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**Morphometrics in the Genus *Amenia*
and Revisionary Notes on the
Australian Ameniinae (Diptera: Calliphoridae),
With the Description of Eight New Species**

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ABSTRACT. The Ameniinae comprise seven genera, of which six occur in Australia; the largest, *Amenia*, is restricted to this country. Previous studies left some uncertainty about the status of several taxa in *Amenia*, and Part 1 of this study applies morphometric methods to the problem. These analyses show that *Amenia longicornis* comprises two geographically isolated, morphologically distinct forms. One occurs around the head of Spencer's Gulf in South Australia and north as far as Alice Springs; the other is widespread across the Nullarbor Plain. Similar studies of *A. i. imperialis* and close relatives show that *A. i. imperialis* and *A. i. dubitalis* are clearly separable by head shape; also, that two other "forms" of *A. i. imperialis* can be distinguished: one occurring in northwestern Australia and arid areas of New South Wales and Queensland, the other in the vicinity of Cooktown, Queensland. Likewise, the two subspecies of *A. leonina*, *A. l. leonina* and *A. l. albomaculata* are morphometrically separable, but with some sign of intergradation, as well as the existence of distinct "forms" of *A. l. albomaculata* in the New England area of New South Wales and on the Eyre Peninsula, South Australia. Finally, *A. chrysame* is shown to comprise two morphometrically separable "forms", occurring north and south of the 26th parallel.

In Part 2, the subfamily Ameniinae is reviewed, with descriptions of eight new species: two in *Stilbomyella*, four in *Paraplatytropesa*, and two in *Amenia*. The last represent morphometrically recognised siblings of *A. imperialis*. Also, the subspecies of *A. imperialis* are raised to full specific rank, as are those of *A. leonina*; genus *Formosiomima* is relegated to synonymy under *Amenia*; the New Guinean *Platytropesa simulans* is newly recorded from north Queensland; and the known ranges of several other species are extended with new records. In Part 3, phenetic studies are offered to support the existing classification within the subfamily, and its zoogeography and possible evolutionary history are discussed. It seems not unlikely that the Australasian taxa stem from a *Paramenia*-like ancestor, that originated in western New Guinea as sister to the mainly Oriental *Catapicephala*. One or more of its descendant species then entered Australia from the north, dispersing, with further concurrent speciation, in a clockwise fashion around the continent.

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The Ameniinae comprise a clearly demarcated group of seven genera that have had a somewhat chequered taxonomic history. Originally placed in Tachinidae (because of the apparent presence of a subscutellum), the studies of Crosskey (1965) have led to a general acceptance that they are best placed in Calliphoridae. Of the seven genera, six occur in Australia and two of these (*Amenia* and *Paraplatytropesa*) are known only from this country. Specimens resemble blowflies, but with metallic colours, often boldly marked with white spots or bands.

In his detailed studies of the subfamily, Crosskey (1965, 1969, 1972) had to leave several questions with rather tentative answers: principally, the taxonomic status of several populations in *Amenia* of which there were too few specimens to allow firm decisions to be made. Since then the material available in Australian collections has grown considerably, as have our facilities for fast and accurate processing of numerical data. Morphometric analyses of adequate material have now provided reasonable answers to some of these questions. At the same time, new and intriguing problems have appeared.

Part 1 of this paper deals with the morphometrics of the populations mentioned, plus a parallel study of a related species. The taxonomic conclusions are formally stated in Part 2, which also includes observations on several other genera of Ameniinae. Finally, in view of our now-abundant information about these handsome flies, I add in Part 3 some numerical studies relevant to the classification of the subfamily and some informed speculation about their zoogeography.

Biology

We still know very little of the biology of the Ameniinae, but the available evidence suggests that all species are macrolarviparous and parasitic as larvae in land-snails. Practically all that is known was summarised by Ferrar (1976). He described the rather distinctive macrolarviparous reproduction of species of *Amenia* and *Paramenia* and collected records of parasitisation of land-snails by species of *Amenia*, *Paramenia*, and *Formosiomima*. To these I can now add a record for *Silbomyia* and four more for *Amenia* (*imperialis*, *dubitalis*, *leonina*, and *longicornis*; see Part 2). Crosskey (1969) also noted that species of *Stilbomyella* and *Platytropesa* are attracted to snails. The parasitic habit helps explain the considerable variation in size that is sometimes observed in ameniines (through truncated development caused by death of the host). It may also help explain some puzzling features in the systematics of the group. At present, the great need is for further rearing, from carefully identified hosts.

Methods and methodology

Ordinations. For morphometric studies, selected characters were measured with a micrometer eyepiece or, in a few cases, scored subjectively. The data were designed for statistical analysis rather than taxonomic description and are not presented here in full. However, copies can be provided by the author on request. Apart from simple statistics, the analyses employed two main techniques: (a)

principal component analysis (PCA) of the correlation matrix, i.e., with character vectors normalised by standardisation; components were equally weighted by the option of normalising scores so that their squares sum to unity (my programme COMPAK); (b) multiple discriminant function analysis (MDA), using the canonical variate programme in the GENSTAT package. The use of MDA was entirely heuristic. Significance tests were ignored, because the necessary conditions, of uniform variances, etc., were clearly violated.

A word is in order concerning the application of ordinations to taxonomic studies. An ordination by, for instance PCA, provides a 2-dimensional, visual display of phenetic relations that are discoverable in the data; and, if (for instance) components have been normalised, the relationships depicted owe nothing to the effects of correlation between characters over the whole group. Suites of correlated characters are extracted and equally weighted. On the other hand, well-defined subgroups (if reasonably similar) may appear as parallel, elongate, even linear, clusters, just because of individual, within-subgroup correlations. Devotees of MDA seem sometimes to regard this as damning. Per contra, I find it useful, to confirm the objectivity of the groups to which one is about to apply MDA.

Here, and in ordinations at large, great care must be taken not to read too much into perceived clusters. On their own they can do little more than generate hypotheses that may be worth testing. On the other hand, if one has some independent, external criterion (hypothesis) for forming clusters, patterns on an ordination diagram may provide very satisfying confirmation (or, for that matter, an incongruent pattern, or even absence of pattern may disconfirm the hypothesis). This argument may, of course, be turned around. In the present case I have started with taxonomic hypotheses taken from the literature, and sought confirmatory clustering patterns in the ordinations. However, I have also searched the diagrams for lower-level clusters of specimens that are related geographically or ecologically: this, in the reasonable belief that such correlations are worthy of further scrutiny. In some cases little more could be found; but in others, further characters were then found that confirmed the distinctiveness of a "local" population. This in turn has generated credible hypotheses that help explain the observed patterns.

Measurements used. A suite of 16 male characters was selected, taken from the literature and/or suggested by preliminary testing; as follows:

- 1 Frons width (*Frw*); the minimum distance between the eye margins.
- 2 Frons length (*Frl*), from lunula to margin of anterior ocellus.
- 3 Parafacial width (*Pfw*), at mid-length.
- 4 Gena width (*Gnw*), from eye-margin to subcranial pit (the latter is seen in lateral view as a small but distinct, pit-like depression near the ventral angle of the triangular epistomal projection).
- 5 Face length (*Fcl*), measured between the level of the vibrissae and that of the antennae bases.
- 6 Intervibrissal distance (*Ivb*).
- 7 Length of antenna (*Ant*), from base of long seta on segment 2 to apex of segment 3.

- 8 Eye height (*Eyh*), its maximum dimension in half-facial view.
- 9 Head width (*Hdw*), in facial view.
- 10 Strength of outer vertical bristle (*Ovb*); scored as 0 for absent and 1–3 for successive degrees of strength (estimated subjectively).
- 11 Strength of upper orbital bristle (*Uob*), lateral to ocelli; scored as for number 10, but 0–2 only.
- 12 Wing length (*Wgl*), from humeral crossvein to apex.
- 13 Distance from angle of vein M1 direct to margin (*AMI*).
- 14 Costal bow (*Csb*), measured as the maximum displacement of the inner margin of the costa from a line between the apices of subcosta and humeral crossvein.
- 15 Basal width of the facial carina (*Cwb*), measured between the apices of the second antennal segments.
- 16 Maximum width of the facial carina (*Cwm*), usually at about two-thirds length.

General. The morphological terminology follows that of Colless & McAlpine (1991).

Many features are illustrated in Crosskey (1965), as are the particular attributes of many species. The computer programmes used are mainly my own, but most well known phenetic packages, such as NTSYS, provide similar facilities.

All holotypes are deposited in the Australian National Insect Collection, as are other specimens unless otherwise specified. Specimens denoted as “examined” are *ipso facto* paratypes unless expressly excluded (ICZN, para. 72b).

Abbreviations for bodily dimensions are given above, for institutes, as follows: AM—Australian Museum, Sydney; ANIC—Australian National Insect Collection, CSIRO, Canberra; QDPI—Queensland Department of Primary Industries; QM—Queensland Museum; SAM—South Australian Museum; UQ—University of Queensland Insect Collection; VM—Museum of Victoria. NP—National Park.

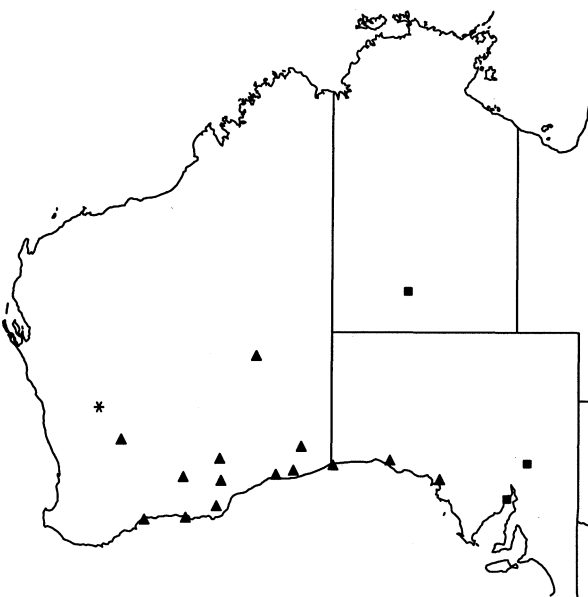


Figure 1. Distributions of forms of *Amenia longicornis* (overlapping records omitted). Filled squares = “eastern form”; filled triangles = “western form”; star = Payne’s Find.

PART 1. MORPHOMETRICS

Amenia longicornis (Malloch)

Crosskey (1965) saw only 12 males and four females of this species, but marked variation in several characters was clearly evident. To quote Crosskey: “Male specimens from South Australia have short antennae, a short facial carina which is regularly elongate in facial view, a broader vertex, rather strongly developed outer vertical setae and a strongly marked forward bowing of the costal margin of the wing; most males from Western Australia, on the other hand, have elongate antennae and a long rather lanceolate facial carina, a narrower vertex, very weak or hair-like outer vertical setae and no well marked bowing forward of the costa”. On the few specimens available these characters suggested a gradual transition from one form to the other, and Crosskey could only speculate on the possible existence of an East-West cline.

The abundant material now available shows that male (but not female) characters provide a clear geographic division into eastern and western populations (Fig. 1). The former is, as far as known, isolated in the Flinders Ranges and around the head of Spencer Gulf in South Australia, extending north to the vicinity of Alice Springs. The latter occurs across the Nullarbor Plain and has been taken as far east as Nunjirkompita (longitude 134°20'E); but is rare or absent between there and Iron Knob in South Australia (longitude 137°09'E). For instance, it was not taken during intensive collecting at Poochera (longitude 134°50'E), whereas numerous specimens were taken a few days later around the head of the Great Australian Bight (longitude ca 131°00'E). To the west, there is a more or less continuous distribution as far as the vicinity of Norseman (longitude 121°50'E), extending south to the coast at Esperance and north to Widgiemooltha; but only 5 specimens are known from areas further north or west. These include an enigmatic specimen from Payne’s Find, 500 km northwest of Norseman (see below).

The analyses that follow concentrate, therefore, on possible differences between the isolated populations, and on possible clinal variation on an east-west axis.

In all 54 males were studied. The eastern population was represented by only 8 (3 from Wilpena Pound and 5 from the Whyalla-Iron Knob area)—a meagre sample, but (I believe) sufficient to support the conclusions reached. The western specimens included the holotype (from an unknown locality in Western Australia) and samples of from one to ten specimens from 15 localities covering the known range. In general, sample sizes were so small that MDA was applied only to the East-West contrast.

PCA yielded 3 components that together explained 89% of variation. Examination of scores on component 3 showed that specimens were scattered more or less at random on that axis, so it was considered no further. Component 1, explaining 70% of variance, was an “overall size” component, with most dimensional characters showing substantial loadings of the same sign. Component 2 explained a further 13% of variance, contributed principally by *Ant* and *Fcl* (positive), with

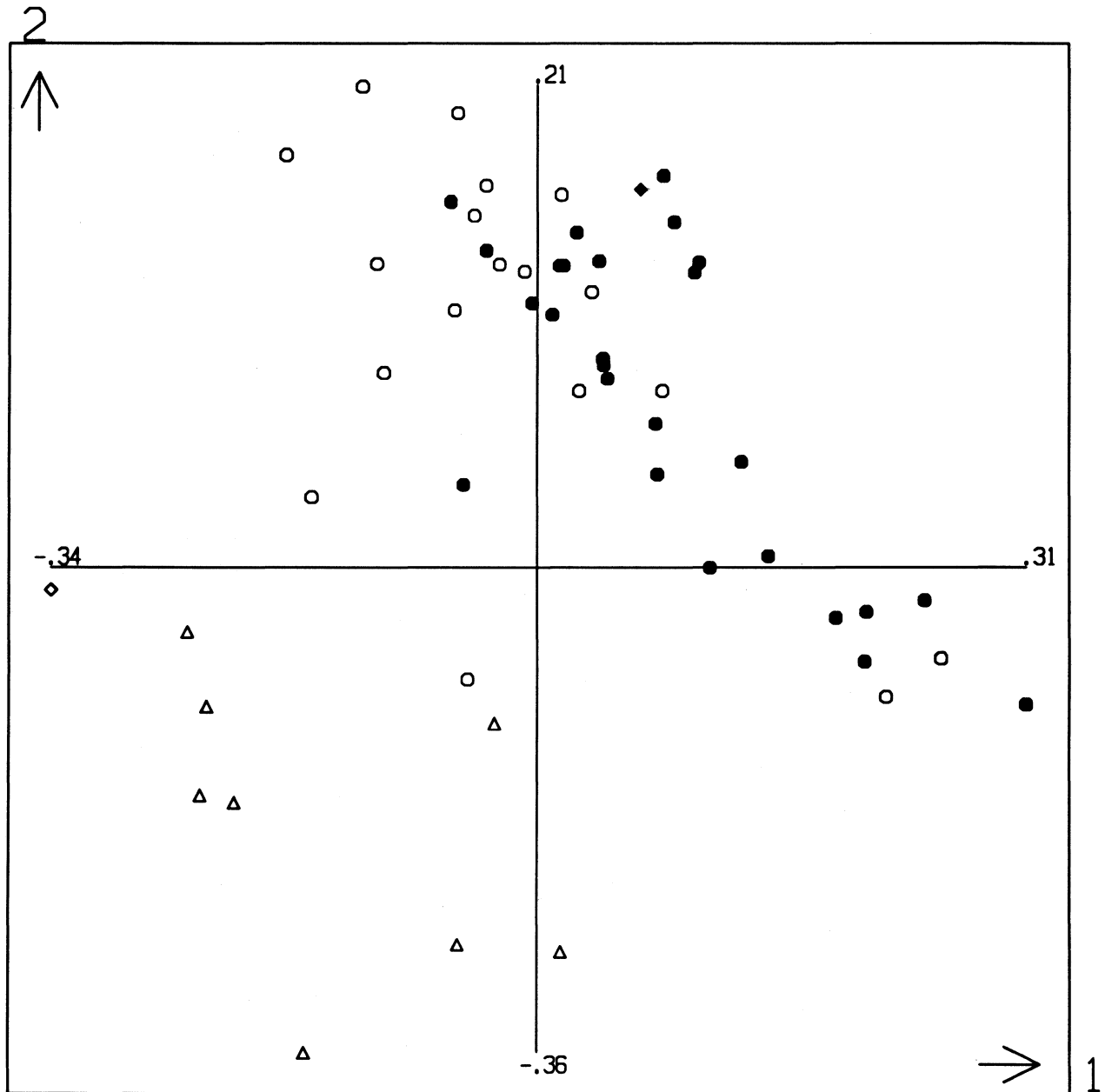


Figure 2. Ordination of 54 male specimens of *Amenia longicornis* on PCA axes 1 and 2. Open triangles = "eastern form"; open circles = "western form" from east of 125°E; filled circles = the same, west of 125°E; filled diamond = holotype; open diamond = Payne's Find specimen.

secondary contributions from *Uob* and *Cwm* (negative). In the ordination shown in Fig. 2, which plots scores on component 1 against those on component 2, it can be seen that eastern and western populations are clearly differentiated on component 2. An exception is a specimen from near Madura, W.A., with an unusually short (perhaps aberrant) antenna, but even it falls outside the envelope of points for the eastern specimens. On component 1, although the eastern specimens tend to be larger, 4 out of 8 fall within the range of the western population. The specimen from Payne's Find, however, is clearly differentiated from all others by its size.

Thus, eastern and western populations are clearly separated by a complex that included 5 of the 6 characters noted by Crosskey; significant variation was not confirmed for vertex width, but was found in one extra character (development of upper orbital bristle). While important, the bristle characters were not crucial. PCA of dimensional characters alone yielded an ordination (not shown) very similar to Fig. 2, with (as expected) component 2 dominated by *Fcl* and *Ant*. Interestingly, the two populations are simply and completely separated by "shape" of the carina, as indexed by the ratio *Cwb/Cwm* (Table 1; note that apparent overlap of ranges is due to rounding).

Table 1. Selected ratios and MDA scores discriminating eastern and western forms of *A. longicornis* (8 and 45 specimens respectively). "Payne's Find" specimen shown separately. For abbreviations, see text.

Character	Eastern form		Western form		Payne's Find
	Range	Mean	Range	Mean	
Cwb/Cwm	0.7–0.8	0.77	0.4–0.7	0.61	0.80
(Frw+Eyh-Fcl)/Hdw	0.5–0.5	0.51	0.4–0.5	0.42	0.49
MDA score	3.7–5.1	4.50	-3.2–1.1	0.65	2.40

Finally, MDA showed eastern and western populations to be completely discriminated by a function for which scores are summarised in Table 1. The major loadings were on *Frw* and *Csb*, with smaller but substantial contributions from *AMI*, *Eyh*, and *Fcl* (the last negative, the others positive). MDA thus confirms the significance of the one remaining character (*Frw*) from Crosskey's set. A crude but effective version of the discriminant function is the ratio $(Frw + Eyh - Fcl) / Hdw$ (Table 1).

A specimen that has recently come to hand (Palm Valley, MacDonnell Ranges, Northern Territory, 21–22 May 1983, G.A. Holloway; AM) allows prospective application of the MDA function. As might be expected, its measurements conform well with those of the Eastern form.

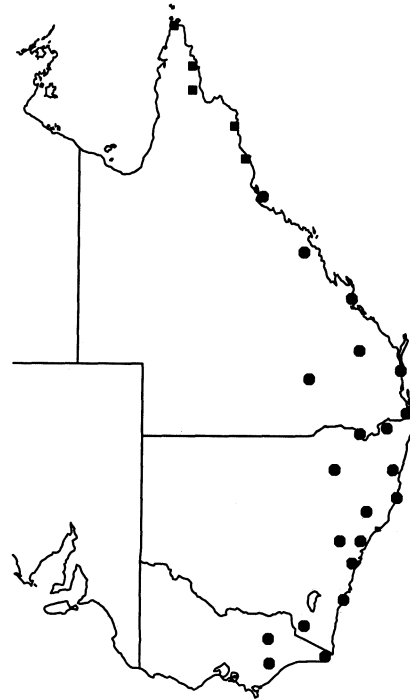
The Payne's Find specimen is exceptional, in that MDA allocates it to the eastern form. Although in many ways similar to the eastern specimens, it is distinguished by its larger size, intermediate scores on principal component 2 and the discriminant function, and, of course, its immense geographic separation. Its status remains obscure—especially since its two nearest neighbours (from Walyahmoning Rock) are quite normal "western" specimens.

Figure 2 includes a suggestion of differentiation, perhaps clinal, *within* the eastern form (there is an apparent tendency of specimens from the same locality to cluster on component 2). However, there is clearly no suggestion whatever of such a phenomenon in the western form. Note the wide scatter of specimens in the samples from east and west of longitude 125°00'. PCA of western specimens alone (not shown) releases them from within-group correlation effects (the linear clustering seen in Fig. 2); and, as expected, they scatter more or less at random on components 1 and 2. That is to say, the variation observed by Crosskey turns out to involve, not a simple cline, but two distinct geographic forms—with, perhaps, clinal variation within one of them. We may add to that the intriguing hint of a north-western population (Payne's Find) that resembles the *eastern*, rather than the western form (Table 1).

Amenia imperialis Robineau-Desvoidy

Crosskey (1965) recognised that *A. imperialis* could be readily distinguished from the very similar *A. dubitalis* Malloch; but, in view of the closeness of that similarity and an apparent separation in their geographic ranges, he preferred to relegate the latter as a subspecies of the former. Accumulated material now shows that the degree of

geographic separation is negligible, the range of *A. dubitalis* being almost completely included within that of *A. imperialis* (Figs 3–6). The consequent likelihood that the two are in fact perfectly "good" biological species calls for more detailed study of their morphological distinctness.

**Figure 3.** Distribution of *Amenia dubitalis* and *Amenia crinita* (overlapping records omitted). Filled circles = *A. dubitalis*; filled squares = *A. crinita*.

Crosskey's characterisation of the two forms now requires some amendment (see Part 2, below), but his sole dimensional character—the width of frons or vertex—clearly applies. Preliminary tests pointed to correlated variation in other parameters of head shape, although other bodily dimensions showed no sign of significant variation.

