata "aurolineata" (Till.)	vs *Eusynthemis guttata* (Selys) s. str.	Theischinger & Watson, unpubl.
Eusynthemis brevistyla "subjuncta" (Till.)	vs *Eusynthemis brevistyla* (Till.) s. str.	Theischinger & Watson, unpubl.
Austrocordulia refracta Till. (short spine larva)	vs *Austrocordulia refracta* (long spine larva)	THEISCHINGER & WATSON, 1984
PLECOPTERA:	Eustheniidae	
Stenoperla wongoonoo Thei.	vs *Stenoperla kuna* Thei.	THEISCHINGER, 1983b
	Gripopterygidae	
Dinotoperla cobra Thei.		THEISCHINGER, 1982b
Dinotoperla parabrevipennis Thei.	cf. Tab. IV	THEISCHINGER, 1982b
Neboissoperla monteithi Thei.	cf. Tab. IV	THEISCHINGER, 1982b
Riekoperla sp. near *R. rugosa* (Kimmins)	vs *Riekoperla rugosa*	Theischinger, unpubl.
Trinotoperla yeoi Perk.	cf. Tab. IV	THEISCHINGER, 1982b
	Austroperlidae	
Austroheptura picta (Riek)	cf. Tab. IV	Theischinger, unpubl.
MEGALOPTERA:	Corydalidae	
Archichauliodes neoguttiferus Thei.	vs *Archichauliodes guttiferus* (Walker)	THEISCHINGER, 1983a
Archichauliodes deceptor Kimmins	*Archichauliodes plomleyi* Kimmins	THEISCHINGER, 1983b

THE SOUTHERN HIGHLANDS

The southern highlands include the most substantial alpine areas in Australia, and surround its highest peak, Mt Kosciusko (2,228 m). The high country is snow-covered in winter to well below the tree-line, which is at about 1,500-1,800 m. The freshwater insect fauna includes a component of distinctively high alpine species, many of which have no close counterparts at lower altitudes. In addition, there are species which, like those of the northern tablelands, have close congeners nearby. As mentioned above, many Plecoptera of the southern highlands have their closest relatives far to the north, in the high country beyond the Hunter River. There are also apparent outliers of the southern highland fauna in the Kanangra Walls region of the Great Dividing Range, at approximately 34° S, south of the Blue Mountains, and in rainforest on the south coast of New South Wales near Minnamurra, at approximately 34° 50'S. However, despite this variability of distribution, there often appears to be faunal discontinuity at about the latitude of Canberra (35° 17'S) (Fig. 1.6).

Table IV lists the southern highland species of Odonata, Plecoptera and Megaloptera, including high alpine as well as other forms, and their counterparts to the north. All the southern species, except those confined to the high alps, have closely related northern congeners (including species with known southern limits at or near the Hunter Valley); there are no species of these old southern genera in the region 2-3° north of Canberra that do not have close relatives in the southern highlands.

DISCUSSION

Three of these four regions of taxonomic disjunction in old southern genera — the Carnarvon Gorge, the southern margin of the northern tablelands of New South Wales, and the northern limit of the southern highlands — are characterised by taxonomic differences at or below the level of closely related species-pairs. The fourth, the gap between the Paluma Range and Eungella, appears to be deeper in that species from the northern side often have no close southern relatives.

Extrapolating from the interpretations that have been placed on similar levels of disjunction in Odonata elsewhere in Australia [e.g., *Austroagrion cyane* in south-western and south-eastern Australia and the presumably parental form now represented in eastern and northern Australia by *A. watsoni* Lieft. (WATSON, 1981; LIEFTINCK, 1982); the *Argiolestes pusillus* complex in south-western Australia and the *A. griseus* complex of the east (WATSON, 1977); and the Tasmanian forms of *Ischnura heterosticta* and *Synthemis eustalacta*], the formation of these taxonomically close pairs can be interpreted as consequences of events that took place during the Pleistocene and Holocene. Certainly, they

Table IV

Odonata, Plecoptera and Megaloptera with northern limits of distribution in the southern highlands of New South Wales, and close northern congeners

