

Current status of the *Drosophila melanogaster* species-group (Diptera)

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ABSTRACT. The *Drosophila melanogaster* species-group, established by Sturtevant (1942) for fourteen species, is now known to contain 115 described species here divided into twelve named subgroups (including one newly proposed), as well as further undescribed species. Three of the species, *melanogaster*, *simulans* and *ananassae*, are cosmopolitan; two others, *kikkawai* and *malerkotliana*, are widespread in the southern hemisphere, the latter apparently a recent introduction to South America. The greatest numbers of species otherwise occur in the Oriental region with smaller numbers in the Ethiopian, eastern Palaearctic and Australian regions and in several islands of the South Pacific. *D.rajasekari* and *D.raychaudhurii* are synonymized with *D.biarmipes*; also *D.andamanensis* Parshad & Singh is synonymized with *D.andamanensis* Gupta & Raychaudhuri.

Introduction

The classification of the genus *Drosophila* is complicated by the very large number of species (over 1300) now known. Almost all of the species have been assigned to subgenera, and within their subgenus most species have also been assigned to a species-group and, in some cases, to a subgroup or even to a 'complex' within a subgroup.

Sturtevant (1942) established the *Drosophila melanogaster* species-group within the subgenus *Sophophora* to include fourteen species. The group was more recently reviewed by Bock & Wheeler (1972), who summarized all available information on the distributions, synonymies and relationships of the forty-six species which had been described to that date, provided descriptions of an additional twenty-seven new species (a further two were contributed by F. J. Lin), and discussed several further poorly-known species of questionable affinity to the others.

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Since Bock & Wheeler's (1972) review, a further thirty-seven species have been described in the group, and it is now clear that the *melanogaster*-group may be regarded as one of the largest species-groups in the genus *Drosophila*. The group clearly contains a number of species of considerable genetic interest or potential, and in view of the large number of new species recently described, together with the more coherent picture of many distributions and relationships which has also emerged since the time of the last review, it now seems appropriate to provide a further summary of this large and important group of species.

Definition of the *melanogaster* species-group (Sturtevant, 1942: 29)

As members of the subgenus *Sophophora*, species of the *melanogaster* group are characterized *inter alia* by relatively narrow cheeks and possession (in most species) on the abdominal tergites of dark posterior bands

that are not interrupted in the mid-line (Sturtevant, 1939, 1942). Species of the *melanogaster*-group may additionally be diagnosed as follows (modified after Bock & Wheeler, 1972): yellowish tan (usually) or dusky species; sexual dimorphism in abdominal coloration often present, male abdomen apically entirely shiny black, female abdominal tergites with dark posterior bands only; sexual dimorphism in foreleg almost always present, male fore-tarsus bearing 'sex-comb' of variable size and structure, female fore-tarsus without additional bristles; second oral bristle large; middle orbital bristle (anterior reclinate orbital) small; ventral receptacle (female internal genitalia) long, coiled; testes spiral; male external genitalia comprising genital arch, pair of anal plates and one or two (primary and secondary) pairs of dentate claspers, the whole with numerous long bristles but without micropubescence; male phallic organs almost always with two pairs of parameres (parandrites).

Subgroup classification and notes

The question of division of the *melanogaster*-group into subgroups has been considered several times in the past in recognition of those clusters of species which are evidently most closely related. The first such subdivision (into five subgroups) was proposed by Hsu (1949) on the basis of a detailed study of male external genitalia in a total of only thirteen species. Hsu's classification has, however, been reinforced by subsequent findings and his five subgroups (all now considerably enlarged) are still universally recognized. Okada (1954) added a further two subgroups, Bock & Wheeler (1972) a further four (an undescribed African species was also separated into a fifth unnamed subgroup).

The distribution of species amongst the subgroups is by no means uniform or even approximately so; the *montium*-subgroup contains over half of all species described to date, while several other subgroups have either remained monotypic or include few species only. A summary of the species of each subgroup is provided below together with additional notes on particular species.

I. melanogaster-subgroup (Hsu, 1949: 121)

Abdomen of male shiny black on apical (approximately) half; female abdominal tergites with apical black bands (sixth tergite sometimes entirely black); male with sex-comb consisting of about 7-12 large black teeth arranged in oblique row distally on metatarsus; male external genitalia with primary claspers only.

In external morphology, the seven species of the *melanogaster*-subgroup (Table 1) comprise a compact complex clearly demarcated from the members of all other subgroups. The most characteristic feature of the species is the sex-comb of the males (although superficially similar sex-combs occur in a few other species; cf. *bipectinata* and *parabipectinata*, *ananassae*-subgroup, and *nikananu*, *montium*-subgroup). The coloration is also subtly characteristic in that few species of the other subgroups are as pale, yet possess such clearly defined bands on the abdominal tergites.

Recent studies (Tsacas & David, 1974; Tsacas & Lachaise, 1974; Lemeunier & Ashburner, 1976) have provided strong evidence that the *melanogaster*-subgroup is native to the Ethiopian region. Five of the seven known species are entirely restricted to that region while the remaining two are cosmopolitan, presumably having extended their ranges within historical times in association with human commerce and movements. Since most species of the *melanogaster*-group occur in the Oriental region and adjacent areas, the species of the *melanogaster*-subgroup clearly represent a peripheral radiation, and the absence of obviously close relatives in the Oriental region suggests that the ancestor of the seven Ethiopian species reached the African continent some considerable time ago. (It appears, indeed, that at least three separate *melanogaster*-group invasions reached Africa, since representatives of two other subgroups, *ananassae* and *montium*, also occur there, while the *dentissima*-subgroup is restricted to Africa. Further zoogeographical comments are offered in the Discussion.)