The morphometrics of head shape were, therefore, investigated further in a series of 68 males and 63 females, chosen to cover the full geographic range of each taxon as well as a representative range of body sizes. They comprised 20 males and 20 females each of *A. dubitalis* and the "classical" *A. imperialis* (from coast and adjacent mountains), identified by the characters recommended by

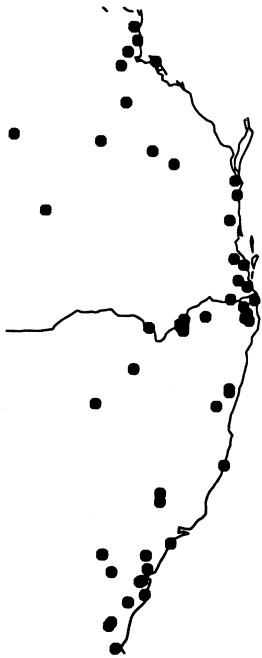


Figure 4. Details of recorded distribution of *Amenia dubitalis* in southeastern Queensland and northeastern New South Wales (compare with Fig. 6).

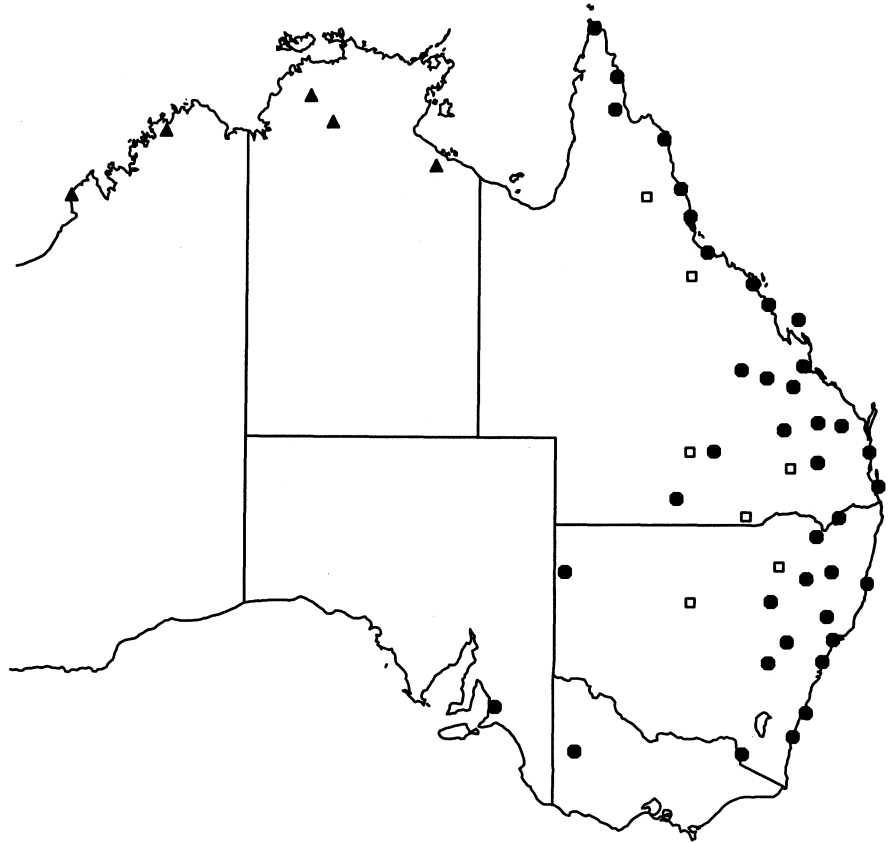


Figure 5. Distribution of *Amenia imperialis* and close relatives (overlapping records omitted). Filled circles = *A. imperialis*; open squares = "arid form"; filled triangles = *Amenia albosquamata*.

Crosskey (1965). The remainder were identified as *A. imperialis*, but came from outlying areas or seemed for other reasons worthy of special scrutiny. In the light of the preliminary tests, 6 dimensions were chosen for measurement: frons width (*Frw*), frons length (*Frl*), gena width (*Gnw*), face length (*Fcl*), eye height (*Eyh*), and head width (*Hdw*). All were measured as described above for *A. longicornis*; this implies that *Frw* was measured towards the middle of the frons in males, but across the posterior ocelli in females.

The close similarity of *A. imperialis* and *A. dubitalis*—and the propriety of analysing them as a single group—was first tested by separate PCA for the 20 *dubitalis* and 20 "classical" *imperialis* males. The 6 loadings on each of the first 3 components from the two analyses (18 paired observations) were almost perfectly correlated ($r = 0.96$). PCA of data for the full set of 68 males then yielded a first, "general size" component explaining 73% of variation. Component 2 explained 18%, with dominant, positive loadings on *Frw* and *Fcl* and negative on *Eyh*. Component 3 explained a further 8%, but provided no obvious taxonomic information and was not considered further.

Figure 7 shows a plot of component 1 against component 2. Not only is *A. dubitalis* clearly separated from *A. imperialis*, but an unexpected pattern of variation is evident within the latter taxon. Two distinct geographic segregates

are separated from the main cluster: one comprising six specimens from localities near Cooktown and two from near Cairns, the other including two specimens from the Northern Territory, eight from the Kimberleys (northwestern Australia), and seven from several arid, inland localities in New South Wales and Queensland. I am calling the former the "Cooktown form" and the latter the "Western form" for the present. Other plots (not shown) show quite clearly that the distinction between *A. dubitalis*, the Cooktown form, and other *A. imperialis* is governed largely by the regression of *Frw* on overall size; a similar regression of *Fcl* on size separates the Western form of *A. imperialis* from all the others. For practical purposes, these distinctions are well reflected in the ratios summarised in Table 2.

Accepting the foregoing groupings, MDA (not plotted) confirms that the 4 groups are indeed clearly identifiable. The first discriminant axis explains 80% of variance and, as expected, is dominated by *Frw*; *Gnw* and *Fcl* also have lesser but substantial loadings. The second explains 19%, with its principal loading on *Frl*. There were lesser but substantial loadings on *Frw*, *Fcl*, and *Eyh* (the first two of these were also prominent on the third principal component). All 4 groups are discriminated on the first axis alone, the second serving mainly to accentuate the distinction between populations of *A. imperialis* from the coastal regions and the "Western form".

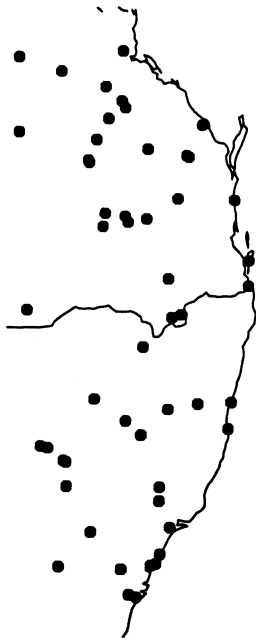


Figure 6. Details of recorded distribution of *Amenia imperialis* in southeastern Queensland and northeastern New South Wales (compare with Fig. 4).

PCA of data for females showed rather similar results, but less clear-cut. The first, “size” component explained 91% of variation; the second explained 4%, with principal loadings on *Frw* and *Fcl*. An ordination on components 1 and 2 (not shown) has the “Cooktown form” mingled with other *A. imperialis*, but specimens of the “Western form” are clearly split off. The remainder form a loose cluster showing a partial separation into *A. dubitalis* and *A. imperialis*.

Further study of the geographic forms of *A. imperialis* revealed that all are distinguishable on additional, qualitative attributes. These are discussed in Part 2 of this paper.

To sum up, *A. dubitalis* and *A. imperialis* are clearly separated, not only by qualitative characters, but also by quantitative parameters of head-shape. Also, morphometrics of “*imperialis*” point to the existence of at least 3 distinct populations. Two are geographically separated, one of them restricted largely to the Northern Territory and Kimberleys, the other to eastern Australia, but with some slight overlap in the interior of New South Wales and Queensland. A third population is everywhere sympatric with the eastern Australian form. The taxonomic implications of these findings are given below in Part 2.

Amenia leonina (Fabricius)

Crosskey (1965), following Paramonov (1957), recognised two subspecies of *A. leonina*, but substituted Macquart’s older name *albomaculata* for Paramonov’s *enderleini*. Crosskey felt that subspecific status was warranted by the degree of allopatry in the known distributions (*A. leonina* in the north, *A. albomaculata* in the southeast), a feature which has, in this case, held up under the increase of material. Basing my concept of the two taxa on the presence (*albomaculata*) or absence (*leonina*) of at least one median marginal bristle on abdominal tergite 3, plus certain male attributes discussed in Part 2, their currently known distributions are shown in Fig. 8.

To examine any correlated morphometric differences, I selected 50 male specimens of each taxon (as identified by the bristle character) and measured *Frw*, *Hdw*, *Eyh*, and *Gnw* (as defined above); also the maximum width of the eye in half-facial view (*Eyw*) and the length of wing-vein R_{4+5} . PCA of the six dimensions showed a fairly clean separation of the two taxa, but with a few highly anomalous specimens from both. There were also signs of the existence of yet another form, represented by several specimens from Eyre Peninsula, South Australia. The PCA results were based mainly on general size and *Frw*, which together accounted for 92% of variation.

A second, more extensive study was therefore made, using all available males—205 in all—and a reduced character set. The latter comprised *Hdw*, *Frw*, and (as a more easily measured, non-head character) the distance between the posterior pair of dorsocentral bristles (*Pdc*). PCA of the three dimensions yielded a first, “size” component on which the two taxa were distributed apparently at random and which took up only 58% of variation. However, components 2 and

Table 2. Ratios (ranges and means) of selected dimensions of *Amenia dubitalis* and forms of *A. imperialis*. Numbers of specimens in brackets.

Ratio	<i>dubitalis</i> (20)	<i>imperialis</i>		
		“Eastern” (24)	“Cooktown” (7)	“Western” (17)
Frw/Fcl	0.3–0.4, 0.39	0.5–0.7, 0.60	0.5–0.5, 0.48	0.6–0.8, 0.67
Frw/Hdw	0.3–0.4, 0.33	0.4–0.6, 0.51	0.4–0.5, 0.42	0.4–0.7, 0.53
Fcl/Hdw	0.6–0.8, 0.65	0.6–0.7, 0.68	0.6–0.7, 0.67	0.8–0.9, 0.84
Fcl/Eyh	0.5–0.6, 0.52	0.5–0.6, 0.57	0.5–0.6, 0.54	0.7–0.7, 0.70
Gnw/Eyh	1.0–1.3, 1.13	1.0–1.2, 1.10	1.0–1.1, 1.08	0.7–0.9, 0.82

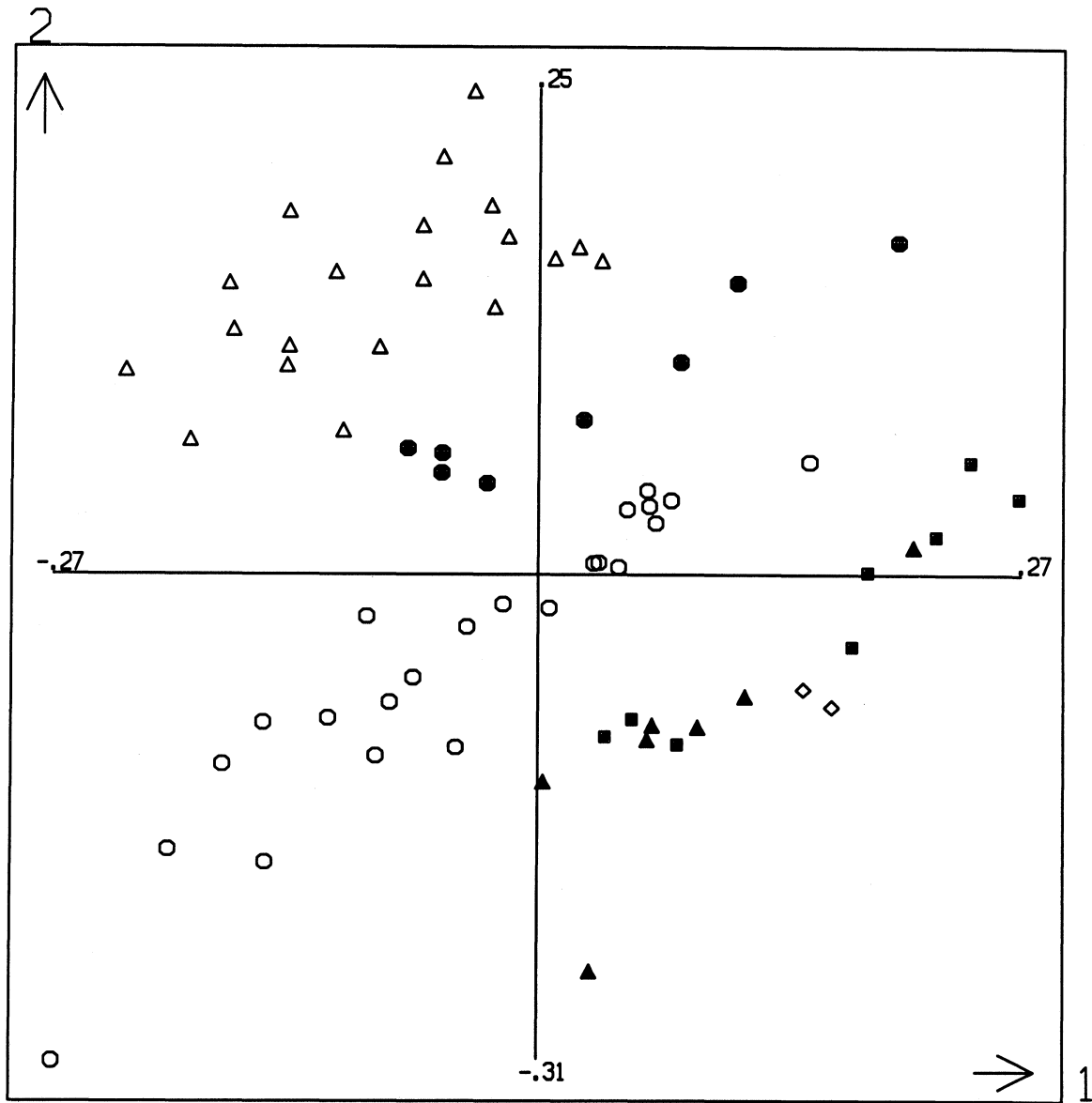


Figure 7. Ordination of 68 males of *Amenia imperialis* group on PCA axes 1 and 2. Open triangles—*Amenia dubitalis*; others—“forms” of *Amenia imperialis*: open circles—typical form; filled circles—Cooktown form; filled squares—western form, Kimberleys; filled triangles—western form, NSW and Queensland; open diamonds—western form, Northern Territory.

3 (with 35% and 7% respectively) were more informative. Component 2 was dominated by *Frw*, and component 3 by a contrast between *Hdw* and *Pdc*. In view of this, and the small number of characters used, the ordination is more clearly presented (Fig. 9, p. 94) as a simple plot of *Frw* against *Hdw*, both scaled by division by *Pdc*. MDA (not shown) gives a very similar result.

Figure 9 demonstrates that “normal” *A. albomaculata* and *A. leonina* are quite well separated by relative head width alone. Frons width serves mainly to distinguish certain exceptional populations of *A. albomaculata* (Fig. 9: “New England” and “Southern” forms). Nor does this reflect any north-south, clinal type of variation. Within each taxon, and omitting the exceptional populations, there is no detectable correlation between normalised head width and latitude.

Another five exceptions are noted on Fig. 9, p. 94: four cases of *A. leonina* with dimensions typical of *A. albomaculata* and one of the converse. These “aberrant” specimens all come from the main area of overlap between *A. leonina* and *A. albomaculata* in southeastern Queensland. In Fig. 9, the 5 “marginal” specimens of *A. albomaculata*, near the centre of the plot, with dimensions close to those of *A. leonina*, also come from the vicinity of Brisbane. On the other hand, 5 other specimens from near Brisbane fall in the main body of the *A. albomaculata* cluster, and are perfectly typical members of that taxon. The same is true of 6 specimens from Noosa, a little north of Brisbane. Also, a further 13 specimens, all collected in the vicinity of Brisbane, came to hand later and were plotted in the foregoing

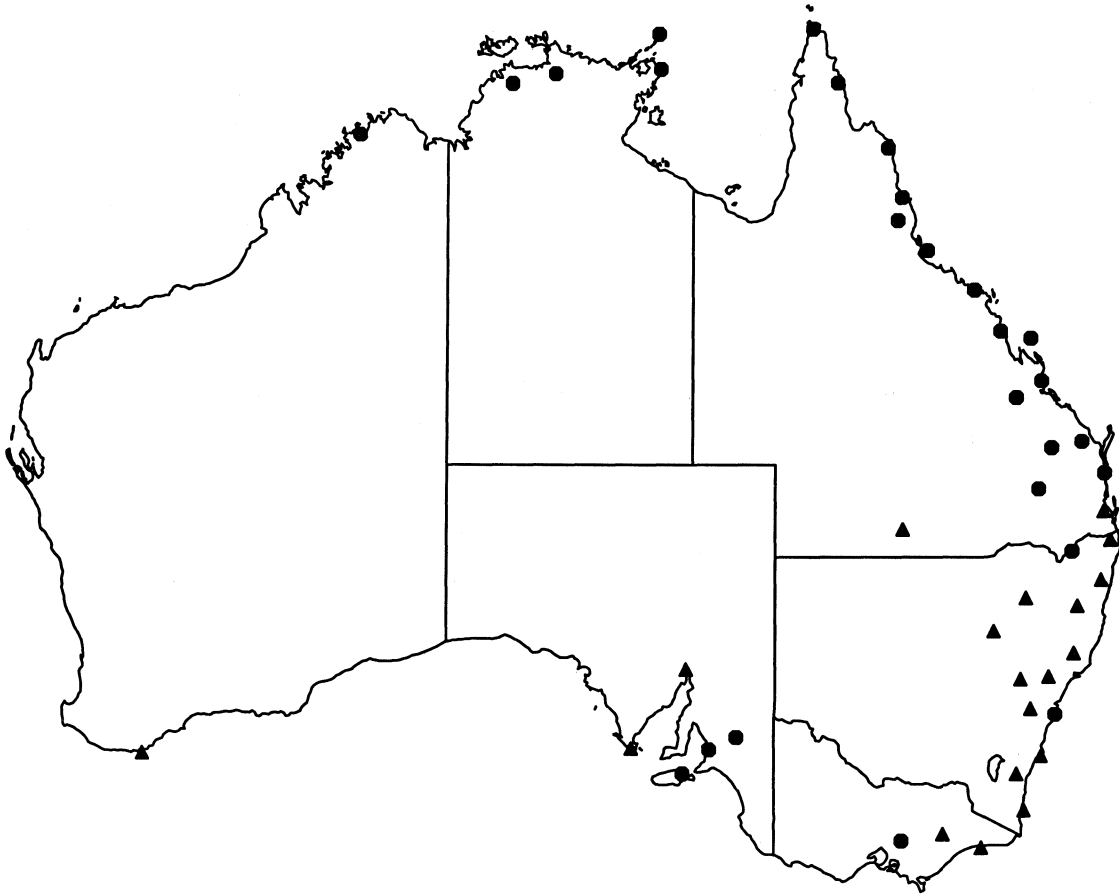


Figure 8. Distributions of *Amenia albomaculata* (triangles) and *Amenia leonina* (circles) (overlapping records omitted).

fashion. Seven *A. albomaculata* would all fall in the appropriate area of Fig. 9, but only 3 out of 6 *A. leonina* would do so; the other 3 would fall in the *A. albomaculata* area.

The simplest explanation of those observations is that some degree of hybridisation is occurring between *A. leonina* and *A. albomaculata* in the general vicinity of Brisbane, with head shape and the bristle character segregating independently in the hybrids. Nonetheless, if such hybridisation is possible it becomes difficult to explain how outliers manage to persist—such as the male *A. albomaculata* from Mackay, deep in the home range of *A. leonina*, and the 4 female *A. leonina* from Sydney.

These results are further discussed in Part 2.

Amenia chrysame (Walker)

Like the several preceding species, *A. chrysame* has a wide distribution in eastern Australia (Fig. 10). To test whether it, too, might display significant geographic variation, a preliminary analysis was made of 6 measurements and 4 bristle characters on a small set of specimens. This suggested that frons-width (*Frw*, as defined above) does, indeed, vary geographically. The ratio *Frw/Pdc* was therefore measured on 100 specimens, selected to cover

the species' range. The ratio proved to have a highly significant regression on latitude ($p < 0.01$). However, a scatter-plot (Fig. 11) shows that the regression reflects, not a regular cline, but an abrupt shift in average frons width at about 26 degrees south. Separate analyses of specimens from north and south of the 26th. parallel show no significant regression on latitude. However, the mean frons ratios were 0.27 and 0.20 respectively—a difference that, although small, is statistically highly significant ($p < 0.01$ for *t*-test).

On present evidence, I would interpret this as simple geographic variation; but the reason for its occurrence is not at all obvious. Perhaps it reflects some ancient physiographic discontinuity that has long since disappeared—indeed, perhaps the same one that gave rise to *A. leonina* and *A. albomaculata*. The matter is further discussed in Part 3.

Figure 11 shows several other interesting features: (a) a deficiency of specimens with relatively narrow frons in places between 28 and 31 degrees south; (b) an apparent surplus of such specimens in places between 26 and 28 degrees south—i.e., in the general vicinity of Brisbane; (c) a deficiency of specimens with relatively wide frons in places between 31 and 35 degrees south. If these represent more than fortuitous statistical fluctuations, I am at a loss to explain them.

