

Australian Endemic *Drosophila*
I. Tasmania and Victoria, including
Descriptions of Two New Species

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Abstract

The endemic *Drosophila* fauna of southern Australia consists principally of species of the typically Australian subgenus *Scaptodrosophila*. In Tasmania and Victoria (but less so further north), the *inornata* group of species within the subgenus predominates. With one exception, none of the southern species is found further north than the upland forest regions of the Queensland-New South Wales border, this being the most northern extension of floral elements of the temperate rain forests of the south.

Species diversities increase with decreasing latitude, presumably because of the dependence of *Drosophila* species on the flora which itself becomes more diverse with decreasing latitude. Evidence is presented for a progressive reduction of niches available or exploited with increasing latitude. In very marginal habitats interspecific variability is low, paralleling low genetic intraspecific variability often found in such habitats. Species distributions are probably highly dependent upon density-independent factors of the climate, so that past climatic shifts would have been important in leading to distribution patterns found today of *Drosophila* populations in 'insular islands of vegetation' surrounded by unsuitable habitats.

Introduction

Until recently the Australian *Drosophila* fauna was very poorly known. This situation was altered dramatically by the publication of a revision based mainly on museum specimens (Bock 1976), and of data from field surveys specifically aimed towards the collection of *Drosophila* species (Bock and Parsons 1975; Parsons 1975; Parsons and Bock 1976); these collections were mainly carried out in rain forests and other permanently damp habitats from the extreme north of Queensland to southern Tasmania. All four major subgenera of *Drosophila* are now known to occur in Australia; of these, the subgenus *Drosophila* is of little interest, there being no recorded endemic species; there have been limited radiations, mainly restricted to the north, in *Sophophora* and *Hirtodrosophila*; while over half of the known Australian endemics are in a major radiation of the subgenus *Scaptodrosophila*. Indeed, in Bock's (1976) monograph, of 71 species restricted to Australia alone or to regions to the immediate north, 45 are *Scaptodrosophila*; this latter number now exceeds 55 as a result of recent intensive survey work.

The proportion of *Scaptodrosophila* species in the total endemic *Drosophila* fauna increases along a north-south latitudinal gradient from northern Queensland to Tasmania, such that 16 of 19 known endemic *Drosophila* species in Victoria and all six in Tasmania are *Scaptodrosophila* (the corresponding figure for northern Queensland is 21 out of 43); this paper is therefore principally a discussion of the

Scaptodrosophila species of the southern part of Australia. It is additionally significant that of the four major subgenera of *Drosophila*, the subgenus *Scaptodrosophila* is the least understood. (The well known and remarkable Hawaiian radiation is in the subgenus *Drosophila*.) The ultimate origin of the Australian *Scaptodrosophila* fauna was probably one or more invasions from Asia (Throckmorton 1975), presumably earlier than those of the other subgenera.

Species, Collection Methods and Site Ecologies

All *Drosophila* species mentioned in this paper are described or revised in Bock (1976) with the exception of two new species, *D. ehrmanae* and *D. louisae*, which are described in the Appendix.

With rare exceptions, southern Australian flies are not attracted to conventional baits such as fermenting fruits and rotting mushrooms. Most flies were obtained by sweeping foliage with a deep net (39 cm diameter). Many of the habitats are characterized by tree ferns and other ferns, often in sheltered locations in mountainside gullies, the highest canopy being *Eucalyptus* spp., but some habitats having trees of *Acacia*, southern beech *Nothofagus* or lillypilly *Eugenia smithii* as well. In addition, especially in Tasmania and western Victoria, *Drosophila* occurs in habitats characterized by sedges, often at the edge of freshwater swamps and small lakes. All habitats have permanent water or considerable wet rotting of leaf litter on the ground.

The habitats are divided into six groups, the first four being warm temperate region rain forests (Webb 1968):

- (1) Tree fern–*Eucalyptus*;
- (2) Tree fern–*Nothofagus*;
- (3) Tree fern–*Eugenia* and many more species than groups 1 and 2;
- (4) Tree fern–*Eucalyptus*–*Acacia* and many more species (including sedges) than group 1;
- (5a) Sedge habitat (Victoria);
- (5b) Sedge habitat (Tasmania);
- (6) On very humid days, flowers often some distance from permanent water. Plants off which flies have been swept include *Prostanthera* (Labiatae), *Cassinia longifolia* (Asteraceae) and *Epacris impressa* (Epacridaceae). Presumably under these conditions the adults are utilizing the nectar of flowers as a resource.

Flies are almost always close to water for all habitats except No. 6. The common Victorian species *D. (Scaptodrosophila) inornata* is distributed in rain forests (Nos 1–4 above) at varying distances from permanent water according to temperature–humidity interactions between a lower boundary of 12°C and an upper one in the 20–30°C range dependent on the humidity (Parsons 1975). Within forest habitats flies were normally on vegetation, often the underside of tree fern fronds, in the 15–20°C range. Sites yielding flies are therefore scattered and often separated from one another by some distance because of these requirements.

The larvae of southern Australian *Scaptodrosophila* species are almost certainly leaf miners of decomposing leaves, utilizing various plant species in areas of low temperature–desiccation stress such as tree fern gullies (Parsons 1975); *D. inornata* larvae have been found on decomposing leaf litter in tree fern crowns. In the laboratory, larvae pupate on wet sand away from the larval medium suggesting pupation

in the soil in the wild. (Most if not all *Scaptodrosophila* species have larvae that 'skip', which suggests separate larval and pupation sites.)

Fermented fruit baiting was successful for three *Scaptodrosophila* species in Victoria, *lativittata*, *enigma* and *fumida*, in orchards, but with the exception of *fumida*, not in habitats Nos 1-6, that is to say, not in native habitats. The above three species occur to northern New South Wales and southern Queensland (*fumida* also occurs in south-western Western Australia), so that they may have spread southwards since European settlement, as orchards were established. Since *fumida* has been collected by sweeping in similar habitats to the other southern *Scaptodrosophila* species, only this species will be considered further.

One other endemic species collected by baiting is *D. (Sophophora) dtspar*, which is attracted to both mushroom and fermented fruit baits in eastern Victoria, but further west has been collected only by sweeping. This species occurs from west of Melbourne to northern Queensland and has been baited frequently to the north of regions considered in this paper, perhaps suggesting some population differentiation within the species.

The lack of success of fermented fruit baiting in Victoria and Tasmania is not surprising since, except in eastern Victoria, forests and sedge habitats lack plants with fleshy fruits. Fungi are plentiful in southern Australia; they are apparently not utilized as a food resource by *Drosophila* species or, if they are, the flies are not attracted to mushroom baits although some Queensland *Scaptodrosophila* species are (Parsons and Bock, unpublished data). Two of the major northern niches are therefore unutilized or unavailable in the south; thus all the data in the tables below refer to swept flies, with the exception of the two *Hirtodrosophila* species, which in eastern Victoria have been found courting on the undersides of bracket fungi (Parsons 1976; Parsons and Bock, unpublished data).