The closest relatives of the species of the *melanogaster*-subgroup remain a matter of speculation. In external morphology the latter most closely resemble the eleven species of the *takahashii*-subgroup; ten of the eleven

TABLE 1. The *melanogaster*-subgroup

Species	Distribution
1. <i>erecta</i> Tsacas & Lachaise, 1974: 193	Africa
2. <i>mauritiana</i> Tsacas & David, 1974: 42	Mauritius
3. <i>melanogaster</i> Meigen, 1830: 85 = <i>fasciata</i> Meigen, 1830: 84 = <i>nigriventris</i> Macquart, 1843: 259 = <i>approximata</i> Zetterstedt, 1847: 2557 = <i>ampelophila</i> Loew, 1861: 231 = <i>uvarum</i> Rondani, 1875: 86 = <i>balteata</i> Bergroth, 1894: 75 = <i>ptiosula</i> Becker, 1908: 156 = <i>emulata</i> Ray-Chaudhuri & Mukherjee, 1941: 215	Cosmopolitan
4. <i>orena</i> Tsacas & David, 1978: 179	Africa
5. <i>simulans</i> Sturtevant, 1919: 153	Cosmopolitan
6. <i>teissieri</i> Tsacas, 1971: 35	Africa
7. <i>yakuba</i> Burla, 1954a: 161	Africa

species of the *takahashii*-subgroup possess the same general coloration and colour dimorphism as the members of the *melanogaster*-subgroup, but the sex-combs of the species of the *takahashii*-subgroup consist of transverse rows of heavy bristles on the first two tarsal segments. Different though the *melanogaster* and *takahashii* arrangements may appear, however, they do not necessarily imply substantial genetic divergence since interspecific crosses are possible in another subgroup between species with sex-combs differing to the same extent (Bock, 1978; *ananassae*-subgroup, *q.v.*). It is conceivable that studies of polytene chromosomal banding homologies might shed additional light on the relationships between these two subgroups. Considerable progress has already been made in the analysis of such relationships within the *melanogaster*-subgroup (Ashburner & Lemeunier, 1976; Lemeunier and Ashburner, 1976).

Notes

1. *D. erecta* is a species of apparently very narrow ecological requirements, associated almost exclusively with fruits of the tree *Pandanus candelabrum* (Lemeunier & Ashburner, 1976).

2. Known only from the island of Mauritius,

D. mauritiana is closely related chromosomally to *melanogaster* and *simulans* (Lemeunier & Ashburner, 1976).

3. *D. melanogaster* is the type species of the subgenus *Sophophora* (Sturtevant, 1939). This best-known of all *Drosophila* species was described by J. W. Meigen (1830) in Volume 6 of his substantial treatise on the Diptera of Europe, although the description of '*Dros. melanogaster*' (as Meigen's other descriptions) was extremely brief. For its historical interest the description is quoted in full [author's translation]: 'Head, thoracic dorsum and legs clay-yellow; abdomen black. The halteres are white, the wings without colour. — From Austria, from Kiel and from Hamburg. — 1 line [i.e., one twelfth of an inch]'. The preceding page of Meigen's treatise contains a description of a '*Dros. fasciata*'. The types of both *melanogaster* and *fasciata* have been lost, but *melanogaster* and *fasciata* are believed to represent male and female respectively of the same species; evidently very old specimens of uncertain origin of '*D. fasciata*' in the collection of the Naturhistorisches Museum Wien (Vienna) are clearly the female of the species now universally known as *melanogaster*. In his catalogue of the *Drosophila* species of the world, Wheeler (1959) listed '*fasciata* Meigen' as 'considered by some authors as prior name (page preference) for *melanogaster* Meigen'. Occasional papers have indeed appeared in which the species has been cited as *fasciata* (e.g. Meltzen *et al.*, 1952), but the citing by Okada (1956) of *fasciata* as a synonym of *melanogaster* fulfills the requirements of Article 24(a) and Recommendation 24A of the International Code of Zoological Nomenclature in establishing *melanogaster* as the valid name. (Where synonymic names have been published simultaneously, the first need not necessarily be selected as the valid name; popular usage had clearly established *melanogaster* as the name of choice.) With the exception of a single specimen which is clearly a different species, the fifteen syntypes of *D. ampelophila* Loew (in the Museum für Naturkunde, East Berlin) are also clearly males (three specimens) and females (eleven specimens) of *D. melanogaster*. [Types of the other species cited in the synonymy above have not been viewed by the author, but the species have been shown to be synonyms of

melanogaster (Wheeler, 1959; Okada, 1956; Bock & Wheeler, 1972).]

4. *D. melanogaster* and *D. simulans* are two of the eight cosmopolitan species (i.e. species which occur in at least parts of all six biogeographic regions) in the genus *Drosophila* (cf. also *D. ananassae* below). Although very widespread, however, the species are restricted in occurrence in most parts of the world to urban or farm environments or other situations in which natural habitats have been modified by man. An exception is the African continent, where the species are widespread in natural habitats; the probable African origin of the *melanogaster*-subgroup has been mentioned above. Both species appear to be absent from South-East Asia; *melanogaster* has been detected in the last 2 years in New Guinea in a few urban environments about Port Moresby and the Sogeri Plateau and is probably a recent introduction.

5. Males of *melanogaster* and *simulans*, frequently collected together, are easily distinguished by examination of the external genitalia; a large clam-shaped process extends from the genital arch in *simulans* while the homologous process in *melanogaster* is considerably smaller. The criteria useful for separating females of the two species are more equivocal, cheek width (narrow in *simulans*, wide in *melanogaster*) perhaps being the better (Gallo, 1973; Bock, 1976).

II. *takahashii*-subgroup (Hsu, 1949: 122)

Abdomen of male shiny black on (approximately) apical half (except in *tanorum*); female abdominal tergites with apical black bands (female unknown in *retnasabapathyi* and *tanorum*); male with sex-comb consisting of short transverse rows of teeth on first two tarsal segments; male external genitalia with primary claspers only (but cf. *tanorum*), clasper with row of large black teeth; anterior parameres of phallic organs large, pointed, apically black.