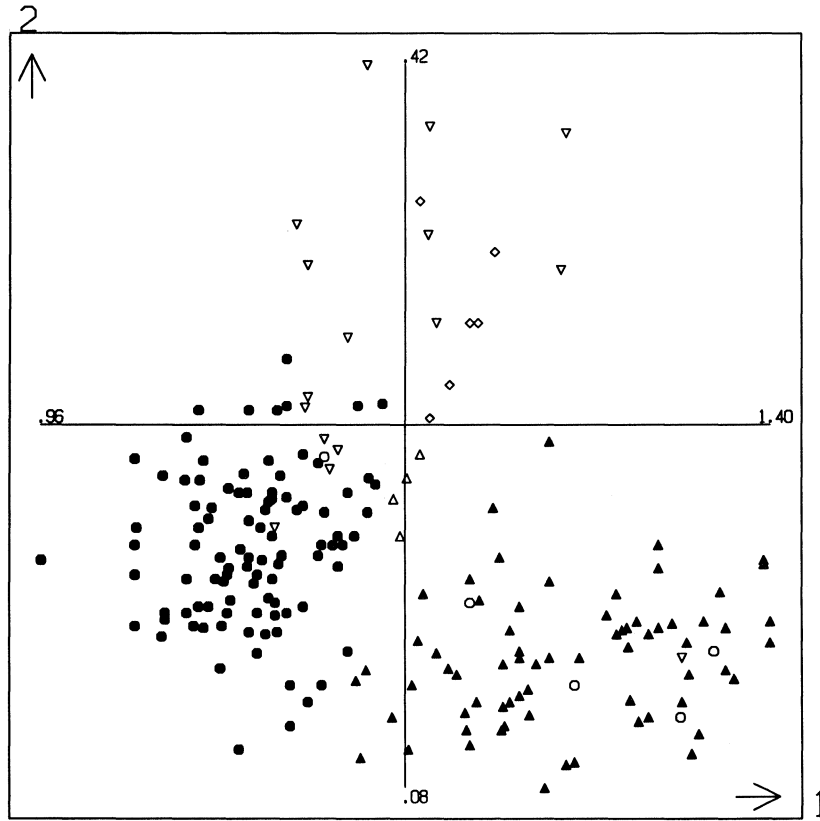


Figure 9. Ordination of 98 males of *Amenia albomaculata* and 107 of *Amenia leonina*; axis 1—*Hdw/Pdc*; axis 2—*Frw/Pdc*. Filled circles—*leonina*; filled triangles—*albomaculata*; open circles—“aberrant” specimens (see text); open triangles—*albomaculata* “marginal” specimens (2 coinciding; see text); open reversed triangles—“New England form”; open diamonds—“Southern form”.

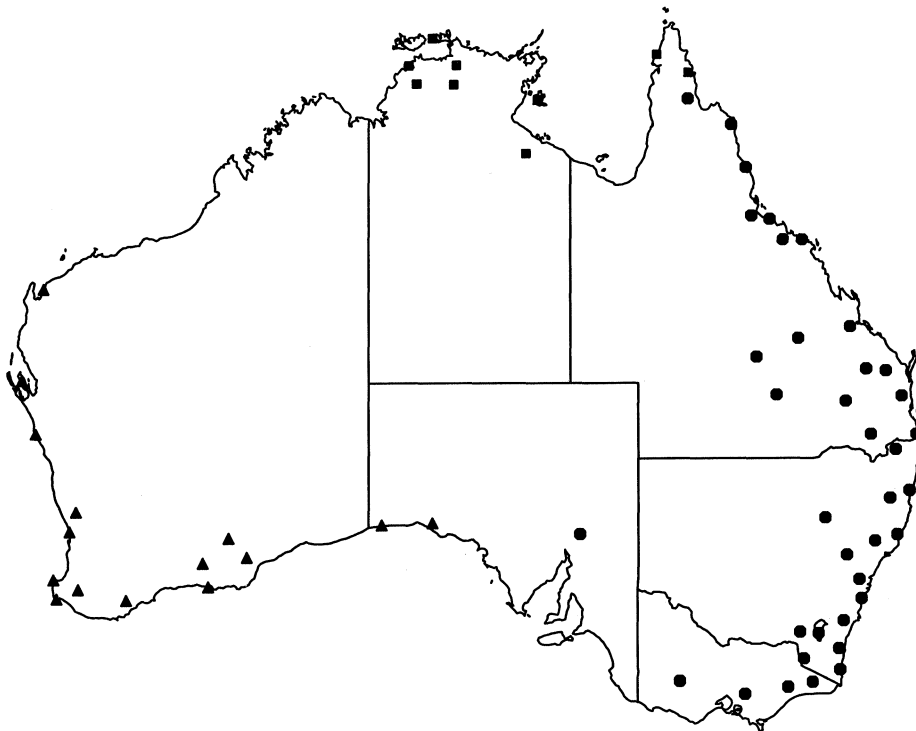


Figure 10. Distributions of *Amenia chrysame* (circles), *Amenia nigromaculata* (triangles), and *Amenia sexpunctata* (squares) (overlapping records omitted).

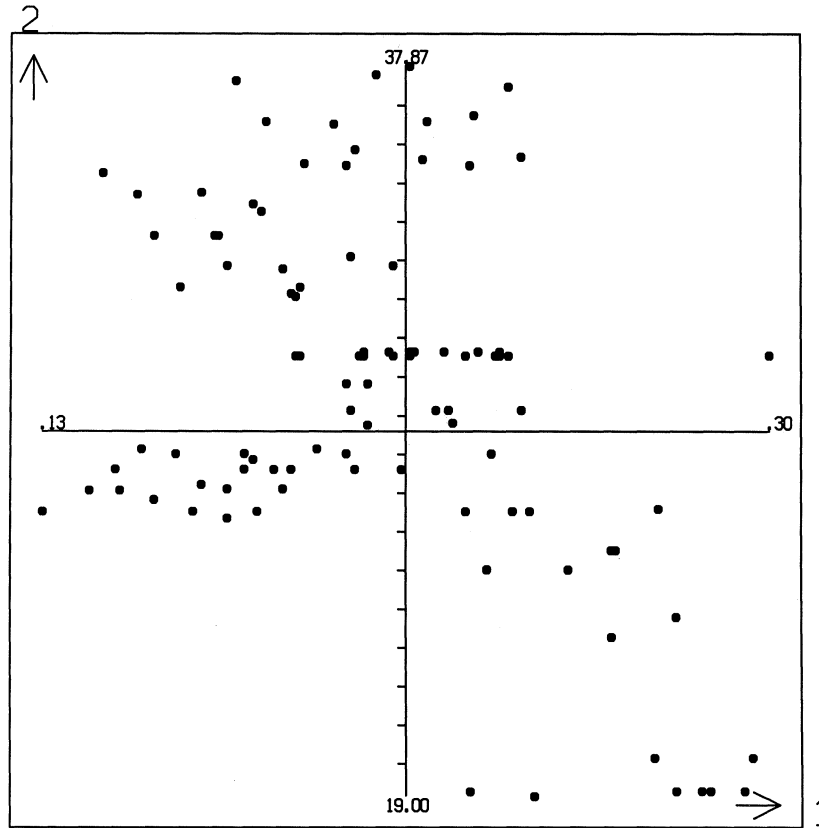


Figure 11. Scatter-plot of 100 specimens of *Amenia chrysame*; axis 1—*Frw/Pdc* (see text); axis 2—latitude (midline marked in degrees).

PART 2. FORMAL TAXONOMY

In this section I formalise the taxonomic decisions foreshadowed in the section on morphometrics and also describe several new species that have come to hand, together with new records and occasional notes on other species. “Specimens examined” are listed only for new species and diagnoses are left to be inferred from the keys. Original descriptions and synonymies are not cited, since they were more than adequately handled by Crosskey (1965, 1969, 1972) and have been recently collated by Kurahashi (1989).

Subfamily AMENIINAE

The diagnosis given by Crosskey (1965) will serve generally to identify Ameniinae:

Calliphoridae with usually metallic coloration; posterior spiracle with cluster of strong hairs on anterior lappet; thorax with weak but distinct development of a subscutellum; head almost always with conspicuous facial carina; postabdomen of female not forming an extensible telescopic ovipositor. And, as secondary attributes: eyes bare; parafacials bare; arista long-plumose; subalar bulla bare; lateral declivity of postalar callus densely long haired; prosternum strongly haired (except in some *Paramenia* spp.); prostigmatic seta

present; prothoracic spiracle dark brown; stem-vein of wing bare; vein M bent angularly forwards; hind tibia with strong apical *pv* bristle (except in *Parameniini*); abdominal sternites very broad and exposed, in female almost always with spinous setae; male terminalia as in Calliphorinae (several other attributes mentioned by Crosskey no longer apply).

To these may be added the presence of infrasquamal setulae on the thoracic mediotergite and the (often) swollen gular area of the head. The last may not always be obvious, but (except in *Amenia* spp.) it is normally detectable. It appears to be absent in other Calliphoridae. The shape of the posterior spiracle is also distinctive; the lappets are roughly equal in area and the posterior one has a smoothly rounded anterior margin and no setulae on the disc (except in some *Catapicephala* spp.). However, the most useful subfamily attribute is still the presence of a tuft of long, dark hairs with fine, “wavy” tips on the anterior lappet of the spiracle. Other calliphorids—e.g., *Chrysomya*—may have a rather similar condition, but the hairs are more normal, not converging into an anterior tuft, and they extend across the posterior lappet as well. Species of *Paraplatytropesa* are a problem, since they may have the lappet hairs weakly, and sometimes not at all, developed; but such specimens may be recognised by the metallic colour, small size, vibrissae level with epistome, parallel inner vertical bristles, and the very prominent swelling of the gular region of the head.

The mainly Oriental genus *Catapicephala* Macquart is now placed in the Ameniinae (Kurahashi, 1989) (see also below, under Parameniini). One species occurs in western New Guinea but none in Australia. *Catapicephala* spp. have the anterior lappet of the posterior spiracle more or less uniformly setose, the length of the hairs varying somewhat between species and sexes. In one female examined, of *C. ingens* (Walker), the hairs were quite sparse and short, but a male of *C. splendens* had them more resembling the ameniine norm, albeit rather inconspicuous. However, the shape of the lappets conforms closely to the rather distinctive form typical of Ameniinae (see above). The subscutellum is also quite well developed, more so, in fact, than in most ameniines. All in all, then, I see no reason to exclude the genus from that subfamily.

I shall refer below to two additional metric characters not employed in Part 1: (a) the relative distance of the bend of wing-vein M to the wing-margin, formalised as the *M-bend index*: the minimum distance from the bend of M_{1+2} to the margin, divided by the distance from the mid-point of the bend to the junction with *i-m*; (b) the *antennal segment ratio*, which is the ratio of the length of antennal segment 3 to that of segment 2, both measured from the junction of those segments on the mesad surface.

Additional species described below necessitate some pruning of Crosskey's (1965) key to genera, to remove attributes that no longer hold good. The following version will serve to identify the vast majority of specimens, if in reasonable condition.

Key to the tribes and genera of Ameniinae

- 1 Head without any strong facial carina between antennae. Hind tibia without definite *pv* apical spine (Tribe Parameniini) 2
- Head with strong facial carina separating antennae. Hind tibia with *pv* apical spine (Tribe Ameniini) 3
- 2 Vibrissae set well above level of epistoma, the latter strongly protruding. Male with eyes approximated at vertex and lacking fronto-orbital bristles *Paramenia* Enderlein
- Vibrissae set level with epistoma, the latter flat, truncate, and not at all protruding. Male with fronto-orbital bristles and with eyes well separated at vertex *Catapicephala* Macquart
- 3 Ocellar setae undifferentiated. Thorax without silver patches on humeri and notopleura. Propleural setulae lacking. Female with strong but normal setae on abdominal S2–4 *Stilbomyella* Malloch
- Head with one or more pairs of clearly differentiated ocellar bristles. Thorax with silvery patches on humeri (except in *Platyropesa* and some *Amenia*). Propleuron setulose (except in some *Paraplatyropesa*). Female with strong spine-like setae on abdominal S2–4 4
- 4 Ventral surface of costa setulose between apices of Sc and R_1 . Scutellum with a pair of strong, erect, often spiniform preapical setae. Frons of male broad, as wide as that of female. Male with strong outer vertical, prevertical and proclinate fronto-orbital bristles, as in female (male not known for *minor*) *Silbomyia* Macquart
- Ventral surface of costa bare between apices of Sc and R_1 . Scutellum usually without erect preapical bristles. Male eyes sometimes strongly approximated. Male sometimes lacking fronto-orbital bristles 5
- 5 Gular region of head often swollen, conspicuous in profile. Scutellum with 6 marginal bristles. Suprasquamal ridge bare. Crossvein r-m placed at about middle of discal cell. Abdominal T3 and T5 usually without lateral pale spots (except in *Paraplatyropesa argentea*). T4 with up to 8 posterior bristles on dorsal and lateral margins (excluding the smaller slightly ventral ones). Male usually with conspicuous long hairs on abdominal S2 and S3 6

- Gular region of head at most inconspicuously swollen. Scutellum usually with more than 6 marginal bristles. Suprasquamal ridge usually with group of tiny setulae adjacent to scutellum. Crossvein r-m placed basal to middle of discal cell. Abdominal T3 and T5 almost always with lateral pale spots. T4 with 10 or more bristles posteriorly on dorsal and lateral margins. Male with short, spiny bristles on abdominal S2 and S3 *Amenia* R.-Desvoidy
- 6 Facial carina conspicuously flattened on anterior surface, separated from epistome by sharp, V-shaped notch. Vibrissae set well above level of epistoma. Hairs of upper occiput pale; genae with pale setulae. Gular region not conspicuously swollen. Mesothorax with at most a trace of silver pruinosity behind humeri *Platytropesa* Macquart
- Facial carina more or less rounded on anterior surface, sometimes separated from epistome by rounded notch. Vibrissae about level with margin of epistoma (except in *Paraplatytropesa argentea*). Hairs of upper occiput dark; genae with at least a few dark setulae. Gular region conspicuously swollen. Mesothorax with silver pruinosity anteriorly, and over humeral, notopleural, prealar and subalar areas *Paraplatytropesa* Crosskey

Tribe Ameniini

Stilbomyella crosskeyi n.sp.

Diagnostic attributes are given in the key to genera.

Genus *Silbomyia* Macquart

The genus is largely Oriental, distributed from India and China to Timor. In Australia, one species (*S. minor*, known from a unique female) is recorded from north Queensland and one (*S. palpalis*, known from 3 males) from northwestern Australia. The genus does not seem well characterised, but I have too little material to attempt a revision.

Silbomyia palpalis Crosskey

I have seen one additional specimen, from the same general area as the type-locality: "W. bank of Turner R. above Kunagunarrina Pool, S. of Port Hedland, W.A., 25 June 1980, B. Duckworth. Map. Ref. = Marble Bar SF50-8-344:155" (AM). It was reared by the collector from a snail, a species of "Quistrachia" (*ms* name).

For the 3 known specimens, the M-bend index (as defined above) is 2.3–4.0.

Genus *Stilbomyella* Malloch

The genus was hitherto known from the Moluccas to New Britain. As predicted by Crosskey (1965), it does occur in Australia as well, and I describe below two new species from North Queensland. One closely resembles the New Guinean *S. gloriosa* (Walk.) (= *S. nigrocostalis* (Doleschall), synonymy by Kurahashi (1989)). The other is more distinct, but is, I think, best placed in this genus.

Holotype: male; 15°47'S 145°14'E, Shiptons Flat, Queensland, 18 October 1980, D.H. Colless, (at light). ANIC No. 6151. The locality is a little south of Cooktown, north Queensland.

Other specimens examined. QUEENSLAND. 4♂♂, same data as holotype, but coll. 19 October 1980. Coomera River, Lamington NP, 1200 ft, 28 May 1966, Z. Liepa, 1♀. NEW SOUTH WALES. 28°42'S 153°17'E, 1 km E Mt Warning, 500 m, 22 November 1976, I.F.B. Common & E.D. Edwards, 1♂. The last two specimens are not paratypes.

Very similar to *S. gloriosa*, as described by Crosskey (1965; as *nigrocostalis*), but differing as follows:

Male. *Body length* 6.8–8.8, mean 7.5 mm (6 specimens). *Head*. Carina (in frontal view) slightly "pinched" above epistome, sides parallel or slightly tapering ventrally on ventral half, a little longer than lunula to anterior ocellus. *Gnw* 0.4–0.5 of *Eyh*, mean 0.43 (7 specimens) (two New Guinea *gloriosa* average 0.48). Antennal segment 3 relatively short, 0.3 of *Hdw* (two New Guinea *gloriosa* average 0.2), usually at most a little shorter than arista. *Thorax*. Propleuron bare. *Wing*. M-bend index 0.8–0.9. *Legs*. Mid tibia with only 1 strong *ad*. *Abdomen*. T3 and T5 with conspicuous pale silvery spots laterally on the ventrally curved part of the tergite. *Genitalia* very similar to those of *gloriosa* (Crosskey, 1965: fig. 37), but cerci distinctly longer than surstyyles.

Female. Secondary sexual differences as for *gloriosa*. Otherwise resembling the male (but see below).

Notes. The above refers to specimens from the type

locality. Another male from Mt Warning, New South Wales, has A3 much shorter, only 0.2 of *Hdw*, and therefore much shorter than the arista (as in *S. gloriosa*), and 2 strong *ad* on the mid tibia. A female from Lamington NP has the same features. Both, however, have the conspicuous pale spots on T3 and T5 that provide the most striking difference from *S. gloriosa*, and I am tentatively placing them as *S. crosskeyi*.

***Stilbomyella anomala* n.sp.**

Holotype: female; Palmerston NP, 1200 ft, Queensland, 18 April 1971, D.A. Duckhouse, (light trap). Ex spirit via ethyl acetate. ANIC No. 6143. The type locality is near the Palmerston Highway, between Innisfail and Millaa Millaa, north Queensland.

A small dark species, body length 7.0 mm.

Female. Head. Interfrons dark brown; parafrontals, parafacials, genae, and postorbits golden pollinose; hairs of genae pale golden. In facial view inner surface of facial ridge dark, continuing as a black line through vibrissa and ventrally along subcranial margin. Frons relatively narrow, 0.2 of head width. Vertical bristles strong, inner verticals decussate, parafrontal with 2 strong proclinate fronto-orbitals and 1 exclinate (prevertical); ocellar bristles not differentiated. Carina in lateral view quite strongly protruding, curved; in facial view, more or less parallel-sided on ventral two-thirds, tapering dorsally; separated from epistome by a distinct but rounded notch. Antenna completely dark; segment 3 a little shorter than carina and than arista. Palps dark. Gena 0.4 of eye height. **Thorax.** Scutum and scutellum metallic green, the former (in glancing light) with trace of silvery frosting on humeri

and notopleura, and (in some lights) an ill-defined median dark vitta. Scutellum with preapical bristles rather erect (but not “spiny”, as typical of *Silbomyia*). Pleura metallic green with large silver-pollinose area over anepisternite and sternopleuron. Propleuron bare. **Legs.** Fore tibia with 1 *pv*, no *pd*. Mid femur with usual group of 3 strong *a* bristles near centre; mid tibia with 2 strong *ad* and 1 *pv*. Hind coxa bare on posterodorsal surface. **Wing.** Costa setulose ventrally between Sc and R₁, as in *Silbomyia*, but not apical to R₁. Membrane strongly infuscated anterobasally, as far back as R₄₊₅, and along M₂ and M₄. M-bend index 0.7. Lower calypter dark on apical half. **Abdomen.** T1+2 dark, other tergites metallic green with apical dark bands in some lights; T3 and T5 with lateral silver-pollinose spots ventrally. T3 with single strong median bristle (presumably an aberration). Sternites dark, with sparse, coarse bristles.

Male unknown.

Notes. Despite the setulose ventral surface of the costa (a “key-character” for *Silbomyia*), *anomala* seems best accommodated in *Stilbomyella* by virtue of the attributes given in the key, especially the unusual lack of differentiated ocellar bristles. As shown in Part 3 (Figs 18–22), it clusters closely with that genus phenetically.

Genus ***Platytropesa*** Macquart

The genus was known from 3 very similar species variously distributed in the Moluccas, New Guinea, the Bismarck Archipelago and North Queensland. One more of these is here recorded from Australia.

Key to species of *Platytropesa*

- 1 Anepisternite metallic, without large white pollinose spot (Bismarck Archipelago) *Pl. dubia* (Malloch)
- Anepisternite mostly covered by large white pollinose spot 2
- 2 Inner eye margin in facial view slightly but distinctly angulate at about level of lunula. Lower calypter with dark marginal colour extending very distinctly on to the membrane, and continuing around posteroexternal angle. Sternopleuron with at most a trace of pale pollinosity, forming a vaguely defined pale area. Fore-tibia usually with 2 *pd* bristles. Male with 2 pairs of proclinate fronto-orbital setae. Male S5 with very long hairs, their apices conspicuously curved downwards and inwards *Pl. auriceps* Macquart
- Inner eye margin in facial view evenly curved, not at all angulate. Lower calypter with dark marginal colour extending at most weakly on to membrane, very slightly or not at all continuing around posteroexternal angle (Australian specimens only). Sternopleuron with distinct pale pollinose spot (Australian specimens). Fore-tibia usually with only 1 *pd*. Male without proclinate fronto-orbital setae. Male S5 with shorter hairs, their apices not conspicuously curved downwards and inwards *Pl. simulans* Crosskey

Platytropesa auriceps Macquart

Crosskey (1965) gives a very detailed description. I give below the salient features, and some others not mentioned by Crosskey.

Male. *Head* in facial view with inner eye margins strongly diverging and distinctly angulate at about the level of lunula. Carina strongly developed, its anterior surface flattened, tapering strongly in upper third towards lunula. Parafacials projecting to form deep foveae in which lie the enlarged antennae. Parafrontal with exclinate prevertical bristle and two proclinate fronto-orbitals; also, numerous black setulae and sometimes several pale ones anteriorly. Interfrons very dark brown, the dark setulae of parafrontal extending on to a marginal strip, but at most a short way on to the disc. Palp dark brown. *Mesonotum* emerald green with variable, usually strong, cupreous hue in glancing lights. Sternopleuron with at most a little pale pollinosity, forming an indistinct pale spot in some lights. *Wing.* M-bend index 0.9–1.3. Calypter with dark marginal colour extending on to membrane as a distinct band, covering some 10–20% of the exposed surface and extending clearly around the posteroexternal angle. *Fore tibia* with 1–2 *p* setae, 1–3 *pd* (usually 2); mid tibia with 2 large *ad*, 1 large *v*, 2 medium *p*, and 2–3 small *pd* setae. *Abdominal venter* with conspicuously long and dense hairs, those on S5 with apices strongly curved downwards and inwards (Crosskey, 1965: fig. 30). *Genitalia* as described by Crosskey (1965: figs 39, 42); cerci in lateral view gently curved, their tips rounded; surstyli more or less parallel-sided, their apices about level with those of cerci.

Female. Generally similar to male, differing as follows:

Angulation of eye margin often less distinct. Carina less strongly flattened anteriorly, tapering regularly towards lunula. Antennae shorter, lying in shallower foveae. Parafrontal setulae much less profuse. Abdominal sternites with spinous setae instead of long hairs.

Distribution. Queensland: Palm Island, Etty Bay, Yungaburra, Kuranda, Cairns (Earl Hill, Ellis Beach), Cooktown (Shiptons Flat, Gap Creek), Iron Range.

