I. The *Drosophila melanogaster* Species Group[1]

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D. melanogaster is probably the best-known species in the genus *Drosophila*. Despite the prominent position which *melanogaster* itself has long occupied in genetic studies, however, the *melanogaster* species group as a whole is not well documented. The majority of the species are confined in distribution to larger or smaller areas within the Australian, Oriental, and eastern Palaearctic biogeographical zones, although the better-known species (*melanogaster, simulans, ananassae, kikkawai*) are more widespread. Most of the many papers in the literature dealing with *melanogaster* group species are concerned with isolated descriptions of new species or local faunal analyses; it is almost 20 years since more comprehensive works have been published (Patterson and Stone, 1952; Okada, 1954), and in that time the number of known species in the group has more than doubled. Studies in recent years on a few of the *melanogaster* group species have provided interesting information concerning patterns of evolution (Ayala, 1965a; Baimai, 1969, 1970b, 1970d; Bock, 1971b).

A large number of stocks of both described and new species of the group is maintained in the University of Texas collection, and indications are that the *melanogaster* group provides very substantial scope for further evolutionary studies. It therefore now seems appropriate, on the basis of the numerous published papers dealing with one or more species and the new material presently available, to provide a comprehensive review of the *melanogaster* species group (taxonomy, relationships, and zoogeography) in the belief that this will be of some assistance in future research on members of the group.

Table 1 presents an indexed summary of the species presently considered to be members of this interesting species group.

The "Species Group" in Drosophila

The "species group," although not one of the more generally recognized levels in the zoological taxonomy, is widely used with reference to *Drosophila* and some comment may be appropriate on its significance.

The fact that evolution is a continual and gradual process is perhaps nowhere better illustrated than in the genus *Drosophila*, where many detailed studies of reproductive isolations, chromosomal homologies and comparative morphology have demonstrated that, amongst the very large number of species in the genus, not a few exhibit an almost continuously variable range of phylogenetic divergence. In some cases it is consequently very difficult, although the "species" itself has been defined clearly enough (Dobzhansky, 1951; Mayr, 1963), to recognize

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TABLE 1

Annotated index of the subgroup names, the species-group names and many of the vernacular names used in the *melanogaster* species group. Subgroup names are in capitals, valid, named species are shown by roman, and synonyms, homonyms, etc. are in italics. A "|" under "Culture" indicates that one or more cultures of the species concerned were available for study in the present project. The last column gives the major page reference in the present article.

Name	Original description or reference	Subgroup affiliation	Culture	Page reference
ampelophila	Loew 1862	....	..	9
IX ANANASSAE SUBGROUP	.....	....	..	35
ananassae	Doleschall 1858	ananassae	+	37
andamanensis	Gupta and Ray-Chaudhuri 1970	ananassae	—	48
apectinata	Duda 1932	....	..	86
approximata	Zetterstedt 1847	....	..	9
asahinai	Okada 1964	montium	—	65
atripex	Bock and Wheeler 1972	ananassae	+	42
auraria	Peng 1937	montium	+	53
auraria "A"	Moriwaki *et al.* 1952	....	..	53
auraria "B"	Moriwaki *et al.* 1952	....	..	53
auraria "C"	Moriwaki *et al.* 1952	....	..	54
baimaii	Bock and Wheeler 1972	montium	+	70
barbarae	Bock and Wheeler 1972	montium	+	62
biarmipes	Malloch 1924	....	..	87
biauraria	Bock and Wheeler	montium	+	53
bicornuta	Bock and Wheeler	montium	+	67
bipectinata	Duda 1923	ananassae	+	46
birchii	Dobzhansky and Mather 1961	montium	|	51
caribea	Sturtevant 1916	....	..	37
clarofinis	Lee 1959	nipponica	—	35
"dark" ananassae	Futch 1966	....	..	38
V DENTICULATA SUBGROUP	.....	....	..	29
denticulata	Bock and Wheeler 1972	denticulata	+	29
XI DENTISSIMA SUBGROUP	.....	....	..	83
dentissima	Bock and Wheeler 1972	dentissima	—	83
dominicana	Ayala 1965	montium	—	52
IV ELEGANS SUBGROUP	.....	....	..	27
elegans	Bock and Wheeler 1972	elegans	+	28
emulata	Ray-Chaudhuri and Mukherjee 1941	....	..	9
errans	Malloch 1933	....	..	37
VII EUGRACILIS SUBGROUP	.....	....	..	31
eugracilis	Bock and Wheeler 1972	eugracilis	+	31
fasciata	Meigen 1830	....	..	9
VIII FICUSPHILA SUBGROUP	.....	....	..	33
ficusphila	Kikkawa and Peng 1938	ficusphila	+	33
gracilis	Duda 1924	....	..	31
greeni	Bock and Wheeler 1972	montium	—	82
hypopygialis	Duda 1924	....	..	87
illata	Walker 1860	....	..	87
immacularis	Okada 1966	suzukii	—	23