The eleven species of the *takahashii*-subgroup (as those of the *melanogaster*-subgroup) are very similar in external morphology, only the *tanorum* male lacking the characteristic

apically black abdomen. There is less variation in the structure of the male genitalia within the *takahashii*-subgroup than within the *melanogaster*-subgroup, but there are some interspecific differences among the species of the *takahashii*-subgroup in the numbers and arrangement of teeth in the sex-combs. The wings of four species (*giriensis*, *nepalensis*, *prostipennis*, *trilutea*) also show a sexual dimorphism, the male wing possessing an apical dark patch or at least some infuscation, while the female wing is clear. Species of the *takahashii*-subgroup occur from eastern Australia north to Japan and west to the Indian subcontinent, but no species is widespread within that area except *D. takahashii* itself.

TABLE 2. The *takahashii*-subgroup

Species	Distribution
1. <i>giriensis</i> Prakash & Reddy, 1977: 597	India
2. <i>jagri</i> Prakash & Reddy, 1979a: 73	India
3. <i>lutescens</i> Okada, 1975: 241 = <i>lutea</i> Kikkawa & Peng, 1938: 533, nec Wiedemann, 1830: 593 = <i>luteola</i> Okada, 1974: 282 (replacement name for <i>lutea</i>), nec Hardy, 1965: 347	Korea; Japan
4. <i>nepalensis</i> Okada, 1955: 388	Nepal; India
5. <i>paralutea</i> Bock & Wheeler, 1972: 15	Thailand; Borneo
6. <i>prostipennis</i> Lin, 1972: 19	Taiwan
7. <i>pseudotakahashii</i> Mather, 1957: 222	Australia
8. <i>retnasabapathyi</i> Takada & Momma, 1975: 36	Malaysia
9. <i>takahashii</i> Sturtevant, 1927: 371	India to Japan; South-East Asia
10. <i>trilutea</i> Bock & Wheeler, 1972: 17	Taiwan; Borneo
11. <i>tanorum</i> Okada, 1964a: 452	Borneo

Notes

1. *D. lutescens* and *D. paralutea* have been shown to intercross to a small extent in the laboratory (Bock, 1972), the polytene chromosomes of the hybrid larvae exhibiting

the asynapsis between homologous arms commonly observed in interspecific crosses, together with evidence of several gene rearrangements. It is conceivable, given the morphological similarities within the subgroup, that attempts at hybridizing other species may also prove successful.

2. *D. pseudotakahashii* is now known to range from northern Queensland to southern New South Wales or possibly Victoria (Bock, 1976, Bock & Parsons, 1978a), often occurring as the dominant fruit-baited species in all categories of rain forest (Bock & Parsons, 1977).

3. *D. tanorum*, known only from the holotype male, was included in the *montium*-subgroup by Okada (1964a, b) because the external genitalia appear to possess two pairs of claspers. As noted by Okada, the genitalia are in other respects typical of those of a species of the *takahashii*-subgroup; the sex-comb also consists of transverse rows of bristles on the first two tarsal segments, an arrangement quite unlike that of any species in the *montium*-subgroup. Bock & Wheeler (1972) provisionally left *D. tanorum* in the *montium*-subgroup, although noting its doubtful position there. Apart from the arrangement of the claspers (to some extent reminiscent of that in the *montium*- and *suzukii*- and, to a lesser extent, the *ananassae*-subgroups) the species is clearly a member of the *takahashii*-subgroup in the structure of the genitalia and seems best now transferred to this subgroup.

III. *suzukii*-subgroup (Hsu, 1949: 122)

Anal plate of male external genitalia with lower bristles clearly differentiated in length and/or thickness from upper bristles; large primary clasper only present, with several sets of different teeth; aedeagus long, slender; anterior and posterior parameres large.

Although fairly easily defined by the structure of the male genitalia, the species of this subgroup are more heterogeneous in external morphology than are the members of most other subgroups. Colour ranges from pale to dark brown. The abdominal colour dimorphism (male abdomen apically black) is present in some species only, and a wing dimorphism similar to that of several species

in the preceding subgroup is also present in four species (*biarmipes*, *pulchrella*, *suzukii*, *tristipennis*). The sex-comb ranges from longitudinal, through oblique and transverse, to absent. Species of the *suzukii*-subgroup have been recorded from India and China to Korea, Japan, Taiwan and Cambodia.

TABLE 3. The *suzukii*-subgroup

Species	Distribution
1. <i>biarmipes</i> Malloch, 1924a: 64 ✓ = <i>rajasekari</i> Reddy & Krishnamurthy, 1968: 202. syn. nov. ✓ = <i>raychaudhurii</i> Gupta, 1969: 54, syn. nov.	India
2. <i>immacularis</i> Okada, 1966: 97	Nepal
3. <i>lucipennis</i> Lin, 1972: 23	Taiwan
4. <i>mimetica</i> Bock & Wheeler, 1972: 25	Malaysia
5. <i>oshimai</i> Choo & Nakamura, 1973: 305	Japan
6. <i>pulchrella</i> Tan, Hsu & Sheng, 1949: 198	India to Japan; Taiwan
7. <i>suzukii</i> (Matsumura, 1931: 366)	India to Japan
8. <i>tristipennis</i> Duda, 1924a: 215; 1924b: 247	India; Nepal; Taiwan
9. <i>unipectinata</i> Duda, 1924a: 215; 1924b: 246	Korea; Japan; Taiwan

Notes

1. The status of *D. biarmipes* has previously been considered doubtful, Malloch's description having been noted to agree with that of *rajasekari* (= *raychaudhurii*), especially with regard to the unusual sex-comb, except for the absence of a mention by Malloch of any strong apical darkening in the male wing (Bock & Wheeler, 1972). The holotype of *biarmipes* has now been examined and, although not in good condition, has been found to possess weak apical darkening on one wing (the other is damaged). Studies on cultures of species possessing the wing coloration dimorphism have indicated that the apical darkening characteristic of the male wing develops with age. The wing is almost or entirely clear on eclosion and the dark patch gradually intensifies over a period of a few days; teneral specimens therefore lack the characteristic coloration and could easily be mistaken for another species. Apart from this general consideration, detailed studies by

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Prakash & Reddy (1976) have revealed considerable variability within the species '*D.rajasekari*' in expression of the wing patch in mature males, the colour ranging from entirely absent to very strong; some individuals even exhibit bilateral asymmetry with respect to colour development. Given the similarities otherwise existing between *biarmipes* and *rajasekari* and the fact that both species occur in the same area, it appears certain that the male described by Malloch was either a young specimen or one in which the wing pigmentation did not develop.