Platytropesa simulans Crosskey

Crosskey (1965) gives a detailed description of New Guinean specimens. I now have Australian specimens, which differ from *Pl. auriceps* as follows:

Male. Inner eye margin smoothly curved. Parafrontals without proclinate fronto-orbital bristles, with more pale setulae anteriorly. Palp usually pale brown, at least apically. Sternopleuron with quite distinct pale pollinose spot, visible in most lights. M-bend index 0.8–0.9 (i.e., slightly, but distinctly less than in *auriceps*). Calypter with dark colour almost completely confined to margin, scarcely if at all extending around posteroexternal angle. Abdominal

S5 with hairs less profuse and rather straight, not conspicuously curved. Cerci more or less straight, slightly hooked at apices; surstyle as described for *auriceps*.

Female. Differs from *auriceps* in shape of inner eye margins, palp colour, pale spot on sternopleuron, and darkening of calypter—though differences not as pronounced as in male.

Distribution. The Australian form is known only from the Iron Range area of Cape York Peninsula.

Notes. There are some quite marked differences between the specimens described above and Crosskey's original description of *Pl. simulans*. These are confirmed by my examination of a female paratype. New Guinean specimens have a much more extensively darkened lower calypter and much less pollinosity on the sternopleuron. The male surstyli of Australian specimens also differ from Crosskey's description and his figures 38 and 41, in more resembling the condition shown for *Pl. auriceps* in his figs 39 and 42. Crosskey does, though, use the term "usually", suggesting that he observed some variation from the shape described.

A case could be made for describing the Australian form as a distinct species; but since it is clearly the local representative of *Pl. simulans*, I am content for the present to leave it under that name.

Genus *Paraplatytropesa* Crosskey

The genus was previously known only from a single Australian species. The discovery of additional species (total now five) necessitates changes to Crosskey's (1965) diagnosis of the genus: only two species with carina as described by him (see below); facial ridges sometimes with setae only near the vibrissae; vibrissae set at least a little above the level of epistome margin in 3 species; frons relatively narrow in 1 species; male lacking orbital bristles in 1 species; fore tibia occasionally with a *p* seta (two species); mid femur with more than 1 strong *a* bristle in two species; hind coxa often setulose on posterodorsal surface; abdomen with lateral pale areas on T5 in 1 species. In addition, hairs on anterior lappet of posterior spiracle (diagnostic of Ameniinae) often small, sparse, and inconspicuous, occasionally absent. Despite these deficiencies, the genus remains distinctive, and recognisable by the attributes given in the key. In all but *argentea* the bend of vein M is relatively remote from the wing margin, with index 1.5–3.0.

It is also noteworthy that, with one exception, the female antennal segment 3 is only some 60–75% the length of that of the male—as in *Platytropesa*. *Paraplatytropesa grandicornis* has them of equal length, as in *Stilbomyella*. Also, all but one species have strongly developed bristling on the abdominal sternites, reminiscent of the condition in *Platytropesa* and *Stilbomyella*. In the exception, *Paraplatytropesa argentea*, both male and female have spines on the sternites, as in *Silbomyia*.

Key to species of *Paraplatytropesa*

- 1 Parafacials golden. Vibrissae set well above level of epistomal margin. Abdominal T5 with lateral silvery spots. Inner vertical bristles strongly converging, decussate *Paraplatytropesa argentea* n.sp.
- Parafacials silver. Vibrissae set at most a little above level of epistomal margin. Abdominal T5 without lateral silvery markings. Inner vertical bristles not converging, usually more or less parallel (in undamaged specimens) 2
- 2 Carina narrow, not confluent with epistome. Protruding portion of lower calypter dark. Facial ridges with setulae confined to region adjacent to vibrissae. Abdominal T3 with conspicuous pale areas laterally 3
- Carina broader, confluent with epistome. Protruding portion of lower calypter pale. Facial ridges with setulae continuing over 50% or more of length. Abdominal T3 without conspicuous pale areas laterally 4
- 3 Carina pale golden, strongly convex and protruding in lateral view. Genae pale golden. Vibrissae about as long as arista, not strongly decussate. Propleuron bare. Male with frons narrow, “waisted”, narrowest in front of ocelli, without strong fronto-orbitals; antennal segment 3 about half as long as head width *Paraplatytropesa parvifrons* n.sp.
- Carina dark brown, not protruding. Genae pale silvery. Vibrissae much longer than arista, strongly incurved, decussate. Propleuron setulose. Male with broader frons, narrowest across ocelli, and with 2 strong recumbent fronto-orbital setae and 1 reclinate; antennal segment 3 about one quarter as long as head width *Paraplatytropesa grandicornis* n.sp.
- 4 Genae pale golden. Fore tibia with a *p* seta. Posterodorsal strip of hind coxa bare. Male with profuse long hairs on abdominal S3 *Paraplatytropesa rieki* Paramonov
- Genae pale silvery. Fore tibia without a *p* seta. Posterodorsal strip of hind coxa often setulose. Male abdominal S3 with only 4–6 long hairs *Paraplatytropesa tropicalis* n.sp.

Paraplatytropesa rieki (Paramonov)

Crosskey did not mention the profuse setulae of the propleuron (not present in some other species). Also, the abdominal sternites have profuse long hairs, not just “a few”. The male genitalia are shown in Fig. 12; note the very short surstyles, which barely project beyond the lateral lobes of T9.

I have two additional specimens, also from central Queensland (Bundaberg, March 1973, and Bin Bin Range, west of Biggenden, December 1974, both coll. H. Frauca).

Distribution (Fig. 26, p. 108). Queensland: Palm Island, Springsure, Collinsville, Bundaberg, Biggenden.

Paraplatytropesa parvifrons n.sp.

Holotype: male; 53 km NE of Alice Springs, Northern Territory, 6 October 1978, D.H. Colless. ANIC no. 6150.

Other specimens examined. NORTHERN TERRITORY: 3♂♂ as for holotype; 1♂, 1♀, as for holotype, but 7 October 1978; 39 km E of Alice Springs, 6 October 1978, 1—all coll. D.H. Colless; 23°38'S 134°15'E, Corroboree Rock, 23 March 1978, 1♀; 23°44'S 134°15'E, 39 km E of Alice Springs, 26 September 1978, 1♀—both coll. J. Cardale.

Resembling *P. rieki*, but differing as follows:

Male. Head (Figs 16, 17). Gena pale golden pollinose,

but parafacials, parafrontals, and postorbitals silver pollinose. Carina much narrower throughout than epistome, strongly convex in lateral view, protruding by about twice the width of a parafacial, forming a notch above epistome, ground colour golden, slightly pollinose. Facial ridges setulose for only a short distance above vibrissae. Vibrissae set a little above level of epistome margin, about as long as arista, incurved. Frons relatively narrow (Table 3), narrowest in front of ocelli; no fronto-orbitals, but dorsal 2–3 interfrontals reclinate. Gular swelling prominent. *Thorax*. Propleuron bare, apparently weakly sclerotised. Hairs on anterior lappet of posterior spiracle 3–6 in number, very inconspicuous. Setulae beneath posterior margin of scutellum sparse, but extending medially well past bases of second marginal bristles (as usual in *Ameniinae*). Lower calypter dark on protruding portion, posterior margin rounded. *Legs*. Fore tibia with 0 or 1 *p*, 1 *pv* seta. Mid tibia with usual 1 strong submedian *a* seta, occasionally (1 out of 6 specimens) with 2. Postero-dorsal strip of hind coxa bare. *Abdomen*. T1+2 dark. T3 metallic green with (viewed from behind) median dark vitta and apical dark band, laterally with conspicuous silvery frosting. T4 metallic green, in some lights broadly cupreous medially and darkened apically, sometimes with a trace of pale frosting laterally. T5 more or less similar to T4. *Genitalia* as in Fig. 13; surstyle relatively broad and almost as long as cerci.

Female. Resembling the male in most attributes, but frons narrowest across ocelli, with 2 strong fronto-orbitals.

Distribution (Fig. 26, p. 108). Known only from the vicinity of Alice Springs, Northern Territory, in very arid habitats.

***Paraplatytropesa tropicalis* n.sp.**

Holotype: male; 17°12'S 144°33'E, 6 km S of Chillagoe, Queensland, 27 November 1981, D.H. Colless (malaise trap). ANIC No. 6149.

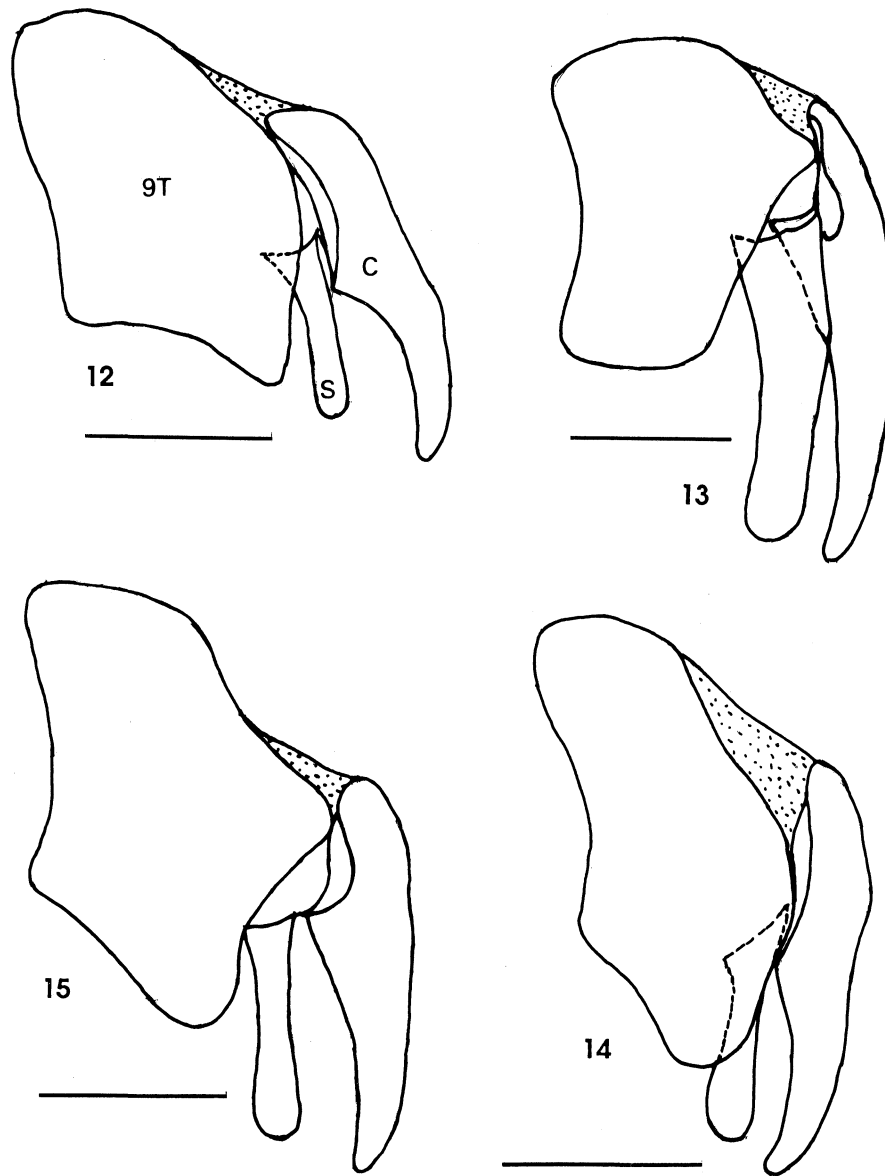
Other specimens examined. QUEENSLAND: 1♂, 1♀, as for holotype; Lakeland Downs Station, SW of Cooktown, 11 September 1969, R.J. Huppertz, 1♀; Helenvale Station, S of Cooktown, 16 September 1969, R.J. Huppertz, 1♀; 13°41'S 143°08'E, Peach Creek, 15 September 1992, P. Zborowski & L. Miller, 1♀ (AM). WESTERN AUSTRALIA: 8 km WSW of Martins Well, West Kimberley, 29 April 1977, D.H. Colless, 1♂; 14°49'S 125°50'E Mining Camp, Mitchell Plateau, 9–19 May 1983, I.D. Naumann & J. Cardale, 21♂♂, 13♀♀; 14°35'S 125°45'E, Lone Dingo, Mitchell Plateau, 9–19 May 1983, I.D. Naumann & J. Cardale, 19♂♂, 10♀♀.

Very similar to *P. rieki*; relevant attributes as follows:

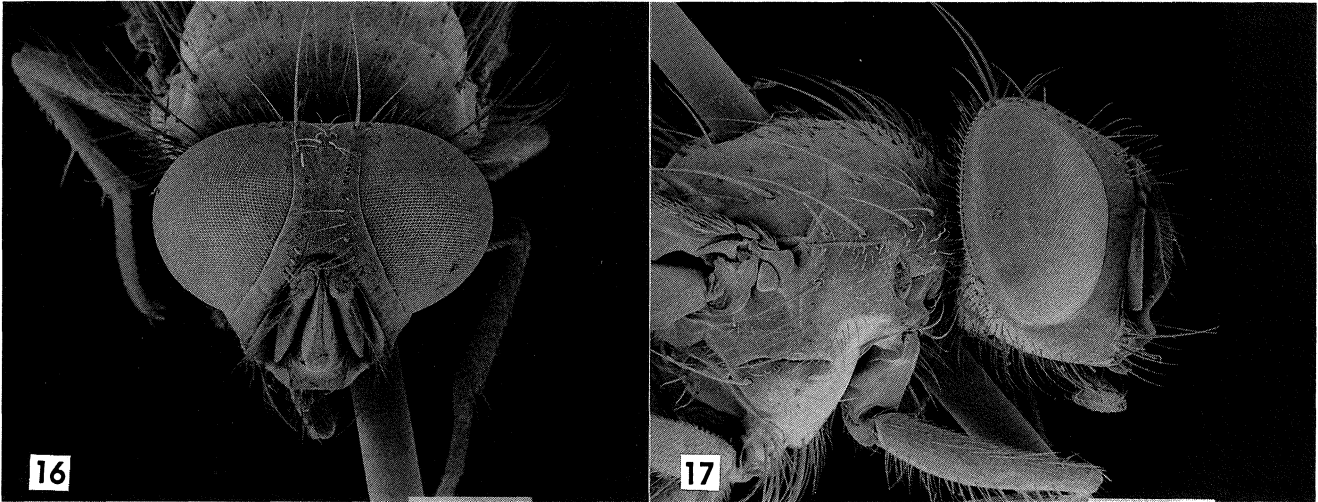
Male. Head (Figs 18, 19). Carina pale brown in ground colour, silver pollinose, confluent with epistome, scarcely protruding past antenna in lateral view. Facial ridge with tiny setulae on some 50–70% of length above vibrissa. Vibrissae set about level with epistome margin, about as long as arista, inclinate but at most slightly decussate. Frons relatively broad (Table 3), with 2 (occasionally 3) strong proclinate fronto-orbitals and 1 (dorsal) exclinate or reclinate. Genae, parafacials, parafrontals, and postorbitals silvery pollinose. Gular region not as strongly swollen as in *rieki*. *Thorax*. Propleuron with profuse setulae. Setulae beneath posterior margin of scutellum sparse, not extending medially past bases of second marginal bristles (as in *rieki*).

Table 3. Selected ratios (ranges and means) for species of *Paraplatytropesa* (numbers of specimens in brackets). Species codes as in Fig. 28. An3l = length of antennal segment 3.

Species			Frw/Hdw	Frw/Frl	Gnw/Hdw	An3l/Hdw
Pa. rie	♂	(4)	0.3–0.4, 0.35	1.5–1.7, 1.52	0.2–0.3, 0.24	0.4–0.5, 0.46
Pa. par	♂	(6)	0.2–0.2, 0.20	0.6–0.8, 0.68	0.2–0.3, 0.23	0.3–0.4, 0.38
Pa. tro	♂	(9)	0.3–0.4, 0.33	1.3–1.6, 1.48	0.2–0.3, 0.23	0.4–0.5, 0.44
Pa. gra	♂	(3)	0.3–0.4, 0.33	1.1–1.2, 1.11	0.1–0.2, 0.16	0.2–0.3, 0.26
Pa. rie	♀	(2)	0.3–0.4, 0.36	1.5–1.5, 1.50	0.2–0.2, 0.23	0.3–0.3, 0.31
Pa. par	♀	(3)	0.2–0.3, 0.27	0.9–1.0, 0.97	0.2–0.3, 0.22	0.2–0.3, 0.28
Pa. tro	♀	(9)	0.3–0.4, 0.34	1.2–1.6, 1.44	0.2–0.3, 0.23	0.3–0.3, 0.29
Pa. gra	♀	(1)	0.32	1.00	0.16	0.26



Figures 12–15. Male genitalia, lateral view. **12**—*Paraplatytropesa rieki*. **13**—*Paraplatytropesa parvifrons*. **14**—*Paraplatytropesa tropicalis*. **15**—*Paraplatytropesa argentea*. Scale bar 0.2 mm; 9T—ninth tergite; c—cercus; s—surstyle.



Figures 16, 17. *Paraplatytropesa parvifrons*, male, facial view (16); lateral view (17). Scale bar 1.0 mm.

Lower calypter pale, posterior angle rounded. Lappet hairs of posterior spiracle numerous in some specimens, but not detected in many others (including holotype). *Legs*. Fore tibia without *p* seta. Postero-dorsal strip of hind coxa with several setulae in about 50% of specimens. *Abdomen*. Tergites metallic green, usually with at least a trace of apical darkening; T1+2 sometimes dark or purplish in some lights, very occasionally with a trace of pale frosting laterally. *Genitalia* as in Fig. 14; surstyli slightly clubbed apically, a little shorter than cerci.

Female. Generally similar to male, but facial ridges setulose over only 20-30% of their length.

Distribution (Fig. 26, p. 108). North Queensland and the Kimberleys; presumably also occurring in intervening areas.

Paraplatytropesa grandicornis n.sp.

Holotype: male; 14°49'S 125°50'E, Mining Camp, Mitchell Plateau, Western Australia, 9–19 May 1983, I.D. Naumann & J. Cardale, ex ethanol. ANIC No. 6152.

Other specimens examined. WESTERN AUSTRALIA: 1♂, 2♀♀, as for holotype; 14°35'S 125°45'E, Lone Dingo, Mitchell Plateau, Western Australia, 9–19 May 1983, I.D. Naumann & J. Cardale, 1♂.

Generally resembling *P. rieki*, with significant attributes as follows:

Male. *Head* (Figs 20, 21). Carina short, narrow, not confluent with epistome, not protruding past antennal segment 3 in lateral view, dark brown with light silvery pollinosity. Facial ridge with setulae only close to vibrissa. Frons relatively broad as compared with head width, but rather short (Table 3), with 2 strong proclinate fronto-orbitals and 1 reclinate. Antennal segment 3 short, only as long as that of female. Vibrissae set a little above level of epistome margin, conspicuously long and strong, incurved,

decussate. Genae, parafacials, parafrontals, and postorbital with silver pollen; gena conspicuously short, truncate (Table 3). *Thorax*. Propleuron with several setulae. Scutellar setulae as for *P. tropicalis*. Lower calypter with exposed portion dark. Lappet hairs of posterior spiracle 1–2 in number, inconspicuous. *Legs*. Fore tibia without *p* seta. Mid tibia with 2–3 strong *a* setae. Postero-dorsal strip of hind coxa setulose. *Wing*. Setulae on basal node of R_{3+4} extending half or more the distance to r-m (in other species, largely confined to the swollen base of the vein). *Abdomen*. T1+2 dark purplish; T3 metallic blue with median dark vitta and apical dark band, and conspicuous, pale silvery lateral patches (in posterior view) extending almost to midline; T4 similar to T3, but pale patches less conspicuous or absent; T5 metallic purplish. S3 with only 4–6 long hairs, S4 without any. *Genitalia* practically identical with those of *P. tropicalis*.

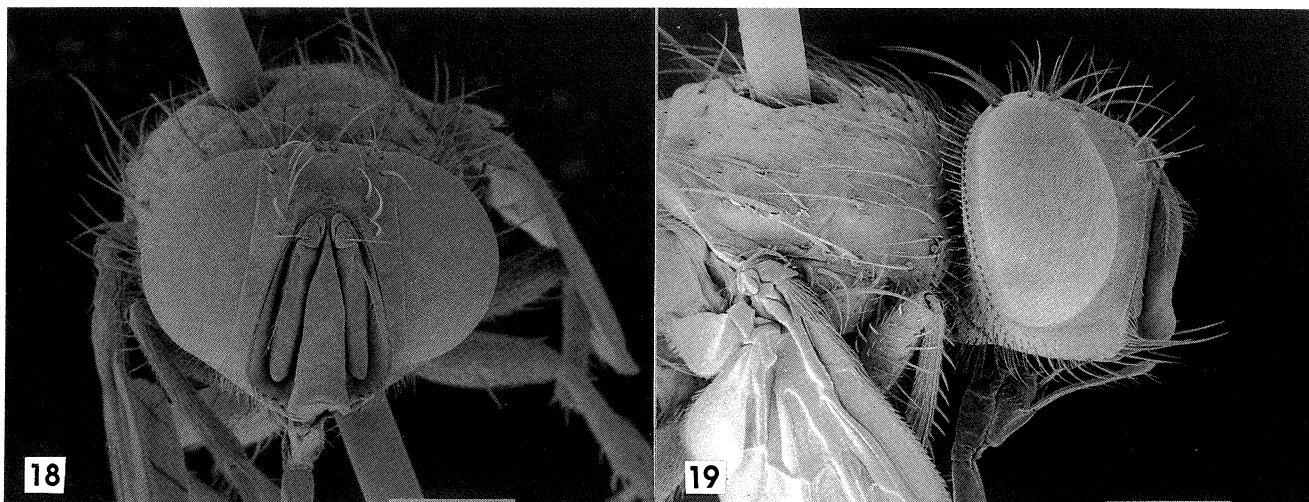
Female. Generally similar to male.

Distribution (Fig. 26, p. 108). Known only from the Kimberleys, Western Australia.

Paraplatytropesa argentea n.sp.

Holotype: male; 12°44'S 143°14'E, 3 km ENE of Mt Tozer, Queensland, 28 June–4 July 1986, D.H. Colless. ANIC No. 6148. The type locality is in the Iron Range area of Cape York Peninsula.