TABLE 1—Continued

Name	Original description or reference	Subgroup affiliation	Culture	Page reference
imparata	Walker 1859	....	..	37
indicus	Parshad and Paika 1964	....	..	22
jambulina	Parshad and Paika 1964	montium	+	67
kanapiae	Bock and Wheeler 1972	montium	+	74
khaoyana	Bock and Wheeler 1972	montium	+	68
kikkawai	Burla 1954	montium	+	57
lacteicornis	Okada 1965	montium	+	65
"light" ananassae	Futch 1966	....	..	38
lini	Bock and Wheeler 1972	montium	+	59
lucipennis	Lin 1972	suzukii	+	23
lutea	Kikkawa and Peng 1938	takahashii	+	15
magnipectinata	Okada 1956	nipponica	—	35
malerkotliana	Parshad and Paika 1964	ananassae	+	47
mayri	Mather and Dobzhansky 1962	montium	+	57
megalopectinata	Takada *et al.* 1953	....	..	35
MELANOGASTER SUBGROUP	.....	....	..	9
melanogaster	Meigen 1830	melanogaster	+	9
miki	Duda 1924	....	..	88
mimetica	Bock and Wheeler 1972	suzukii	+	25
MONTIUM SUBGROUP	.....	....	..	48
montium	de Meijere 1916	montium	—	75
mysorensis	Reddy and Krishnamurthy 1970	montium	—	76
nepalensis	Okada 1955	takahashii	—	20
nesoetes	Bock and Wheeler 1972	ananassae	+	41
nigra	Bock 1971	....	..	48
nigrens	Bock and Wheeler 1972	....	..	48
nigriventris	Macquart 1843	....	..	9
nikananu	Burla 1954	montium	+	76
NIPPONICA SUBGROUP	.....	....	..	34
nipponica	Kikkawa and Peng 1938	nipponica	—	34
orosa	Bock and Wheeler 1972	montium	+	64
pallens	Bock and Wheeler 1972	....	..	48
pallida	Bock 1971			47
pallidosa	Bock and Wheeler 1972	ananassae	+	38
parabipectinata	Bock 1971	ananassae	+	47
paralutea	Bock and Wheeler 1972	takahashii	+	15
parvula	Bock and Wheeler 1972	montium	+	73
pectinifera	Wheeler and Takada 1964	montium	—	75
pennae	Bock and Wheeler 1972	montium	+	61
phaeopleura	Bock and Wheeler 1972	ananassae	+	40
pilosula	Becker 1908	....	..	9
prostipennis	Lin 1972	takahashii	+	19
pseudoananassae	Bock 1971	ananassae	+	48
pseudomayri	Baimai 1970	montium	—	57
pseudotakahashii	Mather 1957	takahashii	—	15
pulchrella	Tan, Hsu and Sheng 1949	suzukii	+	22
punjabiensis	Parshad and Paika 1964	montium	+	65
quadraria	Bock and Wheeler 1972	montium	+	55
rajasekari	Reddy and Krishnamurthy 1968	suzukii	+	23