2. *D.lucipennis* and *D.tristipennis* lack sex-combs.

3. *D.suzukii* was described in the genus *Leucophenga*.

IV. *elegans*-subgroup (Bock & Wheeler, 1972: 27)

Anterior parameres of phallic organs exceptionally long and slender, apically pointed, basally recurved; posterior parameres large, with numerous small finger-like branches; lower portion of anal plate with large tooth (*elegans*) or smaller teeth (*sahyadrii*); sex-comb consisting of transverse rows of bristles on first three tarsal segments; male wing with apical black patch.

This subgroup was established for the single species *D.elegans* which shows some resemblances to members of the *suzukii*-subgroup but possesses highly distinctive male genitalia.

TABLE 4. The *elegans*-subgroup

Species	Distribution
1. <i>elegans</i> Bock & Wheeler, 1972: 28	Philippines; New Guinea
2. <i>sahyadrii</i> Prakash & Reddy, 1979b: 69	India

Notes

1. Formerly known only from the Philippines, *D.elegans* was recently collected in New Guinea (Bock & Parsons, unpublished) in the large tubular flowers of *Ipomoea fistulosa*. It is conceivable that larvae of *D.elegans* could

be living in the fleshy basal tissues of the flowers; a similar situation has been shown to exist in the Australian species *D.(Scaptodrosophila) hibisci* Bock (Cook *et al.*, 1977), larvae of which feed in the decaying tissues of flowers of native *Hibiscus* species that have fallen from the plant.

2. *D.sahyadrii* was included in the *suzukii*-subgroup by Prakash & Reddy (1979b) but morphologically the species is clearly a close relative of *elegans*; *sahyadrii* was further recorded as 'obtained from the flowers of *Ipomoea* species'.

V. *denticulata*-subgroup (Bock & Wheeler, 1972: 29)

Primary clasper only present in male external genitalia; anterior parameres of phallic organs finger-like; fore-femur of male plump, densely pubescent, with posteromedial row of longer bristles; sex-comb consisting only of a few large teeth apically on short metatarsus; abdominal colour dimorphism absent.

TABLE 5. The *denticulata*-subgroup

Species	Distribution
1. <i>denticulata</i> Bock & Wheeler, 1972: 29	South-East Asia; New Guinea; Australia
2. <i>pseudodenticulata</i> Takada & Mochima, 1975: 350	Malaysia

Notes

1. *D.denticulata* is now known to be widespread in rain forests of north Queensland.

2. *D.pseudodenticulata* is known only from two males collected together in West Malaysia.

VI. *eugracilis*-subgroup (Bock & Wheeler, 1972: 31)

Primary clasper only present in male external genitalia; aedeagus large, highly ornate; 'sex-comb' consisting only of two large bristles on distal portion of metatarsus; dimorphism strong, male abdomen apically black, sharply truncated, without protruding genitalia.

The *eugracilis*-subgroup was established for a single distinctive species with a convoluted taxonomic history; the subgroup has remained monotypic. A review of the earlier confusion surrounding the status of this species is given in Bock & Wheeler (1972). The single species of this subgroup is *D.eugracilis* Bock & Wheeler, 1972: 31, *eugracilis* having been proposed as a replacement name; the species was originally described by Duda in the genus *Tanygastrella* together with another species now known to be a member of the subgenus *Scaptodrosophila* (Bock & Parsons, 1978b).

VII. *ficuspshila*-subgroup (Okada, 1954: 43)

Sex-comb longitudinal along entire lengths of metatarsus and second tarsal segment, consisting of row of numerous close teeth on each segment plus several larger teeth on each segment below (deep to) former rows; primary clasper only present in male external genitalia; anal plate with differentiated upper and lower bristles; abdominal colour dimorphism absent.

The most distinguishing feature of the species of this subgroup is the sex-comb; similar sex-combs occur in the *montium*- and *dentissima*-subgroups (see below).

TABLE 6. The *ficuspshila*-subgroup

Species	Distribution
1. <i>ficuspshila</i> Kikkawa & Peng, 1938: 531	Korea; Japan; Taiwan; Andaman Islands; Malaysia
2. <i>smithersi</i> Bock, 1976: 17	Australia

Notes

1. The species of this small subgroup appear to be rare and have remained little known. *D.ficuspshila* is the most widespread species but there are few records of its collection. *D.smithersi*, although recorded from both northern and southern Queensland (Bock, 1976), appears to be very rare.

2. An undescribed species of this subgroup is known from New Guinea (Bock & Wheeler, 1972).

VIII. *nipponica*-subgroup (Okada, 1954: 43)

Sex-comb longitudinal on first two tarsal segments; anal plate of male external genitalia with single large ventromedial tooth; primary clasper only present; aedeagus branched or serrate.

This small group comprises three species known only from Korea and Japan. The abdominal tergites of both sexes of *clarofinis* and *magnipectinata* are highly unusual within the *melanogaster*-group and the subgenus *Sophophora* in possessing apical black bands that are interrupted in the mid-line, a characteristic that appears to have escaped previous comment. Unbroken apical bands (or bands widened in the mid-line) on the abdominal tergites were given by Sturtevant (1939) as a subgeneric characteristic for *Sophophora*, and almost all of the species that have been described since 1939 in that subgenus possess abdominal tergites that are either uniformly coloured or with unbroken apical bands. Apart, however, from this anomalous characteristic, there seems no doubt that the species are correctly included in the *melanogaster*-group. According to the original description of *D.nipponica* the apical bands on the abdominal tergites of this species are not interrupted in the mid-line.