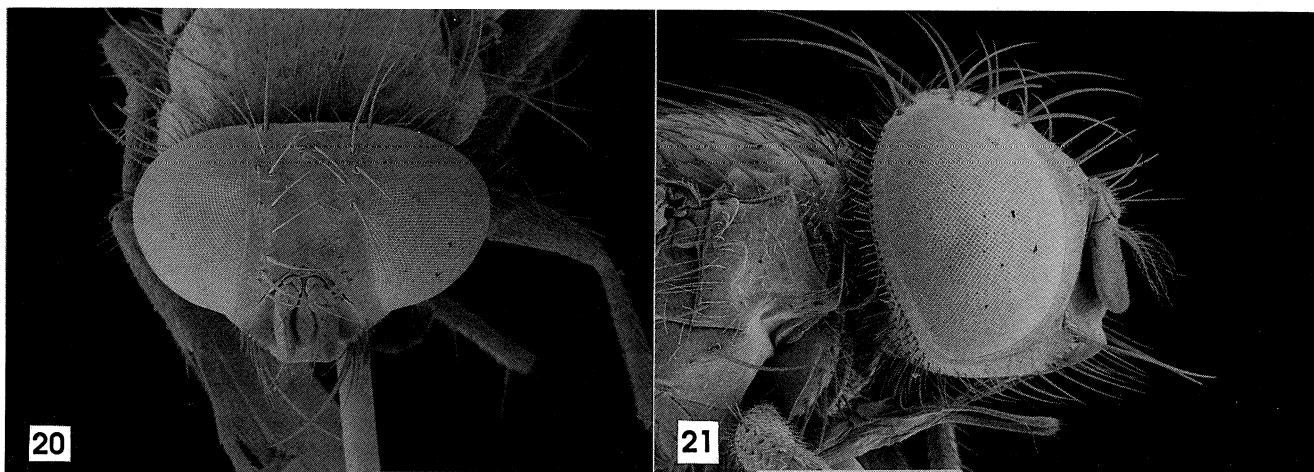
Other specimens examined QUEENSLAND: Banks Island, Torres Strait, 3 June 1969, Neboiss, 1♂ (VM); 12°43'S 143°18'E, 11 km ENE of Mt Tozer, 11–16 July 1986, 1♂; Middle Claudie River, Iron Range, 29 September 1974, G. Daniels, 1♀ (AM); 15°47'S 145°14'E Shiptons Flat, 18 May 1981, 1♂, 1♀; 15°03'S 145°09'E, 3 km N of Mt Webb, 2 October 1980, 1♂; Ellis Beach, N of Cairns, 12 May 1967, 6♀♀. Collected by D.H. Colless unless specified otherwise.



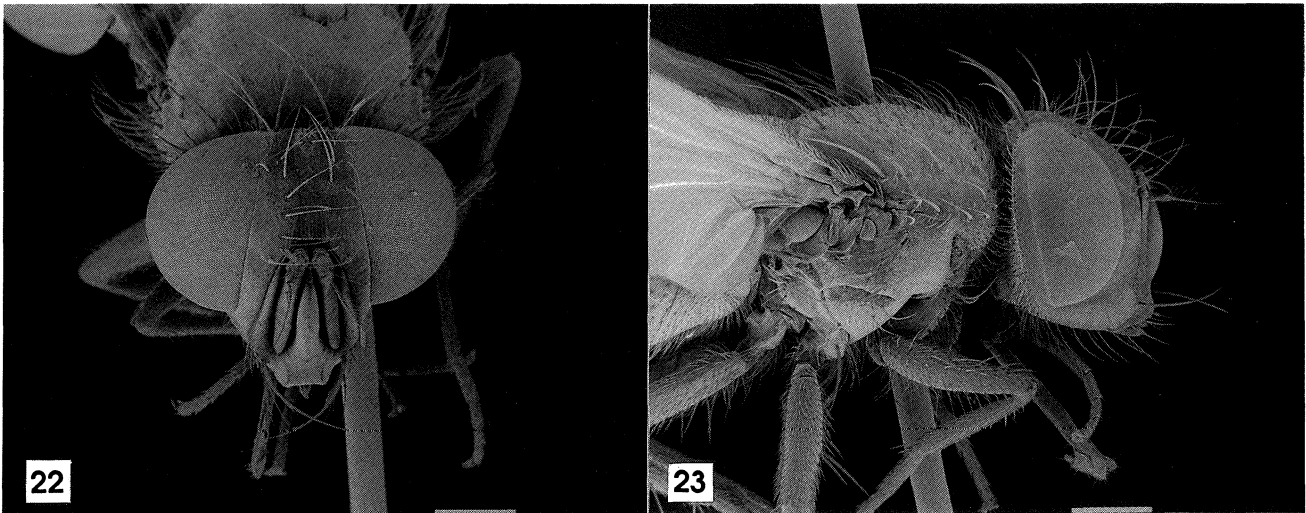
Figures 18, 19. *Paraplatytropesa tropicalis*, male, facial view (18); lateral view (19). Scale bar 1.0 mm.

Male. *Head* (Figs 22, 23) with cerebrale, vertex and a variable amount of parafrontals pale golden pollinose, this merging into silver pollinosity on lateral and ventral portions of parafrontals and most of parafacials, contrasting strongly with deeper golden pollinosity on lower parafacials, genae and postbuccae; postorbits silver pollinose; occiput metallic blue (but with pale pollinosity in some lights). Interfrons rather pale reddish brown. Palps pale brown. Carina and epistoma pale brown with thin pale pollen. Antennal segments 1 and 2 brown, segment 3 pale brown in vicinity of arista, merging into dark brown on the remainder. Parafrontals with sparse dark setulae, few if any along internal margins; interfrons with several dark setulae, none at margins; postbuccal hairs pale golden, those of occiput, parafrontals and genae brown to black. Genal hairs very sparse. Inner eye margins in frontal view only slightly divergent, in some specimens slightly convex below antenna bases. Carina in lateral view protruding, evenly curved, with notch at junction with epistoma; in facial view rounded, not at all flattened anteriorly, tapering from epistoma towards lunula, or somewhat "pinched" on ventral third. In lateral view gular region distinctly swollen,

but less conspicuous than in other *Paraplatytropesa* spp. Inner vertical bristles strong, decussate; outer verticals as large as inner; ocellars strongly developed; parafrontal with 2 strong proclinate fronto-orbitals and exclinate prevertical. Vibrissae set distinctly above level of epistoma, decussate and slightly upcurved. Facial ridges with setulae over about the ventral two thirds. *Thorax.* Scutum metallic green with vague cupreous mottling around hair-bases, but in glancing light thinly silver-pollinose over all presutural area, with smaller prealar and postalar patches. Pleura with conspicuous silver spots on anepisternite and sternopleuron. Propleuron haired. *Wing.* Costa without setulae on ventral surface apical to R_2 , and in some specimens along branches of M and crossveins. Lower calypter mainly pale, darkened on posterior and internal margins. M-bend index 1.0–1.5. *Legs* black, with greenish and violaceous reflections on femora. Hind coxa bare on posterodorsal strip. Fore tibia with 1 *p* bristle and 1 *pd* (rarely) or none; *ad* bristles strongly developed. Mid femur with usual anterior group of very strong bristles; mid tibia with 1 strong *ad*, 1 *v*, 2 *p*, and 0–1 *pd*. *Abdomen.* T1+2 dark violet; T3 metallic blue-green, with silvery lateral spots,



Figures 20, 21. *Paraplatytropesa grandicornis*, male, facial view (20); lateral view (21). Scale bar 1.0 mm.



Figures 22, 23. *Paraplatytropesa argentea*, male, facial view (22); lateral view (23). Scale bar 1.0 mm.

extending to midline in glancing light; T4 blue-green with trace of lateral silver frosting in some lights; T5 with conspicuous pair of lateral silver spots. T3 with usual pair of strong median marginal bristles. Sternites dark, with spiny bristles only (no long fine hairs): S2 with 2–3, S3 with 4–6, S4 with 4–6. *Genitalia* rather like those of *Stilbomyella crosskeyi*, but surstyles distinctly swollen apically (Fig. 15).

Female. As for the male, except that parafrontals, parafacials and genae all uniformly golden pollinose and antennal segment 3 uniformly pale brown.

Distribution (Fig. 26, p. 108). North Queensland (Torres Strait, Iron Range, Cooktown, Cairns).

Notes. This species is rather intermediate between *Platytropesa* and *Paraplatytropesa*, and grounds could be found for placing it in the former. Crosskey in fact suggested this on the label of two specimens that he saw but did not describe. Nonetheless, numerical studies support the course that I have adopted here (see Part 3, below).

Genus *Amenia* Robineau-Desvoidy

Formosiomima Enderlein, 1936: 444. Type species: *Formosiomima imitatrix* Enderlein, 1936: 444, (= *Amenia nigromaculata* Malloch, 1929), by original designation.

Despite the considerable differences in ornamentation between Malloch's *nigromaculata* and other species of *Amenia*, the structural differences are not great. I am therefore reluctant to follow Crosskey in accepting the generic status proposed by Enderlein (see below) and therefore place his *Formosiomima* as a junior synonym.

Despite much further collecting, *Amenia* has been found (as reported by Crosskey, 1965) only in Australia, especially Queensland and New South Wales; it is present in the Torres Strait islands, but absent from Tasmania. It is sharply separated from other genera by the characters given in the key. See also the note on setulae of the suprasquamal ridge under *Paramenia* (below).

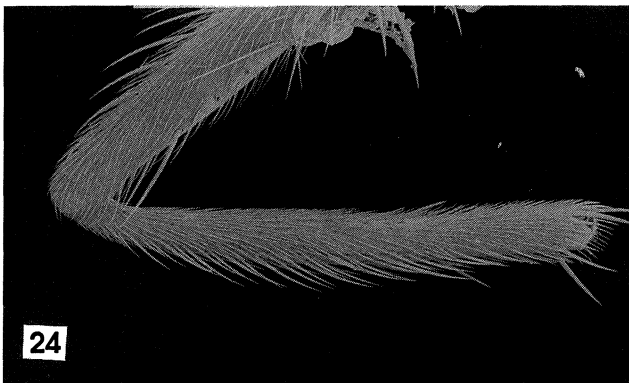
In descriptions of species, I have confined myself to salient, diagnostic features, rather than repeat the detail provided by Crosskey (1965).

Key to species of *Amenia*

- 1 Abdominal T3, T4, and T5 largely pale grey pollinose with conspicuous pattern of large black spots on their posterior margins (3 on T3, 5 on T4, 1 on T5), the marginal setae standing in groups on the spots. Mesonotum with pair of conspicuous submedian prescutellar pale spots *A. nigromaculata* Malloch
- Without such pattern on abdomen and thorax 2
- 2 Scutellum with 3 pairs of marginal bristles 3
- Scutellum with 4–6 pairs of marginal bristles 6
- 3 Postorbites silvery white. Hair of genae and postbuccae brownish black. Male frons narrow, but interfrontal strip distinct to ocelli. General colour emerald or cupreous green *A. chrysame* (Walker)

- Postorbital pale yellow or orange. Hair of genae and postbuccae golden yellow. Male with very narrow frons, parafrontals more or less contiguous. General colour dark blue-green to bluish violet (*leonina* group) 4
- 4 Abdominal T3 almost always lacking submedian submarginal bristles (very rarely with a weakly developed pair); setulae on central third of T3 appressed (angle less than 45° to surface). Male with head only a little broader than distance between posterior dorsocentral bristles (ratio about 1.2 or less); parafrontal setulae usually relatively short and straight; postorbital strip usually not obliterated, pollinose to or almost to innermost postorbital setae *A. leonina* (Fabricius)
- Abdominal T3 with at least one submedian marginal bristle, almost always with 2 or more; setulae on central third of T3 relatively erect (angle of 45° or more to surface; Fig. 25). Male with head distinctly broader than distance between posterior dorsocentral bristles (ratio 1.1 or more, except in specimens from New England); parafrontal setulae usually relatively long and at least a few with sharply bent tips (*albomaculata* forms) 5
- 5 Male with postorbital strip usually more or less obliterated, shiny, anterior to innermost 10 or so postorbital setae *A. albomaculata* (Macquart), typical form
- Male with postorbital strip well developed, not at all reduced, pollinose to outer vertical seta *A. albomaculata*, New England form
- 6 Upper occiput non-pollinose, black and semi-shining. Hair of occiput and postbuccae dark brown or black. Wing with bend of vein M much further from margin than from *m-cu*. Thorax black or dark violet with (inter alia) a pair of conspicuous silvery dorsocentral spots at anterior margin. Abdominal T4 with a pair of small white lateral spots *A. longicornis* (Malloch)
- Upper occiput yellow pollinose over yellow or orange ground colour. Hair of occiput and postbuccae golden yellow. Bend of vein M at most a little further from margin than from *m-cu*. Thorax otherwise, anterior margin without submedian pale spots or with a pair of intraalars and a diffuse median pale area over dorsocentral and acrostichal areas. Abdominal T4 without lateral pale spots 7
- 7 General colour bright green, sometimes cupreous or bluish green. Scutellum usually with 4 pairs of marginal bristles. Abdominal T4 and T5 without submedian pale spots. Bend of vein M usually about as distant from margin as from *m-cu*. Male with eyes widely separated (*imperialis* group) 8
- General colour purplish black. Scutellum with 5 or 6 pairs of marginal bristles. Abdominal T3 and T4 each with a submedian pair of silvery spots. Bend of vein M much closer to margin than to *m-cu*. Male with eyes closely approximated *A. sexpunctata* Malloch
- 8 Upper calypter more than 50% dark, its posterior margin and associated fine hairs dark (or at least brownish) laterally as far as, and including, the external tuft at junction with lower calypter. Male without median marginal bristles on abdominal T3 and hind tibia with conspicuous *ad* fringe of close-set hairs of more or less uniform length (Fig. 24) *A. crinita* n.sp.

- Upper calypter dark on little more than the crescent-shaped lobe adjacent to alula and internally along posterior margin, externally (adjacent to lower calypter) the margin and associated fine hairs pure white or (occasionally) slightly golden. Male with pair of strong median marginal bristles on abdominal T3, and hind tibia with rather sparse, irregular *ad* row of several strong bristles mixed with other, much smaller ones 9
- 9 Exposed portion of lower calypter (not covered by upper one) pale grey with darkened border. Upper calypter all pale. Female with pair of strong median marginal bristles on abdominal T3; antennal segment ratio about 3. Male with *Frw/Frl* about 0.7; antennal segment ratio about 4; wing with costa only slightly bowed beyond apex of Sc (Northern Territory and Kimberleys) *A. albosquamata* n.sp.
- Exposed portion of lower calypter all dark brown. Upper calypter usually with at least a little brown colour on posterointernal lobe. Female without median marginal bristles on abdominal T3 (except in southern specimens of *dubitalis*); antennal segment ratio about 2.5. Male with *Frw/Frl* usually less than 0.6; antennal segment ratio usually about 3; wing with costa conspicuously bowed beyond apex of Sc (Eastern Australia) 10
- 10 Head in direct facial view (lit from above) with conspicuous pale golden pollinosity over genae and parafacials, extending to parafrontals as head is rotated. Male with *Frw/Frl* less than 0.5. Females from south of Brisbane almost always with pair of median marginal bristles on abdominal T3 *A. dubitalis* Malloch
- Head in direct facial view without conspicuous pollinosity on genae or parafacials, at most a narrow band along eye margins (rotation may reveal some thin pale pollinosity). Male with *Frw/Frl* greater than 0.5. Female without median marginal bristles on abdominal T3 *A. imperialis* R.-Desvoidy



Figures 24, 25. 24—*Amenia crinita*, male, hind tibia. 25—*Amenia albomaculata*, male, abdomen, lateral view, to show dorsal setulae on T3. Scale bar 1.0 mm.

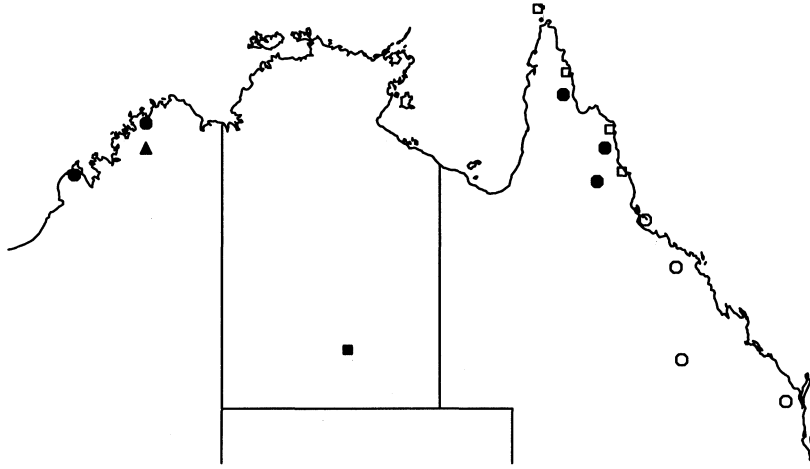


Figure 26. Distributions of *Paraplatytropesa* spp.: filled circles—*tropicalis*; open circles—*rieki*; open squares—*argentea*; filled square—*parvifrons*; filled triangle—*grandicornis*.

Amenia imperialis group

As shown in Part 1, the two “subspecies”, *A. imperialis imperialis* and *A. i. dubitalis* are clearly distinguishable, not only by qualitative characters (Crosskey, 1965), but morphometrically as well. Moreover, *dubitalis* is everywhere sympatric with *imperialis*. The case seems, therefore, overwhelming for treating *dubitalis* as a full species, a course foreshadowed by Crosskey (1965) and one that I shall henceforth follow.

The morphometric study also revealed further differentiation within *A. imperialis*, separating off a “Cooktown” and a “Western” form. As shown below, both of these are characterised by additional, qualitative characters. As the “Cooktown” form is everywhere sympatric with typical *imperialis*, and both sexes can be readily identified, I am awarding it, too, full specific status. The case of the “Western” form is more complicated. Its members from the Northern Territory and Kimberleys also possess distinctive qualitative attributes, but there remain several specimens from arid, inland localities in New South Wales and Queensland. These belong morphometrically in the “Western” form, but are otherwise typical *A. imperialis*. The simplest course, and that which I shall follow here, is to recognise the population from the Northern Territory and Kimberleys as a distinct species, treating the other specimens as variants of unknown status (see below: *imperialis*, “arid form”).

The principal attribute distinguishing *dubitalis* from the others is the pollinosity of the head in frontal view. For its strict application, the head must be viewed from directly in front, with the light coming at an angle of about 60 degrees and from the direction of the vertex. In the above key, and in the descriptions that follow, these conditions are assumed.

The pair of submedian marginal bristles on abdominal T3 is typically present in males and absent in females. However, they may be present as a rare aberration (female *A. imperialis*), or geographically determined (female *A. dubitalis*), or specifically diagnostic (female *A. albosquamata*). Likewise, in male *A. crinita* lack of the bristles is diagnostic. This suggests variability in some “maleness/femaleness” balance,

presumably stemming from some sensitive physiological threshold. A similar phenomenon occurs in species of *Platytropesa* and *Paraplatytropesa*.

Crosskey (1965) commented on the remarkable uniformity of the male genitalia over most of the Ameninae. Dissection of a single specimen from each member shows this to hold for the *imperialis* group, with the possible exception of two features mentioned under *A. crinita* and *A. dubitalis*. These are relatively so trivial that I have not pursued them further.

The group as a whole is well characterised by the attributes given in the key. Its members are readily recognised with the naked eye, by the relatively large size, the brilliant green, bluish-green, or cupreous-green colour, without conspicuous pale markings, and the bright golden face.

Amenia imperialis Robineau-Desvoidy **n.stat.**

Amenia imperialis imperialis Crosskey, 1965: 109.

Dr Crosskey has kindly checked his neotype of *A. imperialis* (in the British Museum of Natural History) and my present application of the name is clearly valid. The species is distinguished from others in the group by the attributes given in the key, in particular the non-pollinose parafacials and the colouring of the calypters, and, in the male, the *ad* setae of the hind tibia and the presence of medial marginal bristles on abdominal T3. Also, the M-bend index is 0.9–1.4 (almost always greater than 1.0) and the antennal segment ratio 2.6–3.5 for males and 2.3–3.4 for females. Crosskey’s male specimen that lacked bristles on abdominal T3 seems likely to have been the new species, *A. crinita*, described below. On the other hand, I have seen a single female specimen (Kandos NSW, 13–15 May 1981, B.J. Day; AM) that has a male-like pair of submedian marginal bristles on abdominal T3. It is otherwise a perfectly normal specimen of *A. imperialis*.

I have one new rearing record: a male (24 km S of Barraba, NSW, 3 April 1990, P. Colman; AM C.329311) reared from *Galadistes marcescens* (Cox) (Camaenidae).

Distribution. Eastern Australia, from Cape York and Torres Strait Islands to Adelaide, largely on the coast and adjacent ranges, but occasionally taken well inland (Fig. 5; the morphometrically distinct specimens are shown separately.)

Amenia crinita n.sp.

Holotype: male; 15°30'S 145°16'E, 1 km SE of Mt Cook, Queensland, 13 October 1980, D.H. Colless, (at light). ANIC 6155.

Other specimens examined. QUEENSLAND: Lockerbie, Cape York, 2 April 1964, I.F.B. Common & M.S. Upton, 1♀; Bamaga, Cape York, 4 April 1964, I.F.B. Common & M.S. Upton, 1♀; Middle Claudie River, Iron Range, 13 September 1974, G. Daniels, 1♂ (AM); Iron Range, 2–9 June 1971, E.F. Riek, 1♀; 15°03'S 145°09'E, 3km NE of Mt Webb, 1–3 October 1980, T. Weir, 2♀♀; same data, D.H. Colless, 1♀; same data, 3 October 1980, D.H. Colless, 1♀; 15°04'S 145°07'E, Mt Webb NP, 28 April 1981, D.H. Colless, 3♂♂, 1♀; same data, 29 April 1981, D.H. Colless, 1♂; 15°16'S 144°59'E, 14 km NW Hope Vale Mission, 8 May 1981, D.H. Colless, 1♂; Leo Creek, McIlwraith Range, near Coen, 2–3 November 1969, 1♀ (UQ); Bayview, Cairns, 16°57'S 145°43'E, 6 December 1991, C.J. Burwell, 1♀ (UQ); Kuranda, F.P. Dodd, 1♂ (SAM); Cairns District, A.M. Lea, 1♂ (SAM); Mt Bartle Frere (East Base), 80 ft, 29 April 1955, K.R. Norris, 1♀; Palmerston East, Innisfail District, 25 January 1991, D.K. McAlpine & B. Day, 1♂, 1♀ (AM).