Results

Scaptodrosophila

Table 1 gives the data by locality (Fig. 1) and Table 2 by habitat. Among *Scaptodrosophila* species, 97% of the flies collected belong to one of the first five species, *inornata*, *collessi*, *fuscithorax*, *rhabdote* and *obsoleta*. In spite of some rather wide differences in male genitalia, these species share several basic morphological features (Bock 1976) and, with the two south-western species *nicholsoni* and *grossfieldi*, form a fairly well defined and presumably monophyletic complex; recognition of this complex as the '*inornata* species-group' (named after the commonest member) is now proposed.

Apart from *parsonsi* from Tasmania and the Mt Cole Forest, and *fumida* from Tasmania, no other *Scaptodrosophila* species occur west of Melbourne or in Tasmania. East of Melbourne there are more species except in West Gippsland, where flies were collected in upland habitats similar to those of the Otway Ranges (west of Melbourne); the lack of additional species is, therefore, not surprising. The increased species diversity east of Melbourne coincides with an increase of floral diversity consequent upon the first intrusion of rain forest types found north of Victoria (Ashton 1969). (In addition, species diversity in the genus east of Melbourne is increased by the occurrence of two *Hirtodrosophila* species on the undersides of bracket fungi.) The *inornata* group, however, dominates all localities, the lowest proportion being 81.3%

from coastal locality 9, and this is due to the presence of many *D. (Scaptodrosophila) exemplar*, an otherwise very rare species, at one site.

Between Sydney and the New South Wales-Victorian border, a preliminary survey collected 78 flies by sweeping, of which 40, or 51.3%, belonged to the *inornata* group; the dominance of this species-group thus lessens towards the north. The species diversity is relatively higher than in eastern Victoria, there being nine *Scaptodrosophila* species amongst only 78 flies; additionally, Bock (1976) listed another eight rare species from this region. By contrast, of the Victorian species recorded in Bock from earlier collections, all except one (*brunneipennis*) are listed in the tables of this paper. Clearly species diversity within the subgenus *Scaptodrosophila* increases towards the north.

Table 1. Distribution of Victorian and Tasmanian species of *Drosophila* by locality

Localities (see Fig. 1): 1, Tasmania; 2, Mt Eccles National Park and Tower Hill; 3, Mt Cole forest and Grampian Ranges; 4, Otway Ranges; 5, Lerderderg Gorge, Mt Macedon and Brisbane Ranges; 6, Kinglake National Park; 7, Dividing Ranges; 8, West Gippsland; 9, Wilsons Promontory and The Lakes National Parks; 10, East Gippsland. All flies collected by sweeping

Subgenus and species	Locality number										Total	
	1	2	3	4	5	6	7	8	9	10		
<i>Sophophora</i>												
<i>dispar</i> Mather				9		2					1	12
<i>Hirtodrosophila</i>												
<i>polypteri</i> Malloch											3	3
<i>mycetophaga</i> Malloch									13			13
<i>Scaptodrosophila</i>												
<i>inornata</i> Malloch	36	8	329	402	85	103	231	250	111	153		1708
<i>collessi</i> Bock	16		10	18	6	46	12	39	30	4		181
<i>fuscithorax</i> Malloch	72			3			1					76
<i>rhabdote</i> Bock	82	50		34	4	6	1	19	1	2		199
<i>obsoleta</i> Malloch							1		1	1		3
<i>barkeri</i> Bock							1		2	2		5
<i>exemplar</i> , Bock									29			29
<i>louisae</i> , sp. nov.						20	9		1			30
<i>notha</i> Bock						1						1
<i>fumida</i> Mather	3					1						4
<i>megagenys</i> Bock									1			1
<i>parsonsi</i> Grossfield	1		1			1	5					8
<i>ehrmanae</i> , sp. nov.							23					23
others											3 ^A	3
No. of <i>Scaptodrosophila</i> spp.	6	2	3	4	3	7	9	3	8	7 ^A		15 ^A

^ASpecies undetermined.

In Table 2, where the data are given according to habitat, the greatest number of species occurs in habitats 3 and 4 where there are tree ferns with more other plant species than in Nos 1 and 2 (from limited data, only members of the *inornata* group were swept off flowering plants); therefore the greatest number of *Drosophila* species occurs in conjunction with the most complex plant associations.

Table 3 lists species diversity data for the four commonest *inornata*-group species. *D. inornata* is the commonest species, except in Tasmania and western Victoria where *rhabdote* predominates; these two species are morphologically more closely related

than they are to *collessi* and *fuscithorax*, which except in Tasmania (*fuscithorax*) and the Kinglake area of Victoria (*collessi*) are not common. *D. rhabdote* is particularly common in the sedge habitats of Tasmania and Victoria. In western Victoria, locality 2 consists of two sedge habitats with only *inornata* and *rhabdote*, and indeed at the more westerly of these only *rhabdote* was found. These are very marginal habitats, since general entomological survey work has revealed very few *Drosophila* further west; thus in marginal habitats species diversities fall to the level of homospecific collections.

All other Victorian habitats have high proportions of *inornata*. Tree ferns are common in most of these habitats (Nos 1–4). Initially, when the frequent association of *inornata* with tree ferns became apparent, it was thought that the latter were being used as a resource; however, it has now become clear that tree ferns are indicators of minimal environmental stress (Parsons 1975). The presence of *inornata* distant from tree ferns in permanently moist areas such as sedge habitats where desiccation–high temperature stresses are lower than in surrounding regions confirms this.

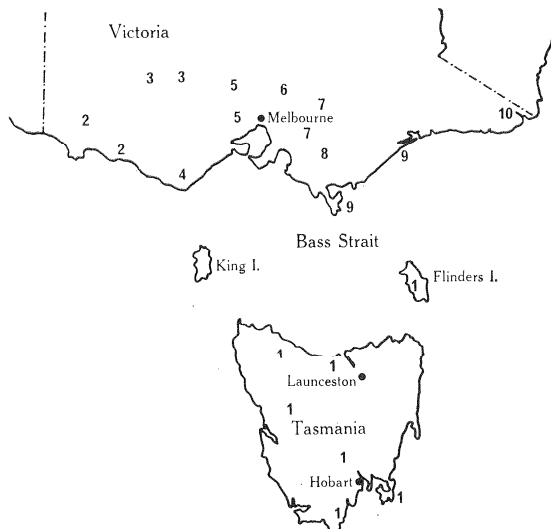


Fig. 1. Localities mentioned in the text. 1, Tasmania. 2, Mt Eccles National Park and Tower Hill. 3, Mt Cole forest and Grampian Ranges. 4, Otway Ranges. 5, Lerderderg Gorge, Mt Macedon and Brisbane Ranges. 6, Kinglake National Park. 7, Dividing Ranges. 8, West Gippsland. 9, Wilsons Promontory and The Lakes National Parks. 10, East Gippsland.