Species occurring: *In, or south from, southern highlands*	*North of highlands, or perialpine*	References
ODONATA:	Megapodagrionidae	
Argiolestes calcaris Fraser s. str.		O'Farrell & Theischinger, unpubl.
Argiolestes griseus intermedius Till.	vs *Argiolestes g. griseus* Selys (*sensu* Tillyard, 1913)	O'Farrell & Theischinger, unpubl.
	Aeshnidae	
Austroaeschna atrata Martin	vs *Austroaeschna subapicalis* Thei.	THEISCHINGER, 1982a
Austroaeschna flavomaculata Till.	vs *Austroaeschna parvistigma* Martin	THEISCHINGER, 1982a
Austroaeschna multipunctata (Martin)	vs *Austroaeschna obscura* Thei.	THEISCHINGER, 1982a
Austroaeschna inermis Martin		THEISCHINGER, 1982a
Telephlebia brevicauda Till.	vs *Telephlebia godeffroyi* Selys	Theischinger, unpubl.
PLECOPTERA:	Gripopterygidae	
Dinotoperla brevipennis Kimmins	vs *Dinotoperla parabrevipennis* Thei.*	THEISCHINGER, 1982b
Dinotoperla eucumbene McL.		THEISCHINGER, 1982b, unpubl.
Dinotoperla hirsuta McL.		Theischinger, unpubl.
Eunotoperla kershawi McL.		Theischinger, unpubl.
Leptoperla sp. near *L. albicincta* Thei.	vs *Leptoperla truncata* Thei.	Theischinger, unpubl.
Neboissoperla alpina McL.	vs *Neboissoperla monteithi* Thei.*	THEISCHINGER, 1982b
Riekoperla tuberculata McL.	vs *Riekoperla* sp. near *R. tubercalata*	Theischinger, unpubl.
Trinotoperla irrorata Till.		McLELLAN, 1971; Theischinger, unpubl.
Trinotoperla montana Riek	vs *Trinotoperla yeoi* Perk.*	THEISCHINGER, 1982b
Trinotoperla nivata Kimmins	vs *Trinotoperla* sp. near *T. nivata*	Theischinger, unpubl.
	Austroperlidae	
Acruroperla atra (Samal)		Theischinger, unpubl.
Austroheptura illiesi Hynes	vs *Austroheptura picta* (Riek)*	Theischinger, unpubl.
	Notonemouridae	
Austrocercella tillyardi (Kimmins)		Theischinger, unpubl.
MEGALOPTERA:	Corydalidae	
Archichauliodes anagaurus Riek		THEISCHINGER, 1983a

* Species found south to the southern margin of the northern tablelands of New South Wales (cf. Tab. III).

must have occurred after the late Miocene, when the uplift of the eastern highlands occurred, and probably after the Pliocene, during which the present patterns of zonal climate were established [cf. papers in KEAST (ed.), 1981]. The least-marked disjunctions presumably followed the rise in sea level which, for example, isolated Tasmania 12-13,000 years ago, and flooded the southern Australian coastal plain along which, it can be argued, *Austroagrion cyane* spread from south-western Australia into eastern South Australia. The more marked disjunctions, however, probably depended on changes in climate during the Pleistocene, creating refugia in which speciation could occur (cf. WATSON, 1977; KEAST, 1981). Unfortunately, as KEAST (1981) has pointed out, the climatic record of the Australian Pleistocene is still relatively incomplete, and there is increasing evidence of diversity in climatic trends in different parts of Australia. We are, therefore, unable to argue confidently about the nature or timing of the events that led to the isolation and taxonomic divergence of populations of Odonata (and other freshwater insects) in the eastern mountain chain.

Clearly, however, the disjunctions occur at regions of present ecological discontinuity which represent, in effect, the "coasts" of ecological "islands". They resemble, on a smaller scale, the extensive discontinuities focussed on in earlier discussions of speciation in Australian dragonflies (e.g. WATSON, 1981). Although some of the gaps seem small in terms of the vagility of many Odonata (though not of Plecoptera or Megaloptera), it must be borne in mind that wide dispersal may be disadvantageous for stream-dwellers (WATSON, 1981, 1982) and that, despite their potential for prolonged, powerful flight, adult Odonata may remain close to their sites of emergence (WATSON et al., 1982).

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