TABLE 7. The *nipponica*-subgroup

Species	Distribution
1. <i>clarofinis</i> Lee, 1959: 43	Korea; Japan
2. <i>magnipectinata</i> Okada, 1956: 113	Korea; Japan
3. <i>nipponica</i> Kikkawa & Peng, 1938: 531	Korea; Japan

IX. *ananassae*-subgroup (Hsu, 1949: 122)

Male external genitalia (except *varians*) with primary and secondary claspers; teeth on primary clasper in two sets; sex-comb absent (*ironensis*) or in transverse, oblique or longitudinal row or rows.

The *ananassae*-subgroup is widespread, with species ranging from Africa across Asia, South-East Asia, New Guinea and northern

Australia to Samoa and Fiji in the South Pacific; one species (*malerkotliana*) is also common in some localities in South America but is probably a recent introduction (see Note 5 below). Most of the species are native to the Oriental Biogeographic region and New

Guinea; the subgroup has evidently expanded westwards to Africa, eastwards into the South Pacific and southwards into northern Australia. One species (*ananassae*) is cosmopolitan.

Notes

1. *D. ananassae* is a cosmopolitan species which is also abundant in the tropical rain forests of South-East Asia and New Guinea. Some colour variation is known in the species, specimens from Samoa and Fiji being appreciably darker than others (Bock & Wheeler, 1972). Additionally, varying degrees of reproductive isolation among *ananassae* populations have been demonstrated (Futch, 1966), and a number of both paracentric and pericentric chromosomal inversions (the latter a rare phenomenon in *Drosophila* species) has been demonstrated. The species lacks dimorphism in abdominal coloration. The genetics of *D. ananassae* has been studied in considerable detail (Moriwaki & Tobari, 1975) and over 150 mutants have been catalogued and, in most cases, assigned to a linkage group; male recombination is also a normal phenomenon in the species and has been known for a long time. [Surprisingly, in view of its very long-standing popularity with respect to other aspects of genetic research, the phenomenon of male recombination in *D. melanogaster* has begun receiving widespread attention only in the last few years (Woodruff & Thompson, 1977).]

2. *D. pallidosa* is a sibling species of *ananassae*, the former restricted in occurrence to Fiji and Samoa and distinguished from *ananassae* by its paler coloration. The male genitalia of the two species are practically indistinguishable, an unusual phenomenon within the genus *Drosophila* where, except in the case of a number of Hawaiian species (Kaneshiro, 1974), even otherwise very similar species usually possess quite different male genitalia.

3. Independent surveys of the Andaman Islands were evidently performed by Gupta & Ray-Chaudhuri (1970) and by Parshad & Singh (1971); the latter paper was overlooked in the last review of the *melanogaster*-group (Bock & Wheeler, 1972). Both Gupta & Ray-Chaudhuri and Parshad & Singh described a '*D. andamanensis*'; the former authors

TABLE 8. The *ananassae*-subgroup

Species	Distribution
1. <i>ananassae</i> Doleschall, 1858: 128 = <i>imparata</i> Walker, 1859: 126 = <i>similis</i> Lamb, 1914: 347, nec Williston, 1896: 415 = <i>errans</i> Malloch, 1933: 21 (replacement name for <i>similis</i>) = <i>caribea</i> Sturtevant, 1916: 335	Cosmopolitan
2. <i>andamanensis</i> Gupta & Ray-Chaudhuri, 1970: 171 = <i>andamanensis</i> Parshad & Singh, 1971: 391, syn. nov.	Andaman and Nicobar Is.
3. <i>atripex</i> Bock & Wheeler, 1972: 43	South-East Asia
4. <i>biplectinata</i> Duda, 1923: 52 = <i>szentivanii</i> Mather & Dobzhansky, 1962: 247	Oriental/Australian; Japan; Samoa and Fiji
5. <i>cornixa</i> Takada, Momma & Shima, 1973: 79	Malaysia
6. <i>ercepeae</i> Tsacas & David, 1975: 134	Réunion Island
7. <i>ironensis</i> Bock & Parsons, 1978a: 102	Australia; New Guinea
8. <i>malerkotliana</i> Parshad & Paika, 1964: 235	India; South-East Asia; Africa; South America
9. <i>micropectinata</i> Takada & Momma, 1975: 43	Malaysia
10. <i>nesoetes</i> Bock & Wheeler, 1972: 41	Micronesia
11. <i>pallidosa</i> Bock & Wheeler, 1972: 38	Fiji and Samoa
12. <i>parabiplectinata</i> Bock, 1971a: 277	South-East Asia; Réunion Is.
13. <i>pereirae</i> Takada, Momma & Shima, 1973: 91	Malaysia
14. <i>phaeopleura</i> Bock & Wheeler, 1972: 40	Fiji
15. <i>pseudoananassae</i> Bock, 1971a: 274	South-East Asia; New Guinea; Australia
16. <i>varians</i> Bock & Wheeler, 1972: 43	Philippines

included their species in the *ananassae*-subgroup while the latter authors included their species in the *montium*-subgroup. Careful comparison of the two descriptions reveals that both groups of workers have described the same species (which is correctly included in the *ananassae*-subgroup). *D. andamanensis* Parshad & Singh, 1971 is thus a synonym of *D. andamanensis* Gupta & Ray-Chaudhuri, 1970. The former name is not a homonym since identical taxa are involved (Article 52, International Code of Zoological Nomenclature), although a homonym was created by Parshad & Singh (1971) in the description of a second species (see Note 2, *montium*-subgroup, below).