TABLE 1—Continued

Name	Original description or reference	Subgroup affiliation	Culture	Page reference
ray chaudhuri	Gupta 1969	....	..	23
rhopaloa	Bock and Wheeler 1972	montium	+	69
rufa	Kikkawa and Peng 1938	montium	+	65
seguyi	Smart 1945	montium	+	77
serrata	Malloch 1927	montium	+	49
similis	Lamb 1914	....	..	37
simulans	Sturtevant 1919	melanogaster	+	10
"species A"	Paterson and Tsacas 1967	....	..	81
"species 2"	Kaneshiro and Wheeler 1970	....	..	42
"species 3"	Kaneshiro and Wheeler 1970	....	..	41
"species 4"	Kaneshiro and Wheeler 1970	....	..	43
"species 5"	Kaneshiro and Wheeler 1970	....	..	40
"species 6"	Kaneshiro and Wheeler 1970	....	..	46
"species 7"	Kaneshiro and Wheeler 1970	....	..	47
"species 8"	Kaneshiro and Wheeler 1970	....	..	48
"species 9"	Kaneshiro and Wheeler 1970	....	..	48
"species 10"	Kaneshiro and Wheeler 1970	....	..	47
"species 11"	Kaneshiro and Wheeler 1970	....	..	47
subobscura	Seguy 1938	....	..	77
II SUZUKII SUBGROUP	.....	....	..	21
suzukii	(Matsumura) 1931	suzukii	+	21
szentivanii	Mather and Dobzhansky 1962	....	..	46
I TAKAHASHII SUBGROUP	.....	....	..	13
takahashii	Sturtevant 1927	takahashii	+	13
tanorum	Okada 1964	montium	—	75
teissieri	Tsacas 1971	melanogaster	—	12
trapezifrons	Okada 1966	montium	—	68
triauraria	Bock and Wheeler 1972	montium	+	54
trilutea	Bock and Wheeler 1972	takahashii	+	17
tristipennis	Duda 1924	suzukii	—	23
truncata	Okada 1964	montium	—	63
tsacasi	Bock and Wheeler 1972	montium	+	79
unipectinata	Duda 1924	suzukii	—	22
uvarum	Rondani 1875	....	..	9
varians	Bock and Wheeler 1972	ananassae	+	43
vulcana	Graber 1957	montium	—	81
vumbae	Bock and Wheeler 1972	dentissima	—	84
yakuba	Burla 1954	melanogaster	+	11

distinct species within a complex of populations exhibiting partial or varying degrees of reproductive isolation from one another. Above the species level, a correspondingly complicated taxonomic hierarchy has been developed in an attempt to group forms within the genus into successively higher levels that reflect true evolutionary relationships. Within the genus *Drosophila* taxonomists have accordingly found it convenient to recognize subgenera, species groups, species subgroups, and within the latter, species complexes, species "clusters," and pairs or groups of sibling species.

Individual species groups within the subgenera of *Drosophila* are defined in

each case, as is a supraspecific taxon in general, by a particular combination of morphological characteristics possessed by and peculiar to all members of the taxon; the "species group" in *Drosophila* does, however, represent a unique level in the taxonomic hierarchy in several important respects.

Firstly, while at least the major subgenera of *Drosophila* are cosmopolitan in distribution, all species groups are largely or entirely endemic to restricted geographic regions. Most of the species of the *melanogaster* group occur in Southeast Asia and New Guinea, Japan, and neighboring areas. (Within these limits of distribution the major subgroups of the *melanogaster* group are largely sympatric. Several species are also endemic to Africa). Other species groups are restricted entirely to one of the six zoogeographic regions of the world.

Secondly, as emphasized by Stone (1962), interspecific hybridization (by direct cross mating) may generally be effected in the laboratory between at least some of the members of a species group, but it has never proved possible to achieve hybridization between members of different species groups (without resort to such techniques as ovarian transplantation). In the *melanogaster* group few hybridization studies have been carried out in spite of the considerable potential of this group for such research, although it has long been known that *melanogaster* and *simulans* may be crossed in the laboratory and indeed do cross in nature (Sperlich, 1962).