This is the “*imperialis* Cooktown form” of Part 1, closely resembling *A. imperialis*, but differing as follows:

Male. *Head:* frons relatively short (Table 2, “Cooktown form”); antennal segment ratio 3.1–3.8. Carina slightly, but distinctly, flatter in profile, less protruding, and therefore less clearly separated from epistome. *Wing:* bend of M relatively closer to wing margin, index 0.6–0.9; upper calypter more than 50% dark, the external margin and associated fringe continuing brown or golden-brown to junction with lower member. *Legs:* hind tibia (Fig. 24) with conspicuous *ad* fringe of close-set bristles of more or less uniform length and strength, about as long as the tibia is wide. *Abdomen:* T3 lacking the usual pair of median marginal bristles. T3 with lateral pale patches reduced, sometimes absent. Genital segments lacking the strong, almost spiny bristles present in other members of the group.

Female. Differing from *imperialis* in the M-bend index and calypter colouration; also, lateral pale patches on abdominal T3 usually absent; antennal segment ratio 2.7–3.2.

Notes. The species was first recognised morphometrically in the male sex only (see Part 1, Fig. 7). Additional diagnostic attributes were later discovered, including the colouration of the calypters, which enabled identification of females. The list of specimens examined includes a number identified since the morphometric studies were made.

Distribution (Fig. 3). North Queensland.

Amenia albosquamata n.sp.

Holotype: male; 14°35'S 124°45'E, Lone Dingo, Mitchell Plateau, Western Australia, 9–19 May 1983, I.D. Naumann & J.C. Cardale. ANIC 6156.

Other specimens examined. WESTERN AUSTRALIA: data as for holotype, 3♂♂, 3♀♀; 14°49'S 125°50'E, Mining Camp, Mitchell Plateau, 9–19 May 1983, I.D. Naumann & J.C. Cardale, 4♂♂, 3♀♀; 8 km S of Cape Bertholet, West Kimberley, 19 April 1977, D.H. Colless, 1♀; Lombardina, 28 May–22 July 1990, G.R. Strickland, 4♀♀; NORTHERN TERRITORY: Brocks Creek, March 1933, T.G. Campbell, 1♂, 1♀; Burnside, 28 March 1929, T.G. Campbell, 1♀; Katherine, 7 January 1964, D. Turner, 1♂ (VM); McArthur River, 48 km SSW of Borroloola, 22 April 1976, D.H. Colless, 1♀; 14°19'S 132°25'E, Katherine Gorge NP, 1 January 1993, G. & A. Daniels, 1♂ (UQ).

This species comprises the Western Australian and Northern Territory populations of the “*A. imperialis* Western form” of Part 1.

Male. Closely resembling *A. imperialis*, differing as follows: *Head:* parafacials sometimes weakly pollinose when head rotated from standard position, away from light (see above); face relatively longer and gena relatively narrower (Table 2, “Western form”); antennal segment ratio distinctly high, 3.5–4.4 due to relatively longer segment 3; arista not reaching apex of segment 3. *Wing:* upper calypter all pale; lower calypter grey or pale, with darker margin. M-bend ratio usually less than 1.0. Costa at most slightly bowed beyond apex of Sc.

Female. Differs from *A. imperialis* in the colour of calypters (as in the male), the presence of a pair of submedian marginal bristles on abdominal T3, and the greater antennal segment ratio, 2.8–3.4.

Distribution. Known only from the Kimberleys, Western Australia, and the Northern Territory.

Amenia imperialis, “*arid form*”

I am using this name for a set of eight males, from arid areas of inland New South Wales and Queensland, that are seemingly intermediate between typical *A. imperialis* and *A. albosquamata*. They cluster with the latter in the ordination described in Part 1, having, for instance, the typically long face and narrow gena and the long antennal segment 3 (ratio 3.2–4.6 for males). However, the calypters resemble those of *imperialis*, as does the M-bend index.

I suspect that this “form” actually belongs to *A. albosquamata*, and that the morphological separation of the latter from *A. imperialis* is slighter than I am here recognising; indeed, the two “species” may represent the extremes of a cline. But without additional material, I am unable to take the matter further.

Specimens examined. NEW SOUTH WALES: Mt Boppy, near Cobar, 25 November 1949, S.J. Paramonov, 5♂♂; 1 mile

NE of Bohena, Pilliga Scrub, 5 April 1951, Key & Chinnick, 1♂. QUEENSLAND: 28 km NNE of Charleville, 18 October 1978, D.H. Colless, 1♂; 17°12'S 144°33'E, 6 km SE of Chillagoe, 27 November 1981, D.H. Colless, 1♂.

Amenia dubitalis Malloch **rev.stat.**

Amenia dubitalis Malloch, 1927: 343.

Amenia imperialis dubitalis Crosskey, 1965: 111.

Differs from *A. imperialis* in the attributes given in the key. The narrow frons of the male is particularly striking and in both sexes the difference in facial pollinosity, while seemingly rather trivial, is conspicuous under the stated conditions of lighting. For both sexes the M-bend index is 0.7–1.2; the antennal segment ratio is 2.2–3.1 for males and 2.4–2.6 for females.

In the one male dissected the surstylus had a subbasal group of 3–4 bristles on the anterior surface, as opposed to a single bristle for other members of the group.

I have one new rearing record: a male (24 km SE of Bonshaw, NSW, 31 March 1990, P.H. Colman; AM) from *Strangesta* sp. (Rhytididae).

Distribution. Eastern Australia, from about Ingham in the north to southeastern Victoria; restricted almost entirely to the coast and adjacent ranges (Fig. 3) A close examination of records shows a marked deficiency from the more inland localities of southeastern Queensland (Fig. 4), as compared with *A. imperialis* (Fig. 6). The area is well-collected and the difference is clearly significant, presumably reflecting some difference in host snails.

Notes. The difference between females from the border area between Queensland and New South Wales and further south, which almost invariably have submedian marginal bristles on abdominal T3, and those from further north, which almost invariably lack them, could well be used to establish two separate subspecies. However, I see no point in taking this step. The change is quite abrupt, at about the latitude of Brisbane: between there and the 25th. parallel, six out of 13 specimens had such bristles, and further north, only one out of 21 (and that very small). Per contra, only two out of 47 specimens from more southern localities (Sydney and Narrabri) lacked such bristles, two had only a single bristle, and two had three bristles.

Amenia chrysame (Walker)

Material now available extends the distribution to far North Queensland and, in the south, to the Flinders Ranges, north of Adelaide (Fig. 10). The morphometric analysis in Part 1 (Fig. 11) revealed a sharp discontinuity in variation at about the 26th parallel, in the vicinity of Bundaberg. Further study shows that males from north Queensland have the postorbital strip less reduced than have those from New South Wales. In the former, the pruinosity can be traced to or almost to the vertex; in the latter it disappears well before the vertex. A slight difference in the shape of the carina, in both sexes, also shows a similar distribution. However,

between the New South Wales border and about Bundaberg, the two forms seem to overlap and intermediates are found. Despite this clear evidence of subspeciation, I see no reason to give it formal recognition.

A. chrysame has the submedian marginal bristles on abdominal T3 very strongly developed, both in size and (in males only) in number (usually 4 or 5, but up to 7 have been seen).

Distribution (Fig. 10). Eastern Australia, predominantly on the coast or nearby ranges, from Cape York to the Flinders Ranges, South Australia.

Amenia leonina group

This group comprises the two taxa treated by Crosskey (1965) as subspecies of *A. leonina*: *A. l. leonina* and *A. l. albomaculata*. As discussed in Part 1, the two are to a large extent allopatric, but with some significant occurrences of each within the range of the other. Males are morphometrically distinct on the basis of relative head width, which correlates with the other characters used in the key above, but in southeastern Queensland, in the general vicinity of Brisbane, intermediate specimens occur, suggesting some degree of introgression of genotypes. However, this could be the result of ecological disturbance, and specimens of *A. albomaculata* from Mackay and of *A. leonina* from Sydney, suggest that introgression is not general. For that reason, specific status seems to me most suitable, and I am restoring the taxa on that basis.

Members of the group can be identified by the characters given in the key. They can be recognised with the naked eye by the large size, the metallic blue or greenish-blue body colour, the conspicuous pair of prescutal dorsocentral pale stripes, and the pale lateral spots of abdominal T3 not extending on to the dorsum. The rather similar *A. longicornis* is usually smaller, purplish-black in colour, and the lateral pale spots on T3 clearly extend on to the dorsum. As in the *imperialis* group, the male terminalia show no attributes useful for identifying the group or its individual species.

Crosskey's (1965) detailed descriptions hold fairly well, and I deal below mainly with additional differences that have appeared in the more abundant material now available. The curious geographic distributions displayed in this group are discussed in Part 3 (Zoogeography and Evolution).

Amenia leonina (Fabricius) **n.sens.**

Amenia leonina leonina, Crosskey, 1965: 113.

The characters given in the key serve, together, by weight of evidence, to identify all male specimens seen so far; but every character fails very occasionally. I have three males (from near Cooktown) that have a small, but distinct pair of submedian marginal bristles on abdominal T3; another three have the parafrenal bristles long and with bent apices; another has the postorbital partly obliterated; and, as shown in Part 1, four others have the broad head typical of *A. albomaculata*. Also, the appressed setulae on

the central third or so of abdominal T3, although almost always evident, were in a few specimens not clearly developed. Nonetheless, in every case the characters jointly gave a convincing identification. The rather greenish hue of the thorax and (sometimes) the abdomen is also of some use. Of other attributes listed by Crosskey (1965), I find that the ocellar setae are by no means “weak”, but usually just as strong as in *A. albomaculata*.

I have examined the specimens of *A. leonina* from Sydney, listed by Crosskey (1965), and can confirm that they are quite definitely of this species.

Distribution (Fig. 8). Largely coastal, from the Kimberleys east to the Queensland-New South Wales border; replaced in New South Wales by *A. albomaculata*, except for one known occurrence in the vicinity of Sydney; then reappearing in central Victoria and the eastern part of South Australia (including Kangaroo Island). The reason(s) for this peculiar distribution remain obscure.

Notes. One of the specimens from South Australia was reared from a “caenenid” snail (sic; ?camaenid).

***Amenia albomaculata* (Macquart) rev.stat.**

Amenia leonina albomaculata, Crosskey, 1965: 115.

There is no difficulty in identifying the species, using the combination of characters given in the key. The submedian bristles on abdominal T3 alone serve for all specimens of *A. albomaculata* seen to date. Of the remaining male attributes, the semi-erect setulae on T3 (Fig. 25) are also reliable, as are the others if the “New England” form (see below) is excluded. Also of some use is the not infrequent reduction or absence of the presutural silvery patch (on the suture, mesad of the presutural bristle), which seems usually present in *leonina*.

I have three enigmatic males from the vicinity of Brisbane that resemble the “New England” form (see below) in having the parafrenal setae as in *leonina*, but the postorbital setae are intermediate between that form and the typical one. Their status remains unclear.

Geographic forms.

Two geographically circumscribed forms were first noticed during the morphometric analyses, by virtue of their relatively broad frons (Fig. 9, p. 94). Fuller study revealed other distinctive attributes.

(a) “New England” form.

This form is represented by 16 male specimens from the New England area, above 1,000 metres. As shown in Fig. 9, the relative frons width, although distinctive, does not completely separate them from typical specimens. However, all have unmodified, pollinose postorbital setae (and hence relatively narrow heads; see Fig. 9); 14 have the parafrenal setulae short and straight; and two have the setulae of abdominal T3 somewhat appressed; i.e., in these attributes they resemble *A. leonina* rather than *A.*

albomaculata. Only one male from that area (from two taken together in New England NP) clearly belonged to the typical form. There are 13 associated females that presumably belong to this form, but cannot be differentiated from the typical one on female attributes.

It seems probable that we have here a population conditioned by adaptation to a different host that frequents higher altitudes. However, its taxonomic status remains unclear.

(b) “Southern” form

This form comprises six males and 11 females from the western shore of Spencer Gulf, South Australia (mostly from the tip of Eyre Peninsula). Two females from Albany, Western Australia, could be included here also. The males are moderately distinct in having the frons relatively wide (Fig. 9, p. 94), and both sexes have the dorsal thorax rather dull and blue-black, rather than the brighter, metallic blue of the typical form. This colour difference is most clearly seen with the naked eye. Also, two females and two males were unusual in having 1–2 discal bristles on abdominal T3.

Considering the isolation of this form from the typical one (Fig. 8), it is perhaps surprising that so little morphological differentiation has occurred. There is certainly insufficient to consider specific status.

Distribution (Fig. 8). Queensland (mainly in the extreme south), New South Wales, and eastern Victoria; reappearing as the “Southern” form in South Australia, west of Spencer Gulf, and at Albany, Western Australia. Not so markedly confined to the coast and adjacent mountains as *leonina*, and extending well inland in the 3 eastern states.

***Amenia longicornis* (Malloch)**

As shown in Part 1, the species comprises two fairly distinct geographic forms: an eastern one, found around the head of Spencer Gulf and north through the Flinders Ranges to the MacDonnell ranges of the Northern Territory, and a western one in places west of about 135° longitude. Although qualifying as geographic subspecies, I see no point in naming them formally.

Two specimens from the Flinders Ranges were reared from snails of the species *Sinumelon hawkerana* Solem (Camaenidae) (near Jonburgh, South Australia, M. Newton, 27 May 1992)

***Amenia sexpunctata* Malloch**

The currently known range of this species (Fig. 10) extends from the general vicinity of Darwin, through Arnhem Land (including the Cobourg Peninsula) and the McArthur River coast, to Cape York Peninsula (vicinity of Weipa and Iron Range). Crosskey doubted its occurrence in North Queensland, due to Paramonov’s (1957) somewhat misleading description of a specimen that had the (eye) “facets very enlarged”. This is in fact true of all males of the species, in that facet size gradually increases from the ventral and posterior margins to the forward-looking area near the middle of the frons; the latter facets are about three times as broad as

the former. However, this hardly differs from the general condition in ameniines, in which the increase is about two times—a figure, moreover, that seems to correlate roughly with size. *Amenia sexpunctata* is one of the largest of the ameniines. Its size, plus its very dark colour and the paired pale spots on abdominal T3, T4, and T5 make it easily recognisable with the naked eye.

***Amenia nigromaculata* Malloch**

Formosiomima nigromaculata Crosskey, 1965: 124.

The species has a largely coastal distribution in southwestern Australia, from Exmouth Gulf in the north and eastwards along the Great Australian Bight as far as Yalata in South Australia (Fig. 10). Although overlapping broadly with *A. longicornis*, it occurs alone along the western and southwestern coasts of Western Australia. This is no doubt correlated in some fashion with the biology of the host-snails, which are species of *Bothriembryon* (Orthalicidae): *B. balteolus* Iredale, *B. bulla* Menke and *B. glauerti* Iredale (Ferrari, 1976).

The phylogenetic evidence in Part 3 (Figs 20–22) suggests that *A. nigromaculata* is the sister species of *A. chrysame*. This is consistent with their complementary distributions in areas that differ markedly in rainfall. Separate generic status for the former species would therefore be quite inappropriate, despite its conspicuously different colour pattern. This is not accompanied by any significant structural differences, and is presumably due to a long period of isolation in southwestern Australia in a different host snail (I am indebted to a referee for the information that *A. chrysame* lives largely (?entirely) outside the range of *Bothriembryon*).

Tribe Parameniini

I am including in this tribe the mainly Oriental genus *Catapicephala*, which was added to the subfamily by Kurahashi (1989), but placed in its own, monotypic tribe

(he also adds West Irian to the range of *C. splendens*). I do this on good phenetic grounds. Examination of a specimen of each sex of *C. splendens* Macquart and a female of the type species, *C. ingens* (Walker), shows that they closely resemble *Paramenia* spp. in the relatively large size, the rather distinctive coloration, the absence of the facial carina and apical *pv* spine on the hind tibia, and the presence of a posthumeral bristle set in front of or a little externally to the presutural bristle. These attributes are probably all plesiomorphic, and the tribe may well be paraphyletic; but that is a small price to pay for a more balanced classification. (A referee has pointed out that, in any case, *Catapicephalini* Kurahashi, 1989 is a *nomen nudum*).

Genus *Paramenia* Brauer & Bergenstamm

The genus, which is confined to Australia and New Guinea, is very distinct: principally in lacking the facial carina, which is well developed in other genera (differences from the non-Australian *Catapicephala* are given in the key to genera). Unlike other ameniines, the prosternal setae may also be reduced or absent, an attribute that was regarded by Crosskey (1965) as of little or no taxonomic use within *Paramenia*. Per contra, I find that there are always at least 2–3 fine hairs present in *P. semiauriceps* (63 specimens) whereas they are almost always lacking (6/7 ♂♂, 9/10 ♀♀) in *Paramenia angustifrons*. I have added this feature to the key below, as well as the difference in relative width of the gena. Crosskey noted the latter feature, but I have used my own system of measurement (see Part 1). I might add that PCA of a set of head dimensions (not shown) clearly separates the two species.

I can add nothing else to Crosskey’s detailed descriptions, beyond noting that both species have a small tuft of setulae on the suprasquamal ridge, as in all the large species of *Amenia* (i.e., excluding *chrysame* and *longicornis*).

Key to Australian species of *Paramenia*

- 1 Males 2
- Females 3
- 2 Eyes almost meeting in midline, frons reduced to a very narrow strip no wider than anterior ocellus. Parafrontals pale yellowish grey or silvery grey pollinosc. Prosternum usually bare *Paramenia angustifrons* Crosskey
- Eyes more widely separated, frons about three times as wide as anterior ocellus. Parafrontals bright yellow pollinose. Prosternum with at least a few fine setae *Paramenia semiauriceps* Brauer & Bergenstamm
- 3 Mid-tibia with at least one weaker, more basal *ad* seta in addition to the submedian one. *Gnw/Hdw* 0.27–0.31, av. 0.30. Prosternum with at least a few fine setae *Paramenia semiauriceps* Brauer & Bergenstamm
- Mid-tibia with one strong isolated submedian *ad* seta. *Gnw/Hdw* 0.22–0.26, av. 0.25. Prosternum usually bare *Paramenia angustifrons* Crosskey

Paramenia semiauriceps Brauer & Bergenstamm

Crosskey (1965) doubtfully assigned to this species a specimen (from Byfield, Queensland) that lacks the second, more basal *ad* bristle on the mid-tibia. I have studied this specimen and find that it clusters clearly with females of *semiauriceps* in a PCA ordination. Apparently the tibial bristling can vary somewhat.

The female from the AM recorded by Ferrar (1976) as reared from *Meridolum gulosum* (Camaenidae) now stands with a labelling correcting that to *M. middenense* McLauchlan.

The distribution is shown in Fig. 27. The range is there provisionally extended to South Australia on the basis of two specimens in the AM labelled (simply) with the name of the state. There are grounds for regarding such records with suspicion, but the implied extension is not unlikely and I am prepared here to accept it.

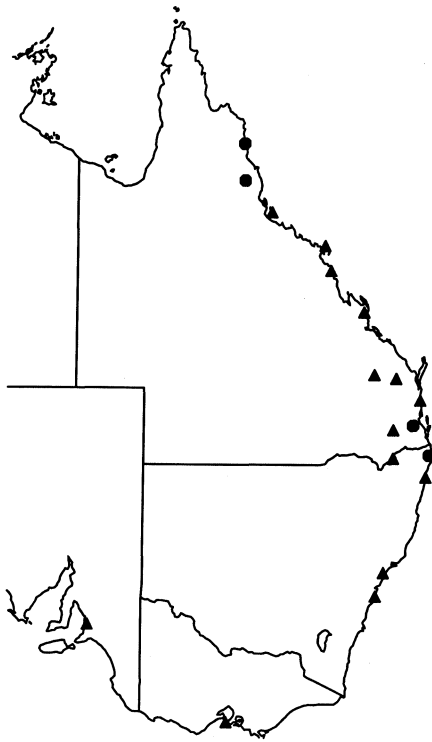


Figure 27. Distributions of *Paramenia* spp.: circles—*angustifrons*; triangles—*semiauriceps*. Records from (simply) “South Australia” are provisional and shown, for want of better, as from Adelaide.

Paramenia angustifrons Crosskey

I have seen two of the the three specimens from Highvale (14 miles NW of Brisbane), Queensland, that Crosskey (1965) thought might represent a new species, largely on the basis of head shape. Using my own system of measurement (which I believe to be more accurate) I find little difference between these specimens and typical *Paramenia angustifrons*, with which they cluster closely in a PCA ordination (not shown).

The range of the species is shown in Fig. 27. It seems restricted to the tropics and subtropics.

PART 3. CLASSIFICATION AND ZOOGEOGRAPHY

I start from the hypothesis that the current classification, as used in Part 2, is reasonable and useful. That is my “positive heuristic” in a Lakatosian “research programme” (Lakatos & Musgrave, 1970). The classification is then compared with the phenetic structure found by numerical studies of a substantial set of characters, in the belief that the degree of such consistency is a measure of the utility of a classification. I also believe that phenetic structure provides a useful hypothesis of phylogenetic structure (Colless, 1970; Saitou & Nei, 1987; Avise, 1994—the last *teste* Wallman & Adams, 1997), which may help illuminate the zoogeography of the group. This is especially true of the Neighbour-Joining algorithm, which, despite its phenetic flavour, was explicitly devised to reveal phylogenetic structure (Saitou & Nei, 1987).

Numerical studies

Phenetic structures were examined using a set of 26 species (listed at Fig. 28) and 54 morphological characters (see Appendix). For the geographically variable *Amenia dubitalis* and *A. chrysame*, the northern and southern forms respectively were employed. The New Guinean *Stilbomyella nigrocostalis* and *S. nitens* were included for comparison with the two Australian species. Also, a female of the Indonesian *Silbomyia mackerrasi* Crosskey was included to fill out that genus, otherwise represented by just four specimens of the two Australian species. For phylogenetic purposes, two related species were also included: *Phumosia surcoufi* (Bezzi) and *Euphumosia papua* (Guérin-Méneville). These were chosen on the criterion of maximum applicability of the characters employed for the study group. The character matrix is shown in Table 5.