D. collessi is often found in the same habitat as *inornata*, usually in low frequencies. Often *inornata* is on the undersides of tree fern fronds while *collessi*, a darker fly, is on sedges. Additionally, *inornata* tends to be closer to permanent water than does *collessi*; there is therefore an apparent microhabitat difference between the two species.

D. fuscithorax is not common in Victoria but in Tasmania it is second to *rhabdote*. *D. fuscithorax* is the southernmost Australian *Drosophila* species recorded so far, at latitude $43^{\circ} 35'S$. at the extreme south of Tasmania, although both *inornata* and *rhabdote* have been found at $43^{\circ} 30'S$. In Tasmania, of the four members of the *inornata* group under discussion, *fuscithorax* and *rhabdote* are common, while in

Victoria inornata is common, and in both states *collessi* makes up usually less than 10% of a collection. The *inornata* group therefore predominates in both states but the relative frequencies of the four species within the group differ; the explanation lies partly in the types of habitat, since sedge habitats predominate in Tasmania and tree fern habitats in Victoria. However, the high frequency of *fuscithorax* in Tasmania cannot be so explained, as it is uncommon in analogous Victorian habitats.

Table 2. Distribution of Victorian and Tasmanian species of *Drosophila* by habitat

Habitats: 1, tree fern-*Eucalyptus*; 2, tree fern-*Nothofagus*; 3, tree fern-*Eugenia*; 4, tree fern-*Eucalyptus*-*Acacia*; 5a, sedge habitat (Victoria); 5b, sedge habitat (Tasmania); 6, flowers some distance from water. All flies collected by sweeping

Subgenus and species	Habitat number							Total
	1	2	3	4	5a	5b	6	
<i>Sophophora</i>								
<i>dispar</i> Mather	1	1	1	4	5			12
<i>Hirtodrosophila</i>								
<i>polypori</i> Malloch			3					3
<i>mycetophaga</i> Malloch	13							13
<i>Scaptodrosophila</i>								
<i>inornata</i> Malloch	869	318	243	188	17	1	72	1708
<i>collessi</i> Bock	64	12	23	63	11	7	1	181
<i>fuscithorax</i> Malloch	3	2		10	1	60		76
<i>rhabdote</i> Bock	5	9	2	26	79	59	19	199
<i>obsoleta</i> Malloch		1	2					3
<i>barkeri</i> Bock			4	1				5
<i>exemplar</i> Bock					29			29
<i>louisae</i> , sp. nov.			1	29				30
<i>notha</i> Bock				1				1
<i>fumida</i> Mather				2		2		4
<i>megagenys</i> Bock					1			1
<i>parsonsi</i> Grossfield	1	5		1		1		8
<i>ehrmanae</i> , sp. nov.				23				23
others			3 ^A					3
No. of <i>Scaptodrosophila</i> spp.	5	6	8 ^A	10	6	6	3	15 ^A

^ASpecies undetermined.

Species diversity can be quantified provided intensive sampling has been carried out, as has been for Victoria and Tasmania (*vide* Emlen 1973). The following index of diversity (D) may be calculated, where p_i is the relative abundance of species: $D = -\sum p_i \ln p_i$. Indices are given in Table 3 for the four common *inornata*-group species; they show diversity to be greatest in Tasmania, as may be expected since it is the only region where *fuscithorax* is common and the other three species are found in reasonable frequencies. The lowest index is for locality 3, a marginal region in which *inornata* almost totally predominates with a few *collessi*. The habitats represented in this locality are Nos 1 and 6, both with tree ferns. Habitat type 6 in this locality is marginal, being the most western site of the Grampian Ranges, and was homospecific for *inornata*. This parallels the homospecific collection further south of *rhabdote* in a sedge region (locality 1, Mt Eccles National Park); the differentiation seems logical since *inornata* is, apparently, mainly a species of tree fern areas and *rhabdote* of sedges.

The two habitats showing the greatest diversities are No. 4, the Victorian diverse tree fern habitat where *inornata* is associated with a high frequency of *collessi*, and No. 5b, the Tasmanian sedge habitat where *fuscithorax* and *rhabdote* are common. In Tasmania, where both of these species occur at the same site, *rhabdote* tends to be collected off sedges somewhat closer to water than does *fuscithorax*, indicating that the former species may be somewhat more susceptible to desiccation stress than the latter. At one site where both of these species were found some *collessi* were also collected further from permanent water than *rhabdote* (as was one male *parsonsi*).

Table 3. Percentages and species diversity indices for the four common species of the *inornata* group
Localities and habitats numbered as in Fig. 1 and Tables 1 and 2

Locality and habitat	<i>inornata</i>	<i>collessi</i>	<i>fuscithorax</i>	<i>rhabdote</i>	Diversity index
Locality 1	17.5	7.8	35.0	39.8	1.24
2	13.8	0	0	86.2	0.40
3	97.1	3.0	0	0	0.13
4	88.0	3.9	0.7	7.4	0.47
5	89.5	6.3	0	4.2	0.41
6	66.5	29.7	0	3.9	0.76
7	94.3	4.9	0.4	0.4	0.25
8	81.2	12.7	0	6.2	0.61
9	78.2	21.1	0	0.8	0.71
10	96.2	2.5	0	1.3	0.19
Total	78.9	8.4	3.5	9.2	0.73
Habitat 1	92.3	6.8	0.3	0.5	0.30
2	93.3	3.5	0.6	2.6	0.31
3	90.7	8.6	0	0.7	0.34
4	65.5	22.0	3.5	9.1	0.94
5a	15.7	10.2	0.9	73.1	0.80
5b	0.8	5.5	47.2	46.5	0.91
6	78.3	1.1	0	20.7	0.56

Since *inornata* has been collected some distance from permanent water, but where it is present simultaneously with *collessi* the latter is further from the water, the field data suggest a sequence for susceptibility to desiccation stress for the *inornata* group: *rhabdote* > *inornata* > *collessi* and *fuscithorax*. In addition, *obsoleta*, the rare Victorian species of the *inornata* group, must be regarded as desiccation-resistant compared with other species in the group, since it occurs from South Australia to central Queensland in open forests (Bock 1976), not necessarily close to permanent water. Presumably, during the evolution of the *inornata* species-group, *obsoleta* managed to invade and occupy more marginal habitats of higher desiccation-temperature stresses than the rain forest-sedge species.