Thirdly, it has generally proved possible to establish in cases so far studied quite detailed interspecific polytene chromosome phylogenies within species groups, either by analysis of the chromosomal rearrangements present in interspecific hybrid larvae where these may be obtained, or by direct comparisons of the banding sequences of the chromosomes of different species where hybrid larvae cannot be obtained, or by a mixture of both methods (cf. Carson and Stalker, 1968a, 1968b, 1968c, 1969; Stalker, 1966; Stone, Guest and Wilson, 1960; Wasserman, 1960). Between species groups, polytene chromosome banding sequences are generally so different that it is impossible to retrace the major steps that have occurred in chromosomal reorganization (cf. the comments of Dobzhansky and Tan, 1936, on *pseudoobscura* and *melanogaster*, members of the same subgenus but different species groups; the gene arrangements of these two species were observed to be "very profoundly different"; but cf. also Yoon, Resch and Wheeler, this Bulletin). Degrees of chromosomal polymorphism, however, vary widely both within and between species groups and are consequently *per se* of little if any diagnostic value as attributes of particular species groups.

In summary it may be generalized that the species group in *Drosophila* represents the results of a major burst of speciation within a subgenus in a particular geographic region.

Historical Considerations Pertaining to the Melanogaster Group

D. melanogaster was described by Meigen in 1830 (from European material) and is thus one of the oldest known members of the genus *Drosophila*. Many synonyms appeared in subsequent decades (*q. v.*), probably due partially to the brevity and imprecision of the original description (amounting to less than thirty

words, without figures), and partly to lack of communication among earlier workers. In the light of the large number of cryptic and sibling species now known in the genus *Drosophila*, modern species descriptions place great emphasis on attention to detail, particularly of the male genitalia, by reference to which the otherwise most similar of species may in most cases be separated.

The Dutch entomologist Doleschall, working on the fauna of the (then) Dutch East Indies, described *D. ananassae* in 1858 ("*ananassae*" from *Ananas sativa*, the pineapple, on which it was collected) from Ambon (= Amboina), a small island off the southwestern tip of Ceram. Doleschall's description, as Meigen's, was also extremely brief and vague, and several synonyms of this species were also subsequently published.

The third species to be described in what is now recognized as the *melanogaster* group was *D. montium* de Meijere 1916, also from the Southeast Asian region (Java). The misidentification of a similar and widespread form as this species by various authors was shown to be an error by Burla (1954a) who examined de Meijere's type and renamed the more widespread species *D. kikkawai*. Both of these species are now known to possess a large number of very similar relatives in the Southeast Asian area, and several more in Africa (*montium* subgroup, *q. v.*), although interestingly *montium* itself is apparently known only from de Meijere's types in the Amsterdam Museum, the species remaining to be rediscovered in the wild.

Sturtevant (1919), in the course of genetic experiments with wild north American strains of *melanogaster*, discovered a new species in Florida (also collected in other areas) morphologically extremely close to *melanogaster* but nevertheless distinguishable in the male sex by reference to the structure of the genital arch. Sturtevant figured the male genitalia of the two species and named the new species, subsequently found to be largely coextensive with *melanogaster* in geographic distribution, *D. simulans*.

In the 1920's and 30's, more extensive work was done on the Oriental and eastern Palaearctic fauna, principally by Duda, and Kikkawa and Peng. Eleven new species now placed in the *melanogaster* group were described in these two decades from this area, in addition to one species (*serrata* Malloch 1927) from Australia. In later years additional new species were described from the same areas and a few have also been described from Africa.