4. The four species *biplectinata*, *malerkotliana*, *parabiplectinata* and *pseudoananassae* are extremely similar in many details of morphology, including male genitalia, and can be hybridized with varying degrees of success in all possible combinations (Bock, 1978); these species have been termed the '*biplectinata*-complex'. However, there are distinct differences among the species in the sex-combs, which consist of short transverse rows of bristles in *malerkotliana* and *pseudoananassae* and considerably longer oblique rows in *biplectinata* and *parabiplectinata*; a hybrid male between one of the first two species and one of the second two possesses a sex-comb of intermediate structure. In spite of the similarities in sex-combs just noted, *malerkotliana* clearly appears to be more closely related to both *biplectinata* and *parabiplectinata* than to *pseudoananassae* (Bock, 1971b, 1978). Abdominal colour dimorphism is absent in *biplectinata*, present in *parabiplectinata* than to *pseudoananassae* (Bock, only of both *malerkotliana* and *pseudoananassae*; in the latter cases subspecies have accordingly been recognized, the typical subspecies of *malerkotliana* possessing the dimorphism while *D. m. pallens* Bock & Wheeler, 1972: 48 lacks it, and the typical subspecies of *pseudoananassae* lacking the dimorphism while *D. p. nigrens* Bock & Wheeler, 1972: 48 possesses it.

5. *D. malerkotliana* (typical subspecies) has been recorded within the last few years in Brazilian forests where it sometimes comprises a high proportion of all flies collected (do Val, personal communication). It appears that the

species is a recent introduction and has adapted very successfully to local conditions.

6. *D. cornixa* and *D. pereirai* were included in the *montium*-subgroup by Takada *et al.* (1973). On both sex-comb structure (transverse rows of bristles in both species) and male genitalia these species are better included in the *ananassae*-subgroup.

7. *D. ironensis*, a small species without abdominal colour dimorphism, lacks a sex-comb, in condition shared by only three other species in the *melanogaster*-group (cf. *suzukii*-subgroup above, *flavohirta*-subgroup below). The species was described from rain forests of northern Australia (Queensland) but is now known to be present in New Guinea (Bock & Parsons, unpublished).

8. Takada & Momma (1975) did not assign *micropectinata* to a subgroup. The structure of the male genitalia places the species in the *ananassae*-subgroup.

X. *montium*-subgroup (Hsu, 1949: 121)

Male external genitalia with primary and secondary claspers, secondary clasper usually with very large bristles (but cf. Note 7 below); sex-comb in almost all species in longitudinal rows of teeth along metatarsus and second tarsal segment (cf. Note 4); abdominal colour dimorphism rarely present, most species possessing shiny yellowish or brown tergites with clearly defined apical black bands in both sexes; abdominal tergites with sparse large apical bristles.

With fifty-nine of the 115 described species in the *melanogaster*-group, the *montium*-subgroup is by far the largest of the twelve subgroups here recognized. Species of the *montium* subgroup are found from Africa to Japan, Micronesia, New Guinea and Australia, and one species (*kikkawai*) occurs in South America as well as in other areas. The 'epicentre' of the subgroup is, however, clearly the Oriental region. Many species are very poorly known, or known from only a single locality; this phenomenon is considered further in the Discussion.

The most distinguishing feature of the species of the *montium*-subgroup is the large longitudinal sex-comb; the coloration, shinier and darker than that of most species of other subgroups, is also characteristic.

TABLE 9. The *montium*-subgroup

Species	Distribution	Species	Distribution
1. <i>agumbensis</i> Prakash & Reddy, 1978: 259	India	29. <i>lacticornis</i> Okada, 1965: 347	Okinawa
2. <i>anomelani</i> Reddy & Krishnamurthy, 1973: 259	India	30. <i>leontia</i> Tsacas & David, 1977: 679	Malaysia
3. <i>artecarina</i> Takada & Momma, 1975: 38	Malaysia	31. <i>lini</i> Bock & Wheeler, 1972: 59	Taiwan
4. <i>asahinai</i> Okada, 1964b: 111	Amami Islands (Japan)	32. <i>longipectinata</i> Takada, Momma & Shima, 1973: 82	Malaysia
5. <i>auraria</i> Peng, 1937: 23	China; Korea; Japan	33. <i>matilei</i> Tsacas, 1974: 148	Africa
6. <i>baimaii</i> Bock & Wheeler, 1972: 70	Thailand; Malaysia	34. <i>mayri</i> Mather & Dobzhansky, 1962: 245	New Guinea
7. <i>bakoue</i> Tsacas & Lachaise, 1974: 197	Africa	35. <i>montium</i> de Meijere, 1916, 205	Java
8. <i>barbarae</i> Bock & Wheeler, 1972: 62	South-East Asia	36. <i>mysorensis</i> Reddy & Krishnamurthy, 1970: 24	India
9. <i>biauraria</i> Bock & Wheeler, 1972: 53	Korea; Japan	37. <i>nigrialata</i> Takada, Momma & Shima, 1973: 85	Malaysia
10. <i>bicornuta</i> Bock & Wheeler, 1972: 67	South-East Asia	38. <i>nigropleuralis</i> Takada, Momma & Shima, 1973: 84	Malaysia
11. <i>birchii</i> Dobzhansky & Mather, 1961: 462	Australia; New Guinea	39. <i>nikananu</i> Burla, 1954a: 160	Africa
12. <i>bocki</i> Baimai, 1979: 237	Thailand; Taiwan	40. <i>orosa</i> Bock & Wheeler, 1972: 64	Thailand
13. <i>bocqueti</i> Tsacas & Lachaise, 1974: 204	Africa	41. <i>palmata</i> Takada, Momma & Shima, 1973: 86	Malaysia
14. <i>brevis</i> Parshad & Singh, 1971: 397, <i>nec</i> Walker, 1852: 411	Andaman Islands	42. <i>paraviaristata</i> Takada, Momma & Shima, 1973: 87	Malaysia
15. <i>burlai</i> Tsacas & Lachaise, 1974: 200	Africa	43. <i>parvula</i> Bock & Wheeler, 1972: 73	Thailand; Malaysia
16. <i>coonorensis</i> Reddy & Krishnamurthy, 1973: 262	India	44. <i>pectinifera</i> Wheeler & Takada, 1964: 176	Micronesia
17. <i>dauidi</i> Tsacas, 1975: 127	Africa	45. <i>penicillipennis</i> Takada, Momma & Shima, 1973: 91	Malaysia
18. <i>diplacantha</i> Tsacas & David, 1977: 681	Africa	46. <i>pennae</i> Bock & Wheeler, 1972: 61	New Guinea
19. <i>dominicana</i> Ayala, 1965a: 620	New Guinea	47. <i>pseudobaimaii</i> Takada, Momma & Shima, 1973: 89	Malaysia
20. <i>exiguittutu</i> Takada, Momma & Shima, 1973: 79	Malaysia	48. <i>pseudomayri</i> Baimai, 1970a: 22	New Guinea
21. <i>flavopleuralis</i> Takada, Momma & Shima, 1973: 82	Malaysia	49. <i>punjabiensis</i> Parshad & Paika, 1964: 241	India; Malaysia
22. <i>greeni</i> Bock & Wheeler, 1972: 82	Africa	50. <i>quadraria</i> Bock & Wheeler, 1972: 55	Taiwan
23. <i>gundensis</i> Prakash & Reddy, 1977: 600	India	51. <i>rhopaloa</i> Bock & Wheeler, 1972: 69	Thailand; Borneo
24. <i>jambulina</i> Parshad & Paika, 1964: 240	India; Cambodia	52. <i>rufa</i> Kikkawa & Peng, 1938: 529	India to Japan
25. <i>kanapiae</i> Bock & Wheeler, 1972: 74	Philippines	53. <i>seguyi</i> Smart, 1945: 56	Africa
26. <i>khaoyana</i> Bock & Wheeler, 1972: 68	Thailand	54. <i>serrata</i> Malloch, 1927: 6	Australia; New Guinea
27. <i>kikkawai</i> Burla, 1954b: 47	Ethiopian, Oriental, Australian, Neotropical and eastern Palaearctic zones	55. <i>trapezifrons</i> Okada, 1966: 93	Nepal
28. <i>kinabalauana</i> Takada, Momma & Shima, 1973: 81	Malaysia	56. <i>triauraria</i> Bock & Wheeler, 1972: 54	Korea; Japan
		57. <i>truncata</i> Okada, 1964b: 455	India; Borneo
		58. <i>tsacasi</i> Bock & Wheeler, 1972: 79	Africa
		59. <i>vulcana</i> Graber, 1957: 309	Africa