It is difficult to comment on the rare species outside the *inornata* group. However, *ehrmanae* is found much closer to permanent water than *inornata*, *louisae* is found in sites similar to *inornata*, and *parsonsi* is found at least as distant from water as *collessi*.

Distributions of Southern Scaptodrosophila in Australia

In Figs 2-7 are plotted the southern and east coast distributions of the Victorian and Tasmanian species in Table 1, with the exception of the two baitable species

fumida and *dispar*. Very few flies were found west of Victoria. The distributions are from extensive recent collections combined with localities listed in Bock (1976). Flies listed by Bock were collected by generalized methods such as sweeping and light trapping not specifically aimed at the collection of *Drosophila* species.

Fig. 2 shows the distributions of *inornata* and *collessi* to be similar, i.e. Tasmania, Victoria, eastern New South Wales and southern Queensland, although in both Victoria and New South Wales *inornata* has been found somewhat to the west of *collessi* and in Queensland somewhat to the north. Additionally there is one record of *inornata* from the south-east of South Australia. The impression gained is one of considerable similarities in distributions, although the resources used presumably differ somewhat in sympatric populations, as already discussed.

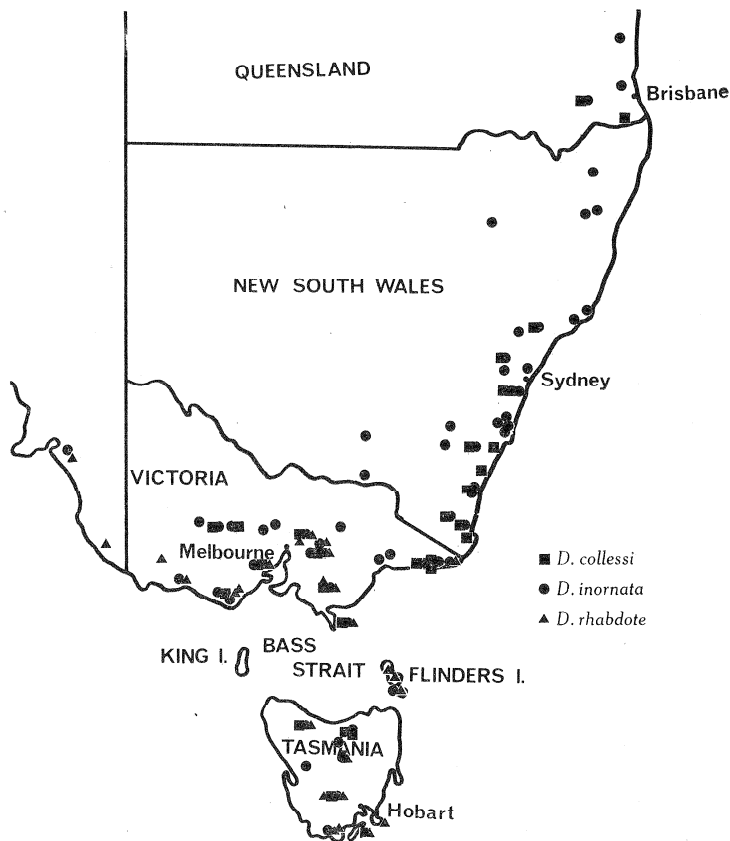


Fig. 2. Distributions of *inornata*, *collessi* and *rhabdote*.

In northern New South Wales and southern Queensland both species are found in upland rain forests at altitudes exceeding 800 m. At these altitudes rain forests have parallels with those further south, since the most northern Australian extension of *Nothofagus*, which occurs in Victoria and is common in Tasmania, is in the McPherson Range just north of the Queensland–New South Wales border.

D. rhabdote is restricted to Victoria and Tasmania with two records from south-eastern South Australia. While it frequently occurs in association with *inornata*, it is

a fly of sedge habitats, especially in Tasmania. The most northern record is at the extreme east of Victoria. *D. rhabdote* is almost always very close to water, as already discussed; the only site where the species was collected off flowers was less than 3–6 m from water on a day of light misty rain. It can be hypothesized that the desiccation stress may become excessive north of Victoria and that it can be regarded as a 'Bass Strait' species. On Flinders I. in Bass Strait, for example, 44 *rhabdote* were collected out of 55 flies (80%), the remaining 11 being seven *fuscithorax*, three *inornata* and one *fumida*.

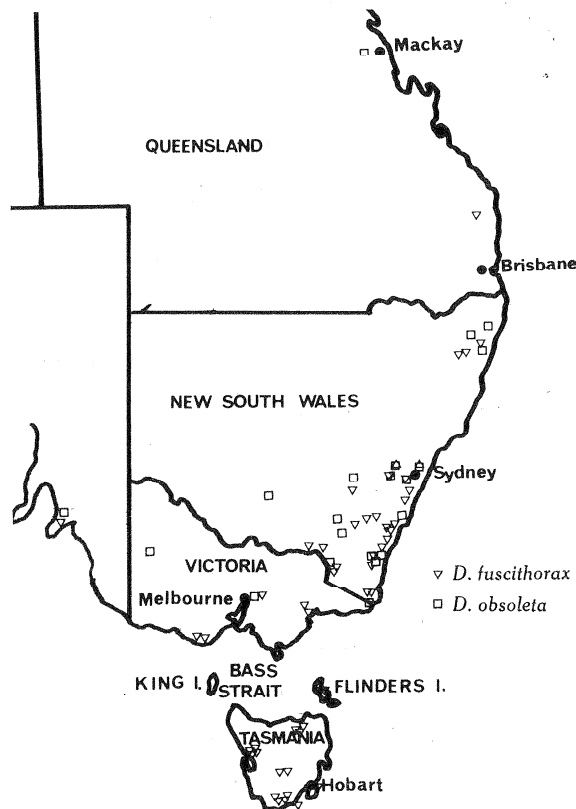


Fig. 3. Distributions of *fuscithorax* and *obsoleta*.

D. fuscithorax (Fig. 3) is the other common Tasmanian species second in frequency to *rhabdote*. On the mainland it is usually at low frequencies, often in sedge habitats, and while being water-dependent it appears less so than *rhabdote* as already discussed; so that its presence to southern Queensland in upland habitats is not surprising. *D. fuscithorax* also occurs in south-western Western Australia and there is a South Australian record. (It may be added parenthetically that the south-west of Western Australia possesses a depauperate *Drosophila* fauna of five *Scaptodrosophila* species. Three of them, *fuscithorax*, *nicholsoni* and *grossfieldi*, belong to the *inornata* group, and indeed *grossfieldi* is almost identical to *inornata* in external morphology and coloration but the male genitalia differ considerably (Bock 1976). The remaining two Western Australian *Scaptodrosophila* are baitable species, *nitidithorax* and *fumida*.)