Sturtevant (1939) established the subgenus *Sophophora* to include those species with "ventral receptacle not finely coiled; posterior pair of Malpighian tubes free, not united at their apices; eggs with two blunt filaments; dark posterior bands of second to fifth abdominal segments broader in median dorsal line, or of uniform width." Included in the subgenus were eight species now placed in the *melanogaster* group and several other species now placed in other species groups. In 1942, Sturtevant established the *melanogaster* species group to include the following fourteen species: *melanogaster* Meigen 1830; *simulans* Sturtevant 1919; *takahashii* Sturtevant 1927; *ananassae* Doleschall 1858; *bipectinata* Duda 1923; *montium* de Meijere 1916; *auraria* Peng 1937; *unipectinata* Duda 1924; *miki* Duda 1924; *rufa* Kikkawa and Peng 1938; *nipponica* Kikkawa and Peng 1938; *ficusphila* Kikkawa and Peng 1938; *lutea* Kikkawa and Peng 1938; and *suzukii* (Matsumura) 1931. Sturtevant defined the *melanogaster* group as follows: "yel-

lowish species; rather long ventral receptacle; medium long spiral testes; no opaque areas on tergites; larvae do not skip; sex-combs present; sterno-index 0.5–0.6; anterior scutellars convergent; apparently native to tropical and subtropical regions of Old World, but several now widely distributed." For reasons apparent below, this diagnosis must now be modified for several respects.

Hsu (1949) undertook a comparative study of peripahllic organs in the family Drosophilidae, giving definitions of many of the species groups of the genus *Drosophila* in terms of the detailed structure and setation of these organs (cf. also Nater, 1953, on the importance of male genitalia in *Drosophila* taxonomy). A definition was not given for the *melanogaster* group as a whole, although within the group Hsu recognized and defined the following five subgroups comprising a total of thirteen species:

1) the *melanogaster* subgroup (*melanogaster, simulans*); "genital arch with large process on posterior margin; one clasper, primary teeth long and somewhat irregularly arranged."

2) the *montium* subgroup (*montium, rufa, auraria, ficusphila*, probably *nipponica*); "a large tooth-bearing secondary clasper present, seemingly originated by separation from anal plate; marginal bristles of primary clasper greatly enlarged."

3) the *takahashii* subgroup (*takahashii, lutea*); "one clasper, simple, with a convex row of long teeth; anal plate usually prolonged on lower portion."

4) the *ananassae* subgroup (*ananassae, bipectinata*); "secondary clasper present, tooth-bearing; primary clasper flat, primary teeth in two groups, some of the marginal bristles especially long and stout."

5) the *suzukii* subgroup (*suzukii, pulchrella*); "toe of genital arch with tube-like process; clasper one, large; primary teeth and marginal bristles separated into two groups."

Wheeler (1949a) listed an additional five species apparently belonging to the *melanogaster* group without being able to assign them to subgroups because insufficient information was provided in the original species descriptions: *illata* Walker 1860; *unipectinata* Duda 1924; *miki* Duda 1924; *serrata* Malloch 1927; and *biarmipes* Malloch 1924. Two of these species (*unipectinata* and *serrata*) were subsequently collected by later workers, redescribed in the more detailed form now generally accepted in *Drosophila* taxonomy, and assigned to subgroups (*suzukii* and *montium* respectively). The remaining three species are unknown apart from their original descriptions (except for Basden's re-examination of the *miki* type); their status is discussed below under the heading "Questionable Species."

Patterson and Stone (1952), in their discussion of the species groups of the genus *Drosophila*, included the eighteen species listed by Wheeler in the *melanogaster* group, adding notes on the geographic distributions of several of the species, most of which are "endemic to the tropical and subtropical regions of the Old World," but *melanogaster, simulans, ananassae* and "*montium*" (= *kikkawai* Burla 1954a) were noted as being considerably more widespread.

The division of the *melanogaster* group into subgroups was extended by Okada (1954), who recognized seven subgroups, viz., *suzukii, nipponica, ananassae, montium, takahashii, melanogaster*, and *ficusphila*. Okada's detailed comparative

study of the phallic organs of the *melanogaster* group species available for study led him to remove *ficusphila* and *nipponica* from the *montium* subgroup and place them in their own subgroups (the latter with another species subsequently described as *magnipectinata*).

At the time of writing, 46 species have now been described which may definitely be included in the *melanogaster group* (cf. Table 1) exclusive of the "questionables." A further 29 species are described in this paper and additional mention is made of several known too imperfectly for formal description.