Because of variation within species, many entries in the matrix represent the *usual* condition as observed over a representative set of specimens. Likewise, some entries were rather arbitrary, due to my inability to draw sharper boundaries between states. The data proved robust under the test of comparing results using odd-numbered characters only, and then even-numbered characters only, with each other and with results for the whole set. This was done using Manhattan distances from range-coded data, sorted by UPGMA and Neighbour-Joining algorithms. Trees were compared by counting shared components (subtrees). The percentages shared were as follows:

Neighbour-Joining: complete set vs even—70, complete vs odd—74, even vs odd—56.

UPGMA: complete set vs even—60, complete vs odd—76, even vs odd—68.

All genera and species-groups recognised in Part 2 above remained practically intact using both reduced sets of data. Changes consisted mainly in rearrangements within genera.

After some preliminary tests of ordinations, phenetic structure seemed most succinctly displayed by the Minimum Spanning Tree (Fig. 28), in which all genera and species groups recognised in Part 2 are clearly clustered. For *Stilbomyella anomala* and *Paraplattytropesa*

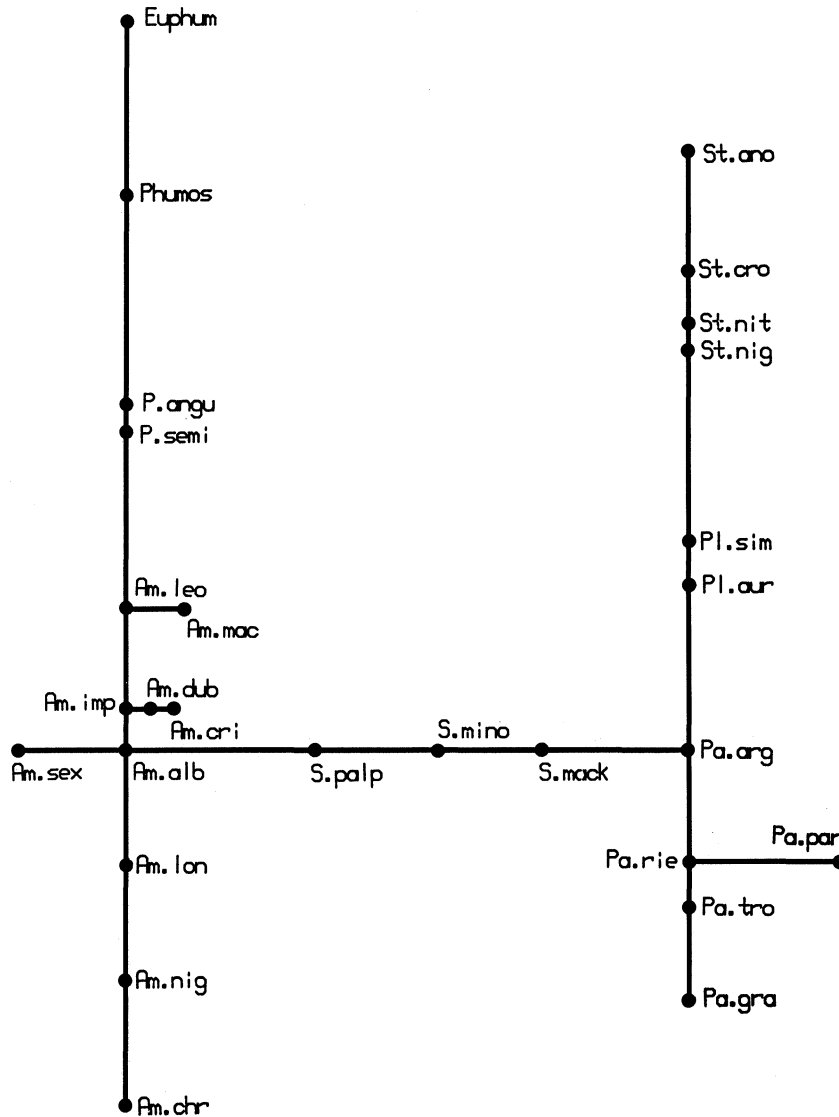


Figure 28. Minimum spanning tree on 26 Ameniini and 2 outgroups; Manhattan distances, to scale. Species codes: Euphum—*Euphumosia papua*; Phumos—*Phumosia surcoufi*; P. angu—*Paramenia angustifrons*; P. semi—*Paramenia semiauriceps*; Am. leo—*Amenia leonina*; Am. mac—*Amenia albomaculata*; Am. imp—*Amenia imperialis*; Am. dub—*Amenia dubitalis*; Am. cri—*Amenia crinita*; Am. sex—*Amenia sexpunctata*; Am. alb—*Amenia albosquamata*; Am. lon—*Amenia longicornis*; Am. nig—*Amenia nigromaculata*; Am. chr—*Amenia chrysame*; S. palp—*Silbomyia palpalis*; S. mino—*Silbomyia minor*; S. mack—*Silbomyia mackerrasi*; Pa. arg—*Paraplatytropesa argentea*; Pa. rie—*Paraplatytropesa rieki*; Pa. par—*Paraplatytropesa parvifrons*; Pa. tro—*Paraplatytropesa tropicalis*; Pa. gra—*Paraplatytropesa grandicornis*; Pl. aur—*Platydropesa auriceps*; Pl. sim—*Platydropesa simulans*; St. nig—*Stilbomyella gloriosa*; St. nit—*Stilbomyella nitens*; St. cro—*Stilbomyella crosskeyi*; St. ano—*Stilbomyella anomala*.

argentea this agreement is gratuitous, since their generic positions were finally decided on phenetic grounds. However, all other detail was derived from the the current classification plus my recent additions.

The phenograms yield a similar result. I computed a set of 10 (Nearest Neighbour, Furthest Neighbour, UPGMA, WPGMA, Lance & Williams Flexible [3], Incremental Sums of Squares [3]) with varying intensities of clustering. Then, following a criterion mentioned in Colless (1994: 521), I chose the one with the least variability in internode length: Furthest Neighbour (Coefficient of Variation = 0.696). This

is shown as Fig. 29, p. 115. That for UPGMA was a close runner-up (C. of V. = 0.716), differing in only 1 component (*A. sexpunctata* shifts position). Again, the classification in Part 2 is well supported. [The criterion just mentioned—C. of V. of internode length—is a measure of what has been called “stemminess” by Fiala & Sokal (1985), and correlates highly with their coefficient].

The Neighbour-Joining algorithm yielded the dendrogram shown in Fig. 30. Rooted by the two outgroups, *Phumosia surcoufi* and *E. papua*, it closely resembles the others; ignoring the outgroups, 75% of its components are shared

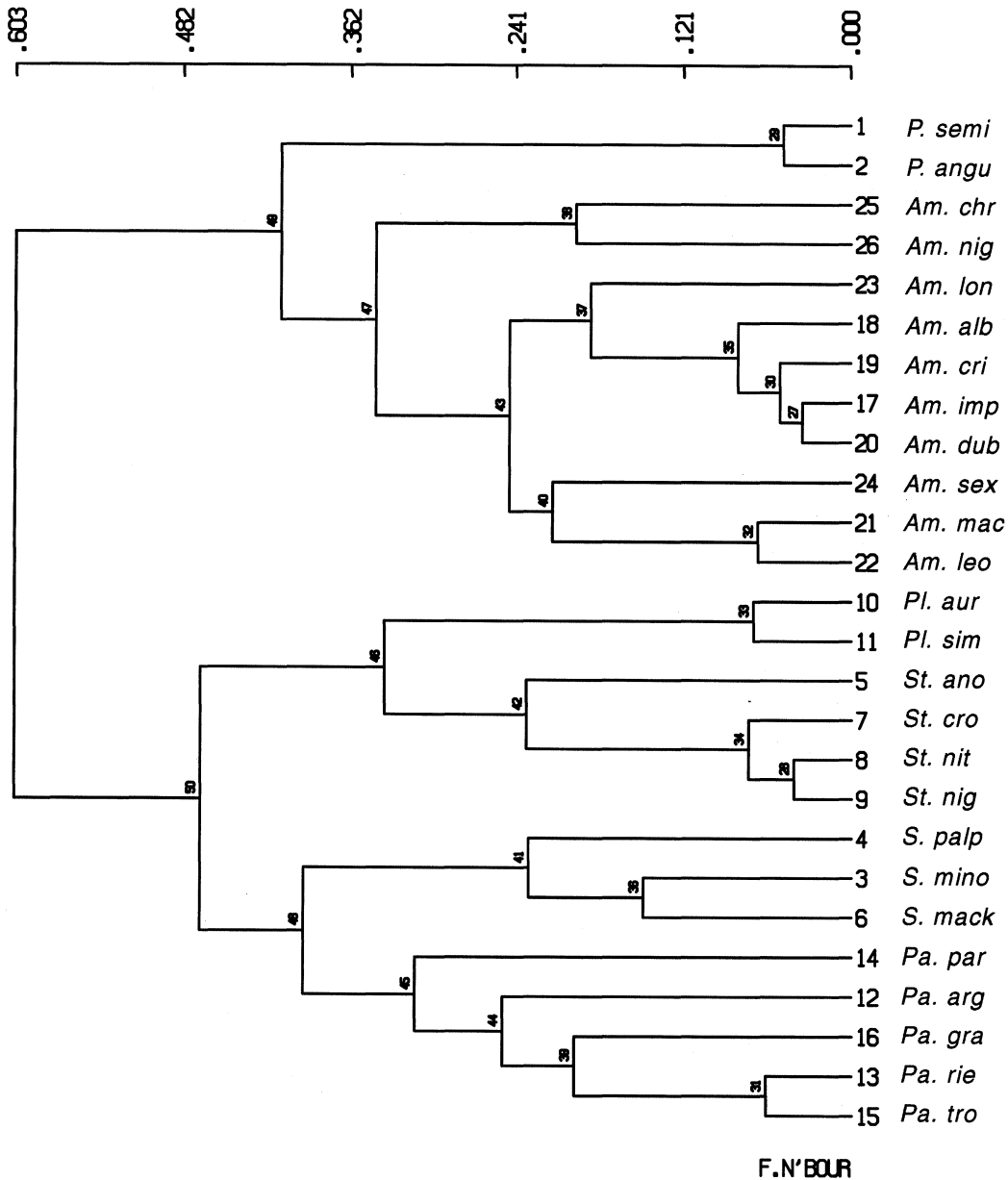


Figure 29. Phenogram for 26 Ameniini; Manhattan distances and furthest neighbour. Codes as in Fig. 18.

with the Furthest Neighbour phenogram. The only major difference lies in the placement of the "primitive" *Paramenia* with *Amenia* in Fig. 29, p. 115, which is explicable as a result of symplesiomorphy. There are grounds, therefore, for accepting the broad details of Fig. 30 as faithfully reflecting the phylogeny of the subfamily.

I conclude that the classification used in Part 2 is in fact a reasonable one: especially as regards the generic placement of *A. nigromaculata*, *St. anomala*, and *Paraplattropesa argentea*. The tribal status of *Paramenia* also seems reasonable. However, it is clear that *Amenia* could itself constitute a tribe of its own, with *Silbomyia*, *Plattropesa*, *Stilbomyella*, and *Paraplattropesa* forming another tribe. Indeed, the phenogram (Fig. 29, p. 115) would argue strongly for such a course. I have, nonetheless, refrained from adopting this formally, because it does

smack of classificatory overkill, and because the new taxon names would have to be defined by complex, polythetic definitions. They would, in my view, serve little if any purpose.

Zoogeography and evolution

It seems very likely that Ameniinae arrived in Australia as immigrants from islands to the north (Colless & McAlpine, 1991), either at some time when the continent was connected to New Guinea, and/or was only narrowly separated from Timor. Crosskey (1965) suggested that *Silbomyia* entered via the Timor route because the genus is absent from New Guinea and the Moluccas. This was made even more likely by the subsequent discovery of *S.*

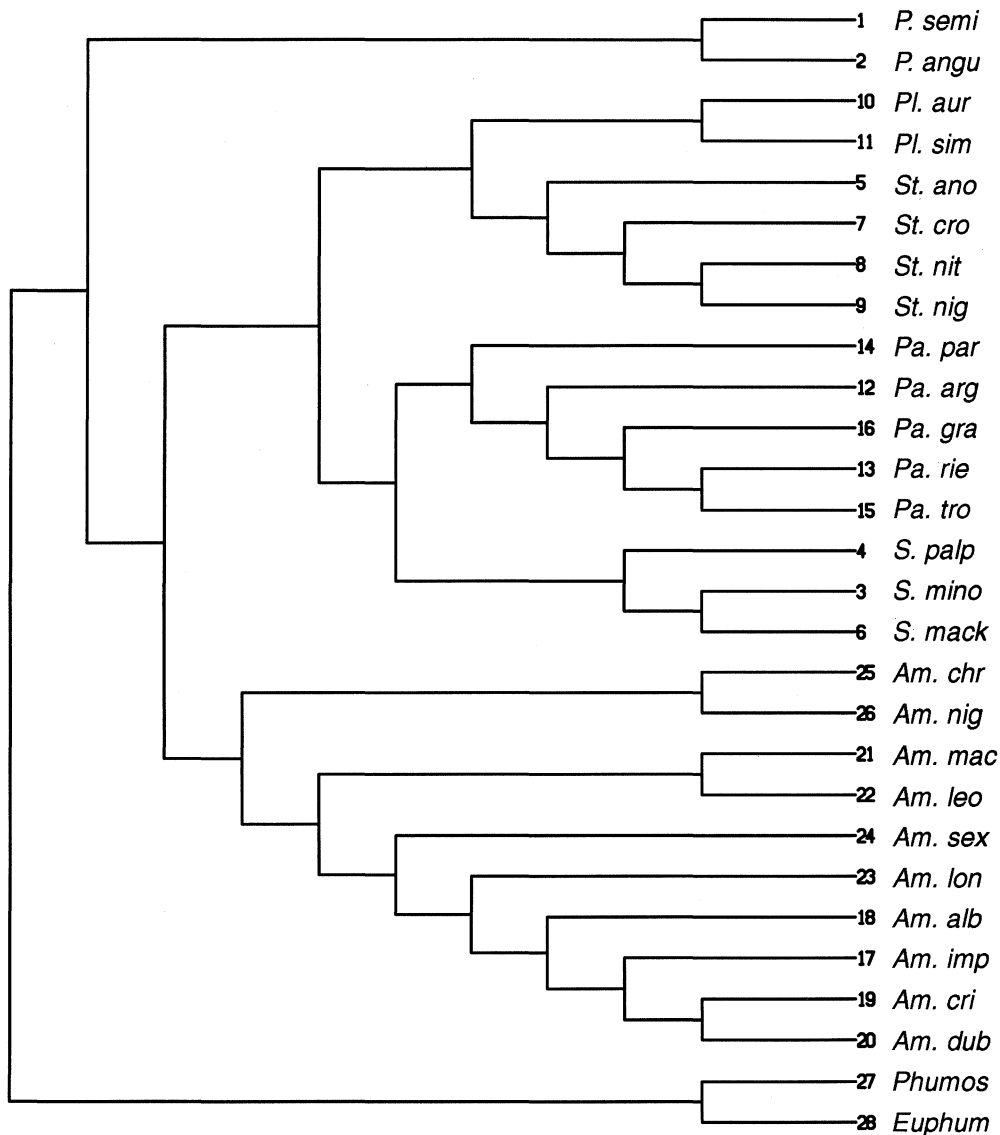


Figure 30. Dendrogram for 26 Ameniini and 2 outgroups; Manhattan distances and neighbour-joining. Codes as in Fig. 18.

palpalis in northwestern Australia. Indeed, the very wide distribution of *Silbomyia*, through India, China, and Southeast Asia makes it a fair candidate to represent the parental stock of the subfamily in Australia. On the other hand, *Platytropesa*, *Stilbomyella*, and *Paramenia*, which are all distributed in Australia, New Guinea and (for the first two) the Moluccas, may well have arrived here from the north. Alternatively, they may have actually originated in Australia and made their way back to New Guinea and islands to the west.

Little of the foregoing is supported by phylogenetic evidence, and it takes no account of the somewhat enigmatic *Catapicephala* (see above). That genus, widely distributed in the Oriental Region (Malaysia, Indonesia, and Taiwan; Senior White *et al.*, 1940), shows distinct resemblances to *Paramenia*, but the attributes concerned are very probably plesiomorphic and do not necessarily

argue for close phylogenetic relationship. Nonetheless, these two are clearly “primitive” genera, and the position of *Paramenia* in Fig. 30 suggests that it, rather than *Silbomyia*, represents the ancestral stock. Its distribution overlaps only slightly with that of *Catapicephala* (*C. ingens*, in western New Guinea), and the Australian ameniines might well have originated in a vicariance event that yielded *Catapicephala* in the Moluccas and *Paramenia* in New Guinea. The latter then entered Australia via Cape York (statements concerning the “evolution”, “migration”, etc., of a genus are, of course, to be construed as referring to some ancestral species that we would place in that genus). There is no evidence whether *Stilbomyella* and/or *Platytropesa* differentiated in New Guinea and migrated into Australia or vice versa; but it does seem plausible that *Silbomyia* evolved on the mainland, along with its sister-group, *Paraplatytropesa*. This would imply that

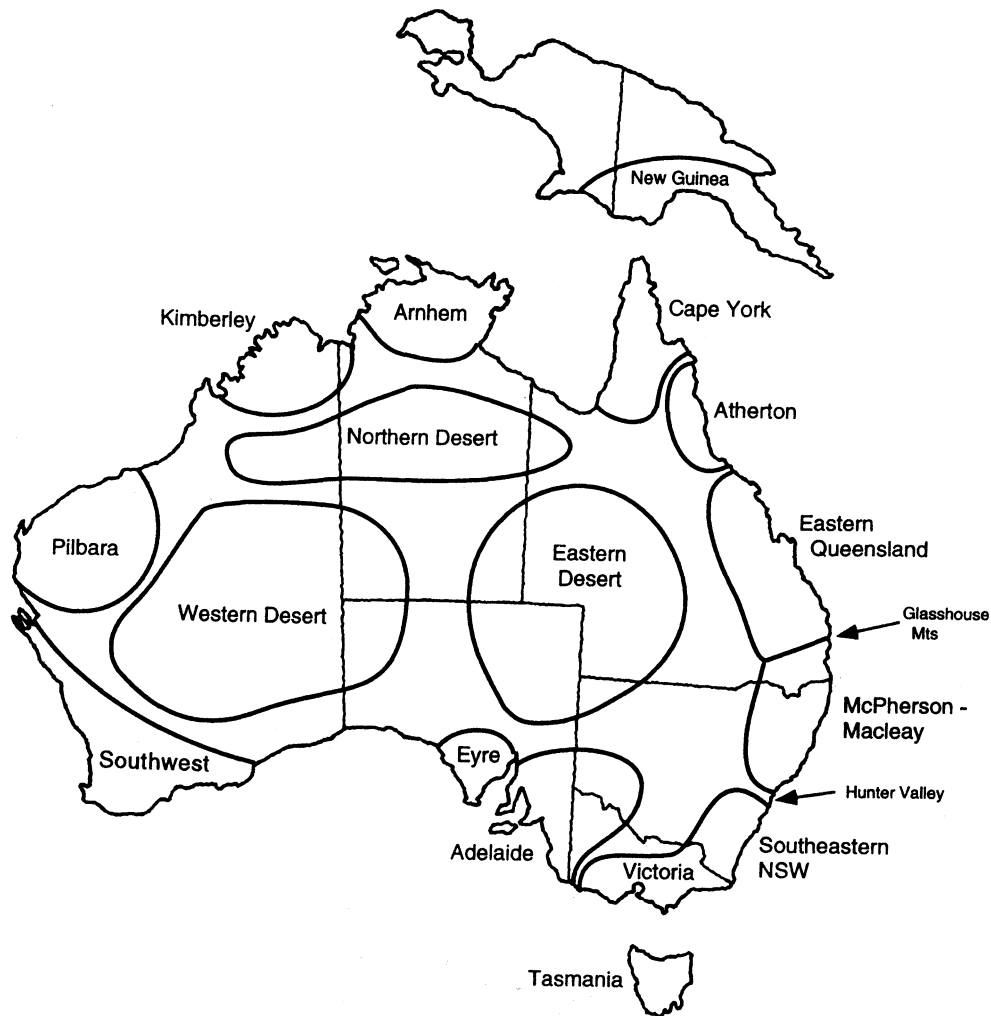


Figure 31. Map of Australia and New Guinea showing “provinces” used in this study (from Crisp *et al.*, 1995).

Silbomyia then back-migrated into Asia via Timor. Alternatively (and more parsimoniously), *Silbomyia* may have originated in Asia and entered Australia independently from the northwest, as in Crosskey’s scenario. I see little hope of a decision on these matters.

The foregoing speculations aside, there remains a body of reasonable evidence supporting the holophyly of all recognised genera, as attested by all methods of analysis. Of relationships within genera, the *imperialis* and *leonina* species groups, within *Amenia*, are credibly holophyletic—scarcely surprising, their members are separable only with careful examination! The grouping of *A. longicornis*, *A. nigromaculata*, and *A. chrysame* also seems credible. As mentioned in Part 2, *A. nigromaculata* is credibly the sister species of *A. chrysame*, on grounds of morphology and distribution; likewise, *A. longicornis* is credibly an earlier migrant to southwestern Australia, and sister species to *A. nigromaculata* + *chrysame*. *Amenia albosquamata* appears to be the sister species to the rest of the *imperialis* group—presumably a western vicariant, but other relationships within the group seem hopelessly obscure. Of others, *A. leonina* is clearly sister to *A. albomaculata*, presumably as north-south vicariants; but the picture is clouded by the

(?)relict populations found in South and Western Australia, which suggest a very complex, but currently unguessable history. Finally, in *Stilbomyella*, *S. anomala* is credibly sister to the rest of the genus, as is *S. crosskeyi* to one or both of the New Guinean vicariants, *S. gloriosa* and *S. nitens*. Of *Amenia*, one can only presume that it evolved from a very early migrant from the north, rapidly differentiating to colonise the whole continent. It is a fair speculation that such a process would have been greatly assisted, even accelerated, by access to an untouched field of host snails.

Turning to distributions, which are now tolerably well known, all ameniines show distinctive ranges that no doubt reflect the history of their dispersal and vicariant evolution. However, we face at the outset the problem that probably all are parasites of land snails and that their distributions will be to an unknown degree influenced by those of their hosts; and no doubt there will have been some coevolution and and/or opportunistic switching of hosts in allopatric populations. But we know so little at present of the actual hosts of ameniine species that, even if the snail phylogeny were credibly established, it would provide little input to zoogeographic studies.