In summary, of the Tasmanian species of the *inornata* group, one species is restricted to the Bass Strait region, and the other three are found as far north as scattered upland regions of southern Queensland.

The remaining species of the *inornata* group, *obsoleta* (Fig. 3), is of open forests rather than rain forests. When found in rain forests it is not necessarily close to water. It is rare but widespread from near Adelaide to central Queensland.

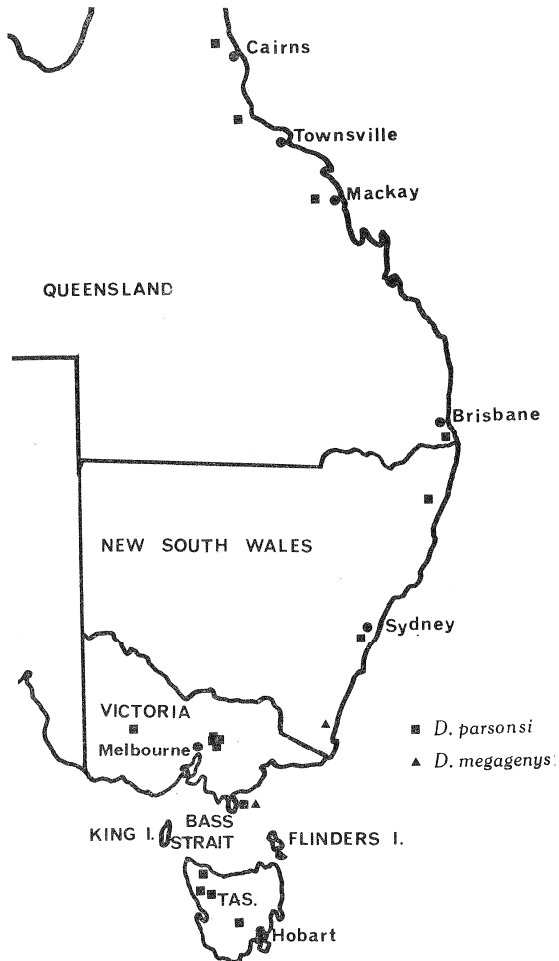


Fig. 4. Distributions of *parsonsi* and *megagenys*.

The remaining Tasmanian species (apart from the baitable *fumida*) is *parsonsi* which is not a member of the *inornata* group. It is a relatively rare species in rain forests from southern Tasmania to northern Queensland (Fig. 4) and spans the greatest range of latitudes of all Australian endemic *Drosophila* species. The records north of Sydney are all from upland rain forests at altitudes over 900 m. In Tasmania it may be somewhat less dependent on close proximity to water than the *inornata* group species. This may be a partial explanation of its range to the extreme north of the continent.

The remaining Victorian species are rarer. Two of the *barkeri* complex of species (Fig. 5) occur from central Victoria to northern New South Wales (*barkeri*, *exemplar*), and the third (*louisae*) has been found in central Victoria and south of Sydney only.

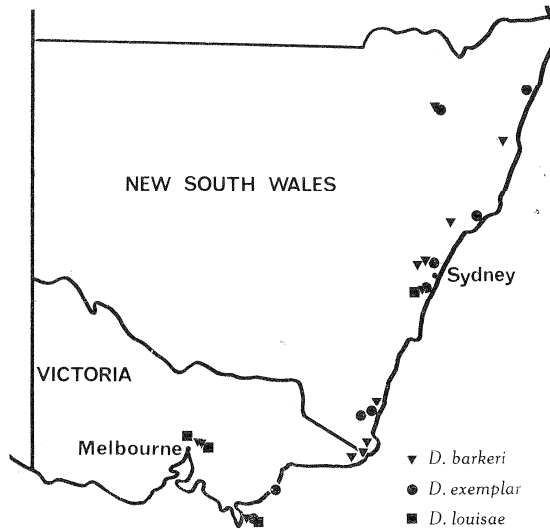


Fig. 5. Distributions of *barkeri*, *exemplar* and *louisae*.



Fig. 6. Distributions of *brunneipennis*, *notha* and *ehrmanae*.

As it is a recently discovered species, its range may ultimately be found to exceed this. These species all occur in rain forest or permanently damp habitats. *D. notha* and *D. brunneipennis* are closely related and have rather similar distributions, being found in more inland habitats than many other species (Fig. 6); they are probably species of damp habitats, not necessarily rain forests. Finally, *D. ehrmanae* (Fig. 6) is a

central Victorian rain-forest species; it is a large species apparently highly sensitive to desiccation, since on days when *inornata* was up to 2 m from water, *ehrmanae* was within 0.5 m of water. This high sensitivity to desiccation may explain its restricted distribution although, like *louisae*, it is recently discovered.

Hirtodrosophila

The two *Hirtodrosophila* species, *mycetophaga* and *polypori*, occur in rain forests from eastern Victoria to upland southern Queensland (Fig. 7). Both court on the horizontal undersides of bracket fungi (Polyporaceae) which grow outwards from the sides of fallen logs or from trees near the ground and normally in permanent shade; the undersides of these fungi are courting territories or leks (Parsons 1976; Parsons and Bock, unpublished data). It is noteworthy too that these are the only two Australian patterned-wing *Hirtodrosophila* species, wing display being prominent during courtship.

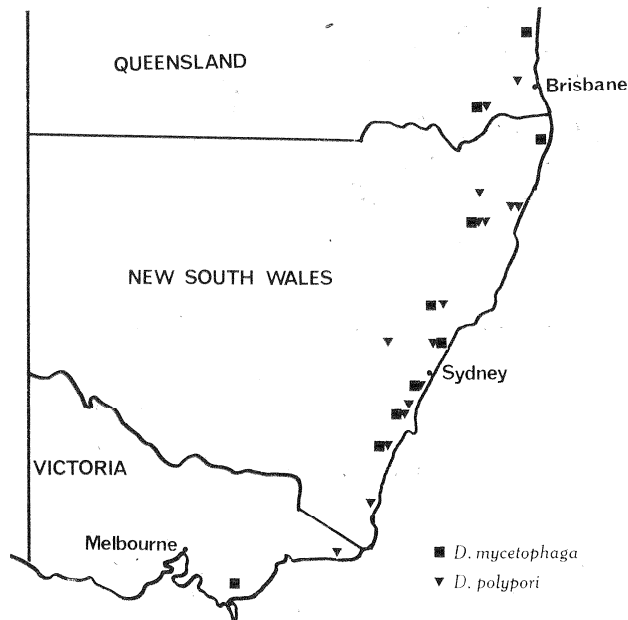


Fig. 7. Distributions of *mycetophaga* and *polypori*.