Definition of the Melanogaster Species Group

Sturtevant (1942) formulated his definition of the *melanogaster* species group on the basis of the limited number of species then known. Several of the species described since the publication of Sturtevant's definition, or included in this work as new, are quite apparently members of the same major line of descent as those *melanogaster* group species known to Sturtevant and agree mostly but not completely with Sturtevant's criteria (e.g. the sterno-index of a number of species lies outside the range of 0.5–0.6). The following modified diagnosis of the *melanogaster* species group is therefore given, although it is realized that discovery of further new species in the future slightly deviant from the criteria given below may again necessitate revision of the definition. (The same considerations of course also apply to the definitions of the subgroups given through the course of this text.)

melanogaster species group:—yellowish or dull dusky species, abdomen of male shiny black distally in many species; ventral receptacle long and coiled; testes spiral, creamish to yellow (orange in *elegans*); no opaque areas on tergites; larvae do not skip; sex-combs present in all except two species of the *suzukii* subgroup; periphallic organs with well-developed genital arch including toe, bearing large bristles but without microtrichia; anal plate with large bristles, in several subgroups with differentiated lower bristles or teeth, in *nipponica* subgroup with a single large black ventromedial tooth; one or two pairs of setigerous claspers present; structures of phallic organs of very variable size and shape but anterior and posterior parameres present in almost all species.

Taxonomy of the Melanogaster Species Group

The following systematic account details the subgroups of the *melanogaster* species group and their diagnoses, treats described and new species within each subgroup, and gives records (as complete as we have been able to make them) of the geographic distribution of each species. Although excellent figures of the male genitalia of several of the described species exist in the literature, the male genitalia of almost all of the described species available to us in culture have been figured together with those of the new species in order to facilitate comparisons of as many species as possible with one another.

Holotype and allotype and five paratypes of each sex of each new species described are deposited in the Genetics Foundation, University of Texas collection, with the exception of the African species described from males only where all available specimens have been retained in the Genetics Foundation collection.

Five paratypes of each sex of each new species described from culture are also deposited in the collection of the U.S. National Museum in Washington, D.C.

1. The melanogaster Subgroup.—Hsu 1949. Univ. Tex. Publ. 4920: 121.

Medium-brown flies, male abdomens black distally. Sex-comb of male an oblique row of rounded black teeth distally on the metatarsus only. Wings clear. Genital arch broad laterally, narrower dorsally; toe with a cluster of long bristles; posterior margin of genital arch with process covering base of clasper (most strongly developed in *simulans*). Anal plate more or less oval, with numerous bristles (and large ventral teeth in *teissieri*). Primary clasper only present, with teeth more or less divisible into two sets—a medial or ventromedial row or cluster of pointed teeth, and lateral to these a row of more blunt, darker teeth. Anterior parameres of phallic organs with long apical sensilla.

1. Drosophila melanogaster

D. melanogaster Meigen 1830. Syst. Beschr. bek. europ. zweifl. Ins. 6: 85. *Type locality*: Europe.

= *nigriventris* Macquart 1843. Dipt. exot. 2,3: 259 (Tsacas, 1967a)
= *approximata* Zetterstedt 1847. Dipt. Scand. Disp. et desc. 6: 2557
= *ampelophila* Loew 1862. Berlin ent. Zeit. 7: 231
= *uvarum* Rondani 1875. Bull. Ent. Ital. 8. 86
= *pilosula* Becker 1908. Mitt. Zool. Mus. Berlin 4: 156
= *fasciata* Meigen 1830. Syst. Beschr. bek. europ. zweifl. Ins. 6: 84
= *emulata* Ray-Chaudhuri and Mukherjee 1941. Indian J. Ent. 3: 215 (Parshad, Narda and Paika, 1964).

General features: As described by Burla (1951); Kikkawa and Peng (1938); Okada (1956); and Patterson (1943).

Sex-comb: Fig. 1; cf. also Table 2.

Periphallic organs: Fig. 2. *Phallic organs*: Fig. 3.