Notes

1. *D. birchii*, originally described as a subspecies of *serrata*, was accorded specific status by Ayala (1965b). The species is rich in chromosomal inversion polymorphism (Baimai, 1970b); no other species of this subgroup appears to have been investigated for inversion polymorphism although the scope for such studies is obviously considerable.

2. *D. brevis* Parshad & Singh, 1971 is a junior homonym of *D. brevis* Walker, 1852: 411, an American species of uncertain relationships

3. *D. kikkawai* possesses several very close relatives, the species concerned [*anomelani*, *barbarae*, *brevis* (see Note 2 above), *diplacantha*, *leontia*, *lini*, *mysorensis* and *pennae*] having, together with *kikkawai*, been termed the 'kikkawai-complex' in a review by Tsacas & David (1977); the two species *kikkawai* and *leontia* were noted to possess identical male genitalia (cf. Note 2, *ananassae*-subgroup).

4. While a longitudinal sex-comb on the metatarsus and second tarsal segment is typical of species of the *montium*-subgroup, four species (*exiguitata*, *gundensis*, *nikananu* and *paraviaristata*) possess smaller sex-combs. A further comment on *paraviaristata* is given in Note 7 below. The male genitalia of *gundensis* and *nikananu* clearly place these species in *montium*-subgroup. The male genitalia of *exiguitata* are somewhat atypical but the species should probably be retained in the *montium*-subgroup at least until further information on the species (which was described from five males) is available.

5. Tsacas (1974) provisionally assigned *D. matilei* to the *montium*-subgroup. The species possesses a sex-comb which could permit its inclusion in either the *montium* or *dentissima* (see below) subgroups, but the male genitalia are not typical of those of either subgroup and the systematic position of the species remains questionable.

6. *D. montium* was the first species described possessing the sex-comb typical of this subgroup. Before it was realized that many other species possess very similar sex-combs but can almost always be distinguished unequivocally from one another by reference to the male genitalia, there followed a long history of mis-

identifications of other species as '*montium*' (Bock & Wheeler, 1972). The type of locality of *D. montium* is Java and in fact there is no confirmed record of the discovery of this species in Java or in any other area since de Meijere's original description. The holotype of *D. montium* is located, together with twenty-one other specimens assigned to the same species, in the Zoologisch Museum, Universiteit van Amsterdam, Amsterdam. It is quite likely that at least some of the latter specimens represent one or more different species but dissection of the genitalia of male specimens would be necessary to confirm this; specific determination of female specimens would probably be impossible. The genitalia of the *montium* holotype male were figured by Burla (1954b).

7. According to the original description of *paraviaristata*, the sex-comb, although long and consisting of many teeth, is confined to the metatarsus. The male external genitalia lack secondary claspers. The systematic position of this species is unclear; it is here provisionally retained in the *montium*-subgroup.

8. *D. vulcana* was recorded from Malaysia by Takada & Momma (1975). Given that this species is otherwise known only from Africa, the Malaysian determination must be regarded with scepticism.

9. *D. seguyi* has been reported from India (Gupta, 1974). Since this species is also African, the Indian determination must also be regarded with scepticism.

XI. *dentissima*-subgroup (Bock & Wheeler, 1972: 83)

Sex-comb similar to that of typical *montium*-subgroup species, with numerous tightly packed teeth; male external genitalia with one pair of claspers only; anterior parameres of phallic organs apically pointed, black.