North-South Distributions

The north-south distribution patterns of the Victorian and Tasmanian species are summarized in Fig. 8. The broad distributions of four of five members of the *inornata* group are clear. The three *barkeri*-complex species have rather narrower but similar distributions, as do *brunneipennis* and *notha* of another complex. In addition, the two *Hirtodrosophila* species have similar distributions. Of the three remaining species, *ehrmanae* is very localized, *megagenys* (only two females known) very rare and *parsonsi*, although not common, is the most widespread of all.

There are zoogeographic analogies with Darlington's (1961) work on Australian carabid beetles, since a few Tasmanian species of the latter occur as far north as the McPherson Range, although in contrast to *Drosophila* many are distributed only as

far north as Sydney. Except for three species, *ehrmanae*, *louisae* and *megagenys*, all species found in Victoria but not Tasmania are also found in New South Wales north of Sydney. As well as being common, the *inornata* group of species is generally very widespread, although the proportion of flies from this group in collections diminishes rapidly north of Victoria to about 50% up to Sydney and less thereafter. The rarer species with one exception have narrower latitudinal ranges than the common *inornata*-group species *inornata*, *collessi* and *fuscithorax*. The exceptional species is *parsonsi*, spanning 26° of latitude from southern Tasmania to northern Queensland. Darlington records one carabid genus, *Notonomus*, with this range, the

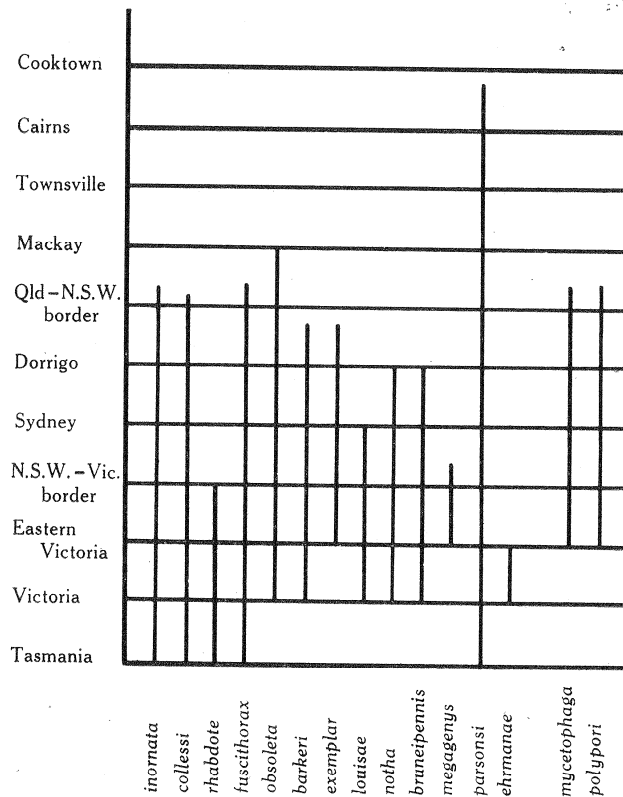


Fig. 8. Schematic north-south distributions of the species under discussion in Figs 2-7.

others having smaller ranges. In conclusion, the ranges of the *Drosophila* species of Tasmania and Victoria all diminish northwards at varying rates. The species of lowland areas in the south move to upland forests in southern Queensland. The northern Queensland upland forests are no higher in altitude than the southern Queensland forests, so the virtual elimination of the southern species in northern Queensland is expected. Certain upland regions of New Guinea having *Nothofagus* forests might repay study.

Discussion

The *Drosophila* species under discussion are mainly of southern warm temperate rain forests at near sea level in Tasmania, of the plateaus and mountains of Victoria,

at wide intervals in eastern New South Wales, and upland regions on the southern border of Queensland, although isolated temperate rain forest elements not investigated for *Drosophila* occur in small patches on the highlands to the north of Cairns (Webb 1959). At lower altitudes in northern New South Wales and southern Queensland there are rare patches of subtropical-type rain forest down to sea level. These forests occur irregularly as far as north Queensland, becoming progressively more tropical (see Webb (1968) for detailed classifications of rain forests); the *Drosophila* fauna therein will be reviewed in due course. In overlapping areas, especially northern New South Wales and southern Queensland, the south temperate and subtropical rain forests may intermix to some extent. There are, in addition, small pieces of rain forest approximating to subtropical rain forest to the south of Sydney (Webb 1959) especially in wet ravines, but much of it has been cleared. The first species of subtropical rain forests do, however, appear in eastern Victoria, in this case with many south temperate species.

The *Scaptodrosophila* species investigated are the non-baitable forms of the south temperate forests, there being effectively no baitable species when these forests are in pure stands. With the first intrusion of subtropical rain-forest trees, the number of non-baitable *Scaptodrosophila* species increases in eastern Victoria and southern New South Wales, presumably due to the greater floral diversity of the forests. However, the eastern Victorian forests and those north to Sydney must be relatively depauperate so far as the fleshy fruit resource is concerned, since only the three baitable Victorian *Scaptodrosophila* species in addition to *D. (Sophophora) dispar* have been attracted to fermented fruit baits. Further north the diversity of baitable species increases to a maximum, possibly in tropical rain forest at the base of Cape York Peninsula (unpublished data). Mushroom baiting is almost ineffective south of Sydney, only *dispar* regularly coming to baits. Again, species diversity from mushroom baiting is high in forests at the base of Cape York Peninsula, new species (especially of *Scaptodrosophila*) being sometimes taken. In general, then, *Drosophila* species diversities increase with decreasing latitude as expected from general biogeographic considerations (Emlen 1973); in the present case the phenomenon is associated with the known dependence of *Drosophila* species on the flora, which becomes more diverse in rain forests with decreasing latitudes (Webb 1968).

The increase in *Drosophila* diversity with decreasing latitude is well illustrated by the increasing diversity towards the north of the yields from the various collection methods, each giving its own spectrum of species and implying increasing niche diversities, as illustrated by differences in resource utilization. The subgenus *Scaptodrosophila* very likely originated in tropical Asia (Throckmorton 1975), so that in southern Australia the fauna probably represents descendants of an old invasion which radiated producing non-baitable species.

Since the southern *Drosophila* species are collected by sweeping, the microhabitats occupied by adult flies can be studied, as shown by detailed studies on *inornata* (Parsons 1975). Subtle interspecific microhabitat differences are now being detected, as already discussed, which in a preliminary way may be related to distribution patterns. As a hypothesis, it can be argued that there is an analogy between the demonstrated importance of high temperature and desiccation in determining the relative distributions of the cosmopolitan species *melanogaster* and *simulans* (McKenzie and Parsons 1974) and for the endemics under discussion. For baitable endemic

species such information is difficult to obtain, since flies are attracted to baits from their preferred microhabitats. As for the cosmopolitan species, the study of the genetic architecture of resistance to environmental stresses will be of interest when the endemics can be bred in the laboratory, especially for those members of the *inornata* group with wide distributions.