Distribution:

AUSTRALIA—Malloch (1927), Mather (1955): eastern; Paterson (personal communication): southwestern.
NEW ZEALAND—Harrison (1952).
SAMOA—Harrison (1954); Malloch (1934a); Wheeler and Kambysellis (1966).
FIJI—Bezzi (1928); Harrison (1954).
GUAM—Bohart and Gressitt (1951).

Table 2

Numbers of teeth (means and ranges) in the sex-combs of three species within the *melanogaster* subgroup; 50 forelegs counted for each species; Australian strains of *melanogaster* and *simulans* used

Species	Mean bristle number	Range
melanogaster	9.68	7–12
simulans	9.28	7–11
yakuba	7.42	6–9

MARQUESAS Is.—Malloch (1933, 1934b).
HAWAII—Bryan (1934, 1938); Momma (1968); Zimmerman (1943).
MICRONESIA—Pipkin (1952); Wheeler and Takada (1964).
NEW GUINEA—Single pinned male in Texas collection.
PHILIPPINES—Texas stock 3135.1.
VIETNAM—Tsacas (1967a).
MALAYA—Texas stock 3033.8 (contamination?).
INDIA—Gupta and Ray-Chaudhuri (1970a, 1970b, 1970c); Parshad and Duggal (1966); Parshad, Narda and Paika (1964); Parshad and Paika (1964); Rahman and Singh (1969); Sturtevant (1927); Vaidya and Godpole (1971).
SEYCHELLES—Lamb (1914).
NEPAL—Okada (1955, 1966a).
CHINA—Kikkawa and Peng (1938); Peng (1937); Tan, Hsu and Sheng (1949).
MANCHURIA—Kikkawa and Peng (1938).
MONGOLIA—Hackman (1968).
AFGHANISTAN—Hackman (1969a).
KOREA—Chung (1955, 1958); Chung and Rho (1958); Kang, Chung and Lee (1958, 1959); Kang and Moon (1968, 1969); Kim (1963); Kim and Paik (1963); Lee (1964a, 1966a, 1966b); Paik (1957); Takada and Lee (1958).
JAPAN—Kaneko (1960); Kikkawa and Peng (1938); Makino and Kanehisa (1951); Makino *et al.* (1955); Momma (1957); Okada (1957); Wakahama (1966).
TAIWAN—Kikkawa and Peng (1938).
RUSSIA—Gershenson (1939); Hackman (1957).
EUROPE—Basden (1951, 1952, 1953a, 1953b, 1954); Burla (1949, 1951); Frydenberg (1955, 1956); Hackman (1954, 1969b); Krimbas (1963); Lever and Sobels (1951); Marien (1966); Monclus (1964); Ortiz (1970); Rasmuson (1955); Schiner (1864); Sobels, Vligin and Lever (1954); Sperlich (1962); Tsacas (1963).
AFRICA—Burla (1954b); Duda (1940) ("*ampelophila*"); Dobzhansky *et al.* (1957); Khishin (1956); Tallantire and Buruga (1971); Tsacas (1967b).
NORTH AMERICA—Johnson (1913a, 1927); Levitan (1954); Malloch and McAtee (1924); Miller and Weeks (1964); Patterson (1943); Patterson and Mainland (1944); Spiess (1951); Stephenson (1963); Wheeler and Throckmorton (1960); Williams and Miller (1952).
CENTRAL AMERICA—Heed (1956, 1957); Hunter and Newball (1961); Johnson (1908, 1913b, 1919); Patterson and Mainland (1944); Townsend and Wheeler (1955); Wasserman (1967).
SOUTH AMERICA—Brncic (1957a, 1957b); Cova Garcia and Suarez (1962); Dobzhansky and Pavan (1943); Duda (1925a) ("*ampelophila*"); Hunter (1960, 1964); Malogolowkin (1951); Mourão *et al.* (1965); Pavan and da Cunha (1947).

2. Drosophila simulans

D. simulans Sturtevant 1919. Psyche 26: 153. *Type locality*: Florida, U.S.A.

General features: As described by Burla (1951); Patterson (1943); and Sturtevant (1919).