The *dentissima*-subgroup was established for the two little-known African species below (cf. Note 5, *montium*-subgroup).

XII. *flavohirta*-subgroup, new subgroup

Sex-comb absent; male external genitalia with one pair of claspers only; body entirely pale

TABLE 10. The *dentissima*-subgroup

Species	Distribution
1. <i>dentissima</i> Bock & Wheeler, 1972: 83	Africa
2. <i>vumba</i> Bock & Wheeler, 1972: 84	Africa

yellowish-tan in both sexes, abdominal tergites without bands.

This subgroup is established for the single species *D. flavohirta* Malloch, 1924b: 354. The species was redescribed by Bock (1976); it is widespread in Australia (although known from few specimens) and, on structure of male genitalia, should be included in the *melanogaster*-group. The body coloration is unique within the group, but is possibly an adaptation to camouflage since the species appears to frequent flowers of *Eucalyptus*.

XIII. Species *incertae sedis*

Bock & Wheeler (1972) listed five species (*apectinata* Duda, 1931: 194; *biarmipes* Malloch, 1924a: 64; *hypopygialis* Duda, 1924b: 254; *illata* Walker, 1860: 168; *miki* Duda, 1924c: 274) which were, or had previously been regarded as, questionable members of the *melanogaster*-group. The last species (*miki*) was assigned to the *obscura*-group, while sufficient information on the remainder was not available to permit definitive judgements.

The systematic position of *hypopygialis* has since been clarified (Bock & Parsons, 1978b), while *biarmipes* is included above in the *suzukii*-subgroup. According to Sturtevant's notes on the type of *illata* ('headless and hopeless'; quoted in Bock & Wheeler, 1972), the status of this species will probably remain forever in question. No further information is available on *apectinata* and the status of this species remains in doubt.

Discussion

It is now clear that the *melanogaster* species-group represents one of the largest adaptive radiations in the genus *Drosophila*, exceeded, perhaps, only by the celebrated explosive speciation of the Hawaiian fauna.

The majority of the species of the *melanogaster*-group occur in the tropical rain forests of South-East Asia and New Guinea, and it thus seems most likely that the group originated in this area with subsequent expansions northwards into the eastern Palaearctic zone, eastwards into Samoa and Fiji, southwards into Australia and westwards into Africa. With the exception of the cosmopolitan species, four subgroups only are not represented in the Oriental region.

The *melanogaster*-subgroup is confined to Africa and Mauritius, evidently representing an early invasion westwards. The *nipponica*-subgroup, a small complex of only three species, is confined to Japan and Korea. The *dentissima*-subgroup, also consisting of few species, is confined to Africa and may have evolved there as a specialized offshoot of the *montium*-subgroup. Finally, the monotypic *flavohirta*-subgroup is unknown outside Australia; *D. flavohirta*, as noted above, appears to be a specialized species although its closest relatives are uncertain.

Accurate ecological information concerning the majority of *melanogaster*-group species is still unavailable but since most species are inhabitants of rain forests, are strongly attracted to fruit baits and are culturable on a laboratory medium suited to fruit-breeding species, it seems most probable that these species feed and breed in decaying rain forest fruits in nature, and that a diet of fruit is the primitive condition for the group. Three species, the members of the *elegans*- and *flavohirta*-subgroups, have apparently adapted successfully to flowers, and, of course, the cosmopolitans have adapted to urban refuse. It is interesting to note that within the general area of distribution of the *melanogaster*-group, other drosophilid radiations have also invaded the 'fruit niche'; members of the *melanogaster*-group must compete with the large *immigrans*-group of the subgenus *Drosophila* and a small number of species of the subgenus *Scaptodrosophila* as well as members of (at least) the genera *Dettopomyia*, *Liodrosophila*, *Sphaerogastrella* and *Zaprionus*. However, species of other dipterous families are almost never collected along with drosophilids at rain forest fruit baits.

After reviewing the seventy-five named species then known, Bock & Wheeler (1972)

predicted that the *melanogaster*-group would continue to grow. Although that prediction has been amply fulfilled — the group has grown by 50% since 1972 — it may confidently be predicted for two reasons that many new species still remain to be discovered. Firstly, recent 'point' studies — collections such as those of Takada *et al.* (1973) and Takada & Momma (1975) focusing on single localities — have yielded appreciable numbers of new species; and secondly, large areas of New Guinea, the Oriental region and Africa are still unexplored. Perhaps dozens of further species await discovery.

Given the state of complexity that the classification of the genus *Drosophila* has now reached, it may finally be appropriate to offer some comments on the subdivision of the *melanogaster*-group. The concept of the 'species-group' within the genus *Drosophila* was considered by Bock & Wheeler (1972), who regarded a species-group as the results of a major burst of speciation (within a subgenus) in a particular geographic region. It might, of course, be argued that such criteria are equally or as validly or even better applicable to subgenera or even genera, and that what are now recognized as species-groups and subgroups within the genus *Drosophila* might better be elevated to the ranks of genera and subgenera. Since this question would involve a restructuring of the entire classification of the Drosophilidae it cannot fairly be considered in isolation, that is to say with reference only to the *melanogaster*-group, and is therefore clearly outside the scope of this paper, but formal recognition of subgroups (or 'quasi-formal' recognition since no provisions are made for species-groups and subgroups in the terms of the International Code of Zoological Nomenclature) may be defended on two grounds. Firstly, long-standing popular usage has given the present system of classification universal acceptance amongst students of the Drosophilidae and any attempt to effect a substantial change would be likely to meet with considerable resistance. Secondly, there are difficulties (as noted in specific cases above) in assigning several species to particular subgroups, that is to say, in deciding in which subgroup the problematical species should be included. If the subgroups were elevated to a higher rank, the problems posed by 'difficult'

and intermediate species would be both more critical and more contentious. For the time being at least, the present system of classification is the most suitable.

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