The distributional similarities within species-complexes have been noted for three members of the *inornata* group, for the *barkeri* and *brunneipennis* complexes, and for the two *Hirtodrosophila* species. From arguments in the literature for general relationships amongst genotype, morphology, physiology and behaviour in a variety of organisms (see Ehrman and Parsons 1976), such similarities would be expected. Similar distributions imply similar but obviously not identical niches utilized; the evidence for associations between behavioural patterns and niches occupied is increasing, especially in rodents. Excellent evidence for an association between behavioural and morphological (structural) phylogenies has been documented by Spieth (1952) for mating behaviour in 21 species-groups of *Drosophila*. Generally, the evolution of mating behaviour has paralleled morphological evolution in the group. More limited evidence for other behaviours in *Drosophila* which fit the same broad trend is discussed by Parsons (1977). The extension of these associations to distribution patterns in nature has been little considered in *Drosophila*, possibly because definitive studies on the ecological genetics of *Drosophila* are to date rare (Parsons 1973).

The two most westerly Victorian sites show no interspecific variability for members of the *inornata* group. These sites are about 40 km from the next sites to the east and so are effectively islands or 'insular islands of vegetation suitable for *Drosophila*'. Two species were collected at each of these more easterly sites, and at the sites next further to the east, three or four species. The fall in species diversity to the west fits data on island biogeography, especially as the westerly sites are less than half the area of those further east. The 'islands' can therefore be regarded as marginal habitats where species diversities would be expected to be low. As already pointed out, species diversities are highest in the non-marginal eastern habitats of Victoria, compared to the western part of the state on the one hand and Tasmania on the other. *D. obsoleta*, the rare open forest species of the *inornata* group, also occurs mainly alone in marginal habitats. Low species variability in marginal habitats is well illustrated in Wilson's (1959) work on the ponerine ants of Melanesia. Dobzhansky and his colleagues (references in Parsons 1973) have shown a similar phenomenon *within* the species *D. willistoni*, which has the highest number of inversion types and the highest percentage of inversion heterozygotes in Brazilian tropical rain forests, with genetic variability diminishing in populations in more marginal habitats. Carson (1958) has demonstrated a similar phenomenon in *D. robusta*. Therefore, if habitats are marginal or distributions peripheral, the species (or populations) may be relatively homogeneous; the *inornata* group extends this conclusion from the interpopulation to the interspecific level in the genus *Drosophila*.

The distribution of Australian rain forests indeed consists of 'islands' of varying size separated by up to several hundred kilometres of comparatively dry country, especially in Queensland. In Victoria and Tasmania distances between rain forest patches are generally less. The forests of east Gippsland are isolated by some distance from forests further west, as is Wilsons Promontory. The Otway Ranges are another

isolated locality. There is also the isolation provided by Bass Strait since about 12,750 years BP (Rawlinson 1974) for isolated *Drosophila* colonies on Flinders I. and colonies in Tasmania. In Tasmania isolation among sites is due to upland cold plateau country as well as comparatively dry country. The present distribution of the *Drosophila* species under consideration suggests that in the past they have moved up and down the coast across what are now comparatively wide gaps of unsuitable country. During a period of higher precipitation than the present, which lasted until about 5000–6000 BP, patches of dry country would have been smaller than at present, permitting contacts among now isolated rain forest patches. The rather depauperate Flinders I. and Tasmanian *Drosophila* faunas presumably must have become established before the time of isolation by Bass Strait.

If, as hypothesized, the distribution of non-baitable *Scaptodrosophila* species is highly dependent upon density-independent factors such as climate (especially temperature and humidity), then climatic shifts known to have occurred in the past could have led to the distribution patterns occurring today, which includes relic populations in northern upland rain forests. This is supported by geological evidence that the Pleistocene glacial periods were characterized by rapid alternation of periods wetter and drier than the present climate of southern Australia (Mulvaney and Golson 1971; Rawlinson 1974). According to Rawlinson (1974) the sequence in southern Australia was: (1) 31,000 BP, low effective precipitation, low temperature and low rainfall; (2) 17,000–30,000 BP, high effective precipitation, low temperature and low evaporation; (3) 12,000–17,000 BP, low effective precipitation, low temperature and low rainfall; (4) 6000–12,000 BP, very high effective precipitation, high temperature and very high rainfall; (5) from 6,000 BP to the present, medium effective precipitation, high temperature, and medium rainfall. Such a situation could permit species to move up and down the coast to give the distributions known today of *Drosophila* occurring in 'insular islands of vegetation' surrounded by unsuitable habitats. Modern agricultural and forestry practices are accelerating this trend, although most major 'islands' must be up to 5000 years old.

Acknowledgments

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Appendix: Descriptions of *D. louisae*, sp. nov., and *D. ehrmanae*, sp. nov.

The two new species recovered in the collections discussed above are described below in the form used previously for the Australian *Drosophila* species (Bock 1976).

✓ *Drosophila (Scaptodrosophila) louisae*, sp. nov.

Types

Holotype ♂: Mallacoota Inlet National Park, Victoria, 16.xii.1974, P. A. Parsons and D. Hay, swept from *Eugenia smithii* rain forest. Paratype ♀: Boyd's Creek, N. of Mallacoota Inlet National Park, Victoria, 14.xii.1974, P. A. Parsons and D. Hay. Both specimens deposited in ANIC.

Distinguishing Features

Carina very prominent, flat. Body entirely brownish; wings faintly brownish. Acrostichal bristles large. Similar in external morphology to some members of the *barkeri* complex (see below) but male genitalia quite distinctive.