Sex-comb: Practically identical to that of *melanogaster*; cf. Table 2.

Periphallic organs: Fig. 4. *Phallic organs*: Fig. 5.

Tsacas *et al.* (1971) give detailed comparisons of the male genitalia of *melanogaster* and *simulans* (as well as those of the interspecific hybrid); a detailed study of genital sclerite homologies between these two species is also to be found in Salles (1947).

Distribution:

AUSTRALIA—Mather (1955): eastern; Paterson (personal communication): southwestern.
NEW ZEALAND—Harrison (1952).

FIJI—Texas collection.
HAWAII—Hardy (1952); Momma (1968); Zimmerman (1943).
KOREA—Kang, Chung and Lee (1958); Lee (1966b).
JAPAN (Ogasawara Is.)—Kikkawa and Peng (1938); Komai (1937).
ADZHARISTAN—Dubinin, Sokolov and Tiniakov (1937).
EUROPE—Basden (1951, 1952, 1953b); Burla (1949, 1951); Frydenberg (1955, 1956); Krimbas (1963); Marien (1966); Monclus (1964); Ortiz (1970); Sobels, Vligin and Lever (1954); Sperlich (1962); Tsacas (1963).
AFRICA—Dobzhansky *et al.* (1957); Khishin (1956); Tallantire and Buruga (1971).
AZORES Is.—Hackman (1960).
TRISTAN DA CUNHA—Frey (1954).
NORTH AMERICA—Levitan (1954); Malloch and McAtee (1924); Patterson (1943); Patterson and Mainland (1944); Spiess (1951); Stevenson (1963); Sturtevant (1919); Williams and Miller (1952).
CENTRAL AMERICA—Heed (1956, 1957); Hunter and Newball (1961); Patterson and Mainland (1944); Townsend and Wheeler (1955); Wasserman (1967).
SOUTH AMERICA—Brncic (1957a); Cova-Garcia and Suarez (1962); Dobzhansky and Pavan (1943); Hunter (1960, 1964); Malogolowkin (1951); Mourão *et al.* (1965); Pavan and da Cunha (1947).
GALAPAGOS IS.—Wheeler (1961).

D. melanogaster and *D. simulans* are largely co-extensive in distribution throughout the Nearctic, Neotropical, Palaearctic and Australian biogeographic zones, and both species are found through a wide range of climates although most frequently associated with human habitations. *D. melanogaster* is a fly of some economic/medical significance; references exist for associations between this species and viruses, bacteria, Schizomycetes and various other classes of fungi, Protozoa, Acarina, and other insects (Greenberg, 1971). Basden (1955) did not find either *melanogaster* or *simulans* amongst Drosophilidae collected north of the Arctic Circle, or in sub-Arctic Norway (Basden, 1956). Harrison (1955) also reported fifty-eight species of Diptera from the sub-Antarctic Auckland Island, but no Drosophilidae at all were included. It may also be appropriate to mention here that although both *melanogaster* and *simulans* occur in New Zealand, no Drosophilidae are endemic to this land (Hennig, 1960). The relative abundance of *melanogaster* and *simulans* is known to be somewhat variable where the two species occur together, although *melanogaster* is generally more common in the colder environments while *simulans* is more abundant in warmer areas. The most striking feature of the distributions of these species is their rarity or absence in the Southeast Asian region where the bulk of the *melanogaster* group species occur; this phenomenon is considered further in the Discussion.

3. Drosophila yakuba

D. yakuba Burla 1954. Rev. suisse Zool. 61: 161. *Type locality*: Ivory Coast, Africa.

General features: As described by Burla (1954b).

Sex-comb: Very similar to that of *melanogaster* and *simulans* but with fewer teeth (Table 2).

Periphallic organs: Fig. 6. *Phallic organs*: Fig. 7.

Distribution:

AFRICA—Burla (1954b), Tsacas (1967b): Ivory Coast; Bock (analysis of Paterson collection): Natal.