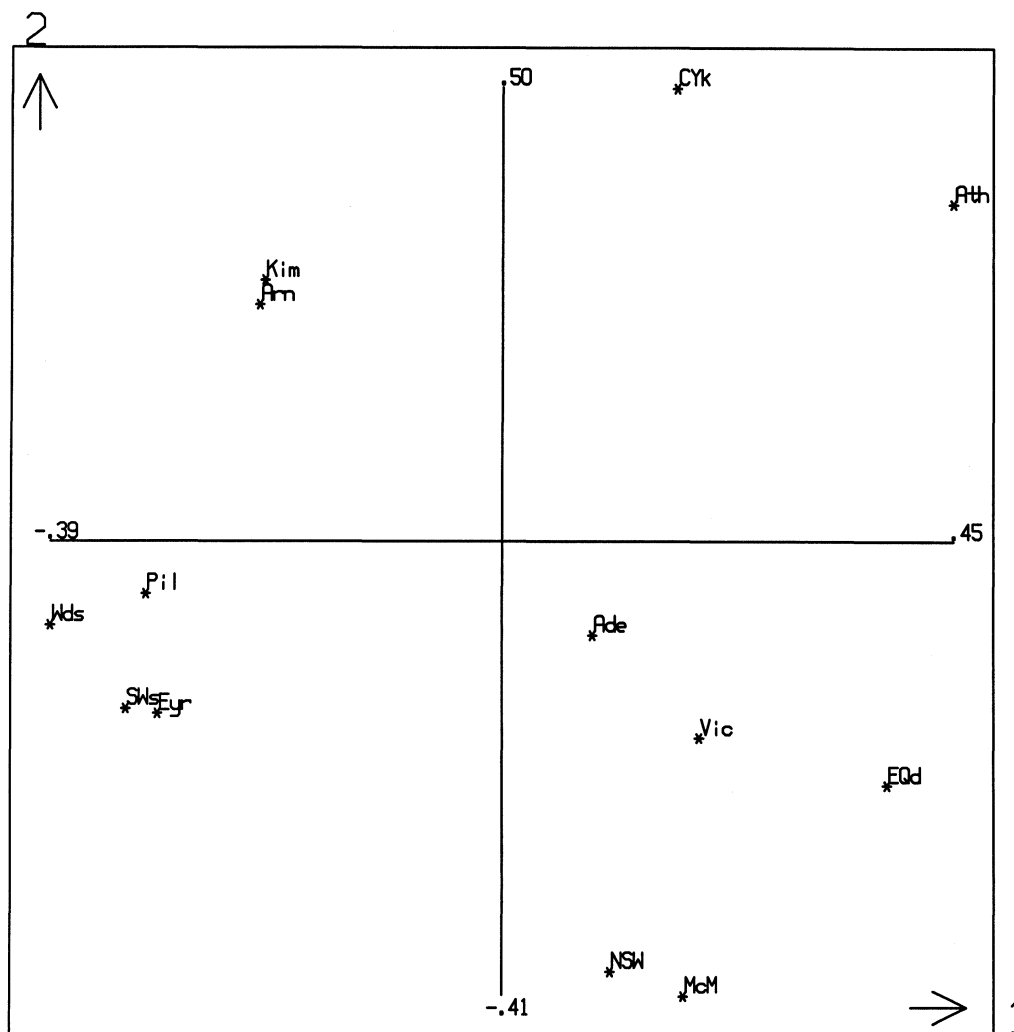


Figure 32. Ordination of provinces on PCA axes 1 and 2 from data in Table 4. Province codes as in Table 4.

Despite these problems, interesting results have been obtained by a purely phenetic analysis of the distributions of Australian ameniines. The starting point was the division of the continent into suitable provinces. For this I chose the recent scheme of Crisp *et al.* (1995), shown in Fig. 31, which incorporates those of earlier botanists, including the classical scheme of Burbidge (1960). It also closely resembles my own scheme (Colless, 1980), based on distributions of Australian Sepsidae (Diptera), and that of Cracraft (1991), based on avian distributions. Due to lack of records from the Northern Desert and Eastern Desert provinces of Crisp *et al.*, those provinces were omitted in the analysis that follows. New Guinea was not considered further, but its close relationship to the Cape York province is demonstrated by the sharing of the genera *Stilbomyella* and *Paramenia* and two species of *Platytropesa*.

Table 4 shows the distributions of ameniine species over these provinces. Seven species were omitted because they are known from only one province and therefore provide little information, as well as causing numerous embarrassing ties in the phenetic analyses. These "presence-absence"

data were subjected to a principal component analysis, which provided the ordination shown in Fig. 32. As shown there, component I crisply divides the continent east-west, along about longitude 138°E; component II likewise divides it north-south along about latitude 20°S. These relationships are also found by computing Manhattan distances between provinces, and from these a minimum spanning tree (Fig. 33). I should stress that these computations treat absence of a species as just as significant as presence (a point hotly contested in various contexts, and one I have no intention of arguing here). The point remains: granting the validity of the results, about which I have no qualms, how are they to be explained?

For a start, there is considerable agreement with the results of Crisp *et al.* (1995), which were based on congruence of cladograms for a number of plant genera. My Figs 32 and 33 show groupings of Southwest + Western Desert, Kimberley + Arnhem, Southeast NSW + McPherson-Macleay, and one of all the eastern and southeastern areas, from Adelaide to Atherton. These all appear in Crisp *et al.* (1995) figure 2 (which omits Eyre

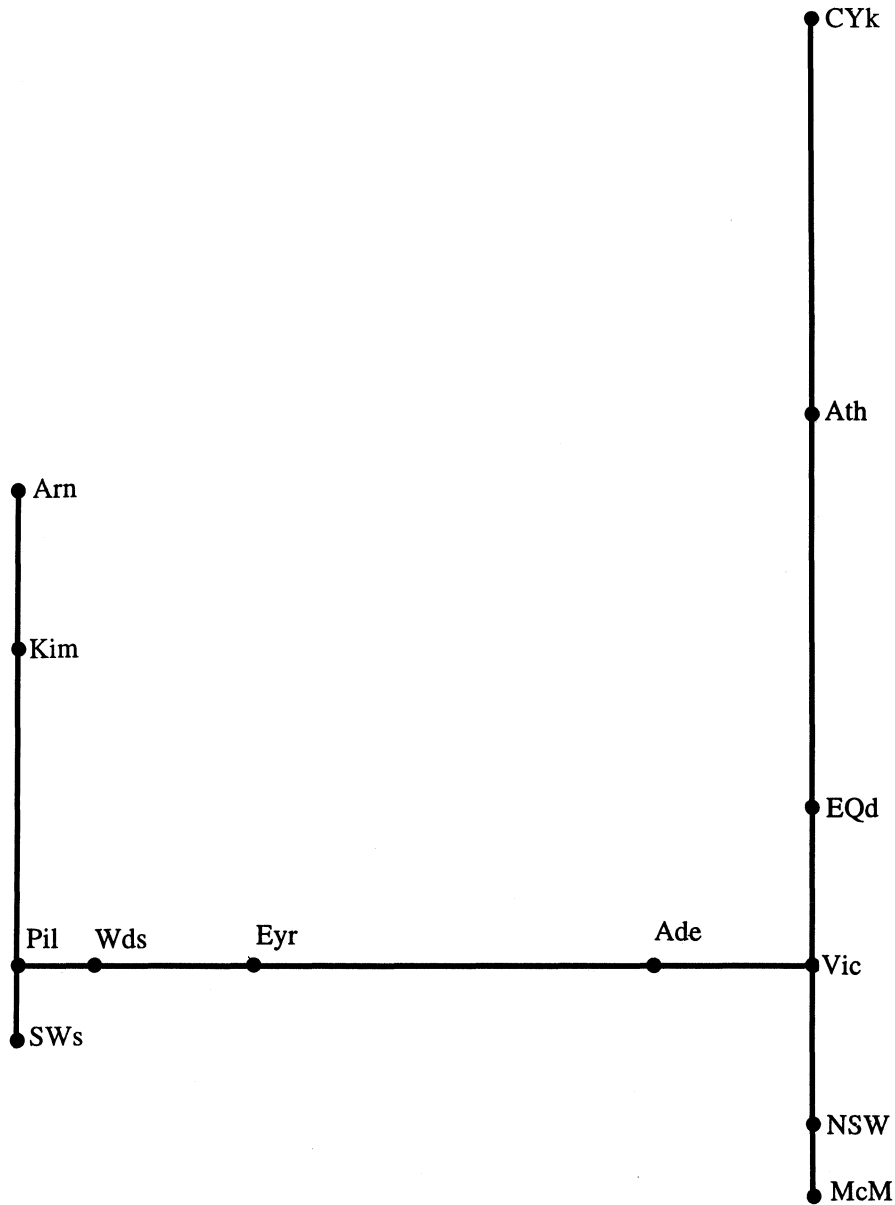


Figure 33. Minimum spanning tree from data in Table 4. Province codes as in Table 4. Arn and Kim are interchangeable due to a tie in distances.

and Pilbara). The notable difference is their grouping of Cape York with Arnhem and Kimberley, rather than Atherton; but my results do agree with those of Ovenden *et al.* (1987) for the bird genus *Platycercus*, which link Cape York with Atherton. The same can also be seen in the results of Cracraft (1982) for a number of bird genera. It is clear, then that ameniines generally have followed an ancient pattern of dispersal that occurs widely in both plants and animals.

It is also clear from (especially) the ordination (Fig. 32) that the overall pattern is primarily geographic: excluding points NSW and McM, the envelope of the remaining points is a tolerable, albeit distorted, map of the Australian coastline! That is, species are shared between provinces to a considerable extent because of simple,

geographic propinquity. This is scarcely surprising, but the very obvious distortions must then be explained some other way. For instance, the wide gap between Pilbara and Arnhem provinces seems to reflect the strong barrier to dispersal raised by the Great Sandy Desert—perhaps not just to dispersal of the flies themselves, but also of appropriate snail hosts. On the other hand, the large gap between Atherton and East Queensland provinces seems, on examination of records, largely due to the failure of New Guinea-linked species of *Platyropesa* (perhaps late arrivals) to penetrate southward, and of *Amenia dubia* to advance northward. The latter may represent a lingering trace of a vicariance barrier between *A. dubia* and the closely related *A. imperialis*. Likewise, the anomalous position of NSW and McM provinces is due largely to the

Table 4. Distribution of selected ameniine species over provinces shown on Fig. 31. **ADE**—Adelaide; **ARN**—Arnhem; **ATH**—Atherton; **CYK**—Cape York; **EQD**—Eastern Queensland; **EYR**—Eyre; **KIM**—Kimberley; **MMO**—McLeay-McPherson; **NSW**—Southeastern NSW; **PIL**—Pilbara; **VIC**—Victoria; **WDS**—Western Desert. Species codes as for Fig. 28.

Species	Province												
	KIM	ARN	CYK	SWS	PIL	WDS	EYR	ATH	EQD	ADE	VIC	NSW	MMO
<i>P. semi</i>	—	—	—	—	—	—	—	•	•	•	•	•	•
<i>P. angu</i>	—	—	—	—	—	—	—	•	•	—	—	—	•
<i>St. cro</i>	—	—	—	—	—	—	—	•	•	—	—	—	—
<i>Pl. aur</i>	—	—	•	—	—	—	—	•	—	—	—	—	—
<i>Pa. arg</i>	—	—	•	—	—	—	—	•	—	—	—	—	—
<i>Pa. tro</i>	•	—	—	—	—	—	—	•	—	—	—	—	—
<i>Am. imp</i>	—	—	•	—	—	—	—	•	•	•	•	•	•
<i>Am. alb</i>	•	•	—	—	—	—	—	—	—	—	—	—	—
<i>Am. cri</i>	—	—	•	—	—	—	—	•	—	—	—	—	—
<i>Am. dub</i>	—	—	—	—	—	—	—	—	•	—	•	•	•
<i>Am. mac</i>	—	—	—	•	—	—	•	—	—	—	—	•	•
<i>Am. leo</i>	•	•	•	—	—	—	—	•	•	•	•	—	—
<i>Am. lon</i>	—	—	—	—	—	•	•	—	—	•	—	—	—
<i>Am. sex</i>	—	•	•	—	—	—	—	—	—	—	—	—	—
<i>Am. chr</i>	—	—	•	—	—	—	—	•	•	•	•	•	•
<i>Am. nig</i>	—	—	—	•	•	•	—	—	—	—	—	—	—

well-known zoogeographic discontinuity in southeastern Queensland (Colless, 1994: 526) that separates the sister species *A. leonis* and *A. albomaculata* (and the morphometric forms of *A. chrysame* and *A. dubitalis*, noted in Part 1); also to the failure of *Stilbomyella crosskeyi*, with sister species in New Guinea, to penetrate further south. Finally, the gap between Adelaide and Eyre provinces seems mainly due to the failure of “eastern” species, such as *A. imperialis* and *A. chrysame* to disperse further westwards.

One final point: the weight of evidence seems to point overwhelmingly to the dispersal of *Amenia* spp., perhaps from Arnhem Land, or at least from Cape York, in a clockwise fashion around Australia. Not a single species is shared between the Pilbara and the Kimberleys, although

the occurrence in the former of *Silbomyia palpalis* may represent a unique crossing of the Great Sandy Desert by the stock of the putative *Silbomyia*-like ancestor, now extinct in the area from which it entered Asia (or Australia!). Penetration of the interior seems to have been slight, involving only the northward extension of *A. longicornis* (Eastern form) and the southward extension of *Paraplatytropesa* (*P. parvifrons*), which meet in the vicinity of Alice Springs,

I have merely sketched some possibilities with respect to these intriguing patterns. There is a clear need for more rigorous investigation, including mathematical modelling of possible mechanisms. It does seem, however, that both dispersal and vicariant speciation have played a role in the distribution of *Ameniinae* in Australia.

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Appendix

Details of the 54 characters and their observed states, as used in numerical analyses, are given below and the character matrix is shown in Table 5. Characters nos. 4, 5, 6, 20, 53, and 54 are unordered; others are considered to be linearly ordered but not polarised; i.e., the numerical codings do not imply plesiomorphy or otherwise in the states coded (see also comments in text).

- 1 Ratio of head width to frons width, male: 1 = 3–5; 2 = 10–20; 3 = >20.
- 2 Apex of arista, male, reaching to: 0 = short of apex of A3; 1 = about level with apex of A3; 2 = a little past apex of A3; 3 = well past apex of A3.
- 3 Carina, separation from epistoma: 0 = none; 1 = slight; 2 = conspicuous.
- 4 Anterior surface of carina: 0 = more or less flattened; 1 = rounded; 2 = sharp.
- 5 Ventral half of carina, male (if flattened, refers to pollinose, flattened surface): 0 = more or less parallel-sided; 1 = tapering dorsad; 2 = tapering ventrad.
- 6 As for 5, female.
- 7 Protrusion of carina in lateral view, male: 1 = at most very slight; 2 = moderate; 3 = conspicuous.
- 8 As for 7, female.
- 9 Orbital bristles, male: 0 = absent; 1 = present.
- 10 As for 9, female.
- 11 Prevertical bristle, male: 0 = absent; 1 = present.
- 12 Inner vertical bristles, female: 0 = more or less parallel; 1 = inclinate; 2 = decussate.
- 13 Outer vertical bristles, male: 0 = not developed; 1 = much shorter than inner; 2 = a little shorter than inner;
- 14 As for 13, female.
- 15 Ocellar bristles, male: 0 = not developed or exceedingly small; 1 = small to moderate; 2 = strong.
- 16 As for 15, female.
- 17 Extent of setulae on facial ridge, male: 0 = close to vibrissa only; 1 = up to 1/4 of ridge; 2 = about 1/2 of ridge; 3 = over 1/2 of the ridge.
- 18 As for 17, female.
- 19 Insertion of vibrissa with respect to margin of epistoma: 0 = about level; 1 = a little above; 2 = well above; 3 = far above.
- 20 Eye margins in facial view, female: 1 = more or less regularly diverging; 2 = more or less parallel; 3 = parallel along frons, then diverging.
- 21 Gular region: 0 = normal; 2 = slightly swollen; 3 = markedly swollen.
- 22 Hairs of dorsal occiput: 1 = pale; 2 = dark.
- 23 Hairs on gena: 1 = pale; 2 = dark.
- 24 Dorsal postorbital strip, male: 0 = normal; 1 = reduced but not obliterated; 2 = median part obliterated.
- 25 Humeral, notopleural, and subalar pale spots on thorax: 0 = absent; 1 = present.
- 26 Prealar pale spot on thorax: 0 = absent; 1 = present.
- 27 Presutural dorsocentral pale stripes on thorax: 0 = absent; 1 = present.
- 28 Broad pale sheen over presutural area of thorax: 0 = absent; 1 = present.
- 29 Notopleural setulae: 0 = few, confined to around bases of bristles; 1 = extending a little on to disc; 2 = extending broadly across disc.
- 30 Posthumeral bristle: 0 = absent; 1 = present.
- 31 Posthumeral bristle with respect to presutural bristle: 0 = laterad or more or less level; 1 = distinctly mesad.
- 32 Number of scutellar marginal bristles: 1 = 6; 2 = 8; 3 = >8.
- 33 Subscutellar setulae: 0 = confined to lateral margin; 1 = extending to a point short of second-last marginal bristle; 2 = extending to or a little past second-last marginal bristle; 3 = forming a complete band.
- 34 Suprasquamal ridge: 1 = bare; 2 = with small tuft of setulae adjacent to scutellum.
- 35 Propleuron: 0 = bare; 1 = setulose.
- 36 Posterdorsal strip of hind coxa: 0 = bare; 1 = with a few setulae; 2 = strongly setulose.
- 37 Fore tibia, *pd* setae: 0 = absent; 1 = present.
- 38 Mid tibia, number of *ad* setae: 1 = 1–2; 2 = 2–3; 3 = 3–4; 4 = 4 or more.
- 39 Mid tibia, number of *pd* setae: 1 = 1; 2 = >1.
- 40 Hind tibia, apical *pv* seta: 0 = absent; 1 = present.
- 41 Wing, ventral surface of 3rd costal sector: 0 = bare; 1 = setulose.
- 42 Costa of male wing: 0 = normal; 1 = conspicuously bowed anteriorly.
- 43 Distance from bend of vein M to crossvein i-m as compared with distance of bend to wing margin: 0 = greater; 1 = about equal; 2 = less.
- 44 Crossvein r-m: 0 = before middle of discal cell; 1 = at middle of cell.
- 45 Setulae at base of vein R₃₊₄: 0 = few only, confined to thickened boss; 1 = extending up to 1/4 distance to crossvein r-m; 2 = extending more than 1/4 distance to r-m.
- 46 Posterior margin of lower calypter: 0 = rounded; 1 = more or less straight but internal angle not produced; 2 = internal angle produced to fit beneath suprasquamal ridge.
- 47 Submedian marginal bristles on abdominal T3, male: 0 = none; 1 = 1 pair; 2 = usually with 4 or more.
- 48 As for 47, female.
- 49 Dorsal marginal bristles on abdominal T4: 1 = up to 10; 2 = usually >10.
- 50 Pale lateral spots on abdominal T3: 0 = none; 1 = very small; 2 = moderate but confined to lateral area; 3 = extending on to dorsum; 4 = forming a complete dorsal band.
- 51 Pale submedian markings on abdominal T3: 0 = absent; 1 = paired spots; 2 = complete dorsal band.
- 52 Pale lateral spots on abdominal T5: 0 = none; 1 = very small; 2 = moderate but lateral only; 3 = extending on to dorsum.
- 53 Setae on abdominal S2–4, male: 0 = short hairs only; 1 = spiny hairs; 2 = long fine hairs; 3 = as 2 but extremely bushy.
- 54 As for 53, female: 0 = short hairs; 1 = strong bristles; 2 = strong spines.

Table 5. States of 54 characters (see Appendix) for 26 species of Ameniinae and two outgroups. For species codes, see Fig. 28 (p. 114).

Species	Characters 1–54					
P.semi	23????0001	0202221123	1210110121	0121010210	0020020022	0312
P.angu	33????0001	0202220123	0211110121	0121010110	0020020021	0312
S.mino	?212?1?1?1	?2?1?2?111	111?110100	?110111??1	?01211110	02?2
S.palp	12100?2?2?	1?2?2?0?1?	1110110100	?110110311	1000021113	001?
St.ano	?221?0?3?1	?2?2?0?111	0?1?000010	?1?0010221	?111111111	01?2
S.mack	?221?1?2?1	?0?2?2?122	111?110101	1110111321	?01211113	03?2
St.cro	2220003101	0202001121	1210000011	1130010111	0011011111	0131
St.nit	2320112201	0202001121	1220000011	1130010111	0011011110	0031
St.nig	2320112201	0202001131	1210000001	1130010211	0011011110	0031
Pl.aur	1020012221	1233222223	1110000021	1110111221	0011211110	0032
Pl.sim	1020012201	1223223231	1110000011	1110121221	0011211110	0032
Pa.arg	1211113221	1233223222	2220110101	1110101111	0011211111	0112
Pa.rie	1000112221	1022222202	2220110101	1110100111	0021011110	0022
Pa.par	1222333301	1022121002	1220100100	?110000111	0020011111	0022
Pa.tro	1000111021	1022223202	2220110100	?100110111	0021011110	0022
Pa.gra	1111210021	1011220112	2220100100	?100110111	0021201111	0022
Am.imp	1220002202	0111221131	0110110111	1211120221	0110121022	0312
Am.alb	1020002202	0112221131	0110110111	1211120211	0100121123	0312
Am.cri	1210002202	0112221131	0110110111	1211120321	0100120020	0312
Am.dub	1310002202	0112221131	0110110111	1221120321	0110121022	0312
Am.mac	3320002102	0112221131	0112111021	1111120211	0010121122	1212
Am.leo	2220002202	0102221131	0111111021	1111110211	0010120022	1212
Am.lon	1020222202	0112221131	0110111001	1210110421	0120021123	0312
Am.sex	2120222202	0102111131	0110010121	1321110311	0000121121	1312
Am.chr	2230222201	0202122131	1112111001	0110110111	0010022123	0312
Am.nig	2220222201	0202222231	0111111011	1321110321	0020022224	2412
Phumos	33??????01	0202020103	0112000131	2120120110	1001210020	0000
Euphum	33??????01	0203121123	0112000020	?131121110	1000020024	2400