Description

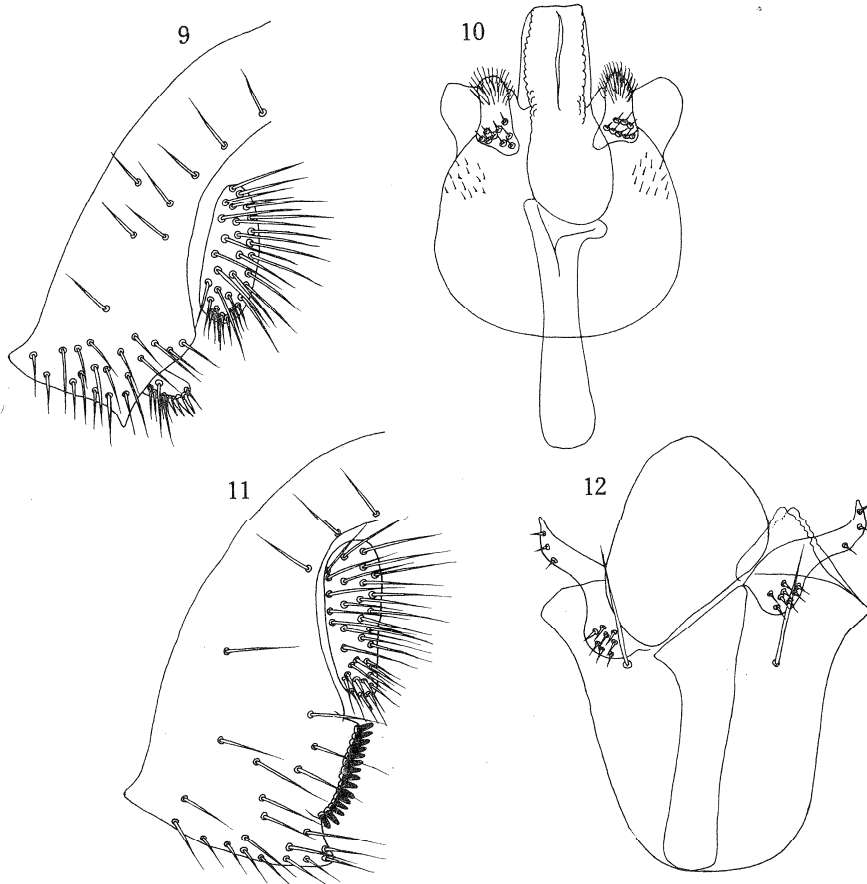
Body length. 3.3 mm (holotype); 3.6 mm (paratype).

Head. Arista with 4 branches above and 2 below plus terminal fork; dorsal rays curved forwards apically, ventral rays straight. Front tan, silvery bordering eyes and about ocelli. 2nd and 3rd antennal segments concolorous with front. Carina prominent, rather narrow above, slightly widening below, flat, squared laterally and ventrally. Cheek curved, wider posteriorly, greatest width 0.15 times greatest diameter of eye. Eyes bare. Orbital bristles in ratio 2:1:2; anterior reclinate orbital posterior and slightly lateral to proclinate orbital, about twice as close to proclinate as to posterior reclinate orbital.

Thorax. Uniformly tan with faint hint of slightly darker longitudinal bands laterally. Acrostichal hairs in 8 rows in front of dorsocentral bristles, *c.* 6 rows, somewhat irregular, between dorsocentrals. Ratio anterior:posterior dorsocentrals 0.6. Prescutellars about as long as anterior dorsocentrals. Anterior scutellar bristles long, divergent. Sterno-index 0.75. Legs concolorous with thorax; preapical bristles on all tibiae; apicals on 2nd tibiae only.

Wings. Hyaline, faintly brownish. *C*-index, 3.3; *4V*-index, 1.5; *5X* index, 1.1; *M*-index, 0.4. 3rd costal section with heavy setation on basal 0.7. Length 3.4 mm (holotype); 3.6 mm (paratype).

Abdomen. All tergites uniformly tan.



Figs 9 and 10. *D. louisae*, sp. nov.: 9, male external genitalia; 10, male internal genitalia.

Figs 11 and 12. *D. ehrmanae*, sp. nov.: 11, male external genitalia; 12, male internal genitalia.

Male genitalia (Figs 9, 10). Clasper small, weak, without the strong rounded black teeth present in most species. Aedeagus large, with fine lateral serrations. Anterior parameres large, with prominent sensillae below and numerous hairs above.

Distribution

As recorded above in Tables 1 and 2 and Fig. 5.

Relationships

Bock (1976) described seven species in which the male genitalia lack true claspers, i.e. completely differentiated claspers with strong teeth; all of these species are also of plain brown coloration. *D. louisae* is clearly allied to this 'barkeri complex' in general coloration and in the structure of its male genitalia; a weak clasper only is present (cf. *concolor*, *exemplar* and *minnamurrae* within the same complex) but, interestingly, although the posterior margin of the genital arch bears strong teeth in the other seven species of the complex, similar teeth are entirely lacking in *louisae*. *D. louisae* does, however, seem best included in the *barkeri* complex.

✓ *Drosophila (Scaptodrosophila) ehrmanae*, sp. nov.*Types*

Holotype ♂: Noojee State Forest, Victoria, 6.i.1976, P. A. Parsons. Paratype ♀: same data as holotype. Both specimens deposited in ANIC.

Distinguishing Features

Body large, brown. Wings with distinct dusky tinge along costal portion, most pronounced apically. Carina very large.

Description

Body length. 4.1 mm (holotype); 4.3 mm (paratype).

Head. Arista large, with 3-4 long curved rays above and 2 straight rays below plus terminal fork. Front as broad as long, deep tan, slightly dusky posteriorly between periorbits and ocellar bristles; slight silveriness present about bases of orbital bristles. 2nd and 3rd antennal segments tan; 3rd slightly dusky anteriorly. Carina large, rather narrow above, considerably broadened below, broadly flattened. Cheek slightly curved, of nearly uniform width, greatest width 0.2 times greatest diameter of eye. Eyes with very sparse, very fine pile. Orbital bristles in ratio 4:2:5; anterior reclinate orbital posterolateral to proclinate orbital. Ocellar and vertical bristles large.

Thorax. Uniformly mid-brown. Acrostichal hairs in c. 8 rows, somewhat irregular, in front of dorsocentral bristles, irregular between dorsocentrals. Ratio anterior: posterior dorsocentrals 0.6. Anterior dorsocentrals close to posterior dorsocentrals. Prescutellar bristles large; acrostichal bristles lateral to prescutellars on each side enlarged to variable extent; pair of acrostichals anterior to prescutellars also enlarged. Scutellar bristles long, subequal; anterior scutellars widely divergent; posterior scutellars crossed. Sterno-index 0.75. Legs tan; preapical bristles on all tibiae; apicals on 2nd tibiae only.

Wings. Translucent, infuscated along posterior crossvein, and costal region more strongly so closer to border, infuscation darkest apically. *C*-index, 3.4; *4V*-index, 1.6; *5X*-index, 1.0; *M*-index, 0.4. 3rd costal section with heavy setation on basal 0.65. Length 4.0 mm (holotype); 4.3 mm (paratype).

Abdomen. Tan; tergites slightly darker apically in paratype.

Male genitalia (Figs 11, 12). Genital arch very broad. Anal plate small. Clasper small, with dense apical row of black teeth. Aedeagus broad, laterally flattened. Anterior parameres apically pointed, with numerous basal sensillae.

Distribution

As listed above in Tables 1 and 2 and Fig. 6.

Relationships

D. ehrmanae is similar in some respects to *brunneipennis*, particularly in size and in structure of the male genitalia; it appears to be related to this species and thus also to the other two members (*notha* and *adelphe*) of the '*brunneipennis* complex' although *ehrmanae* has a rather different wing pigmentation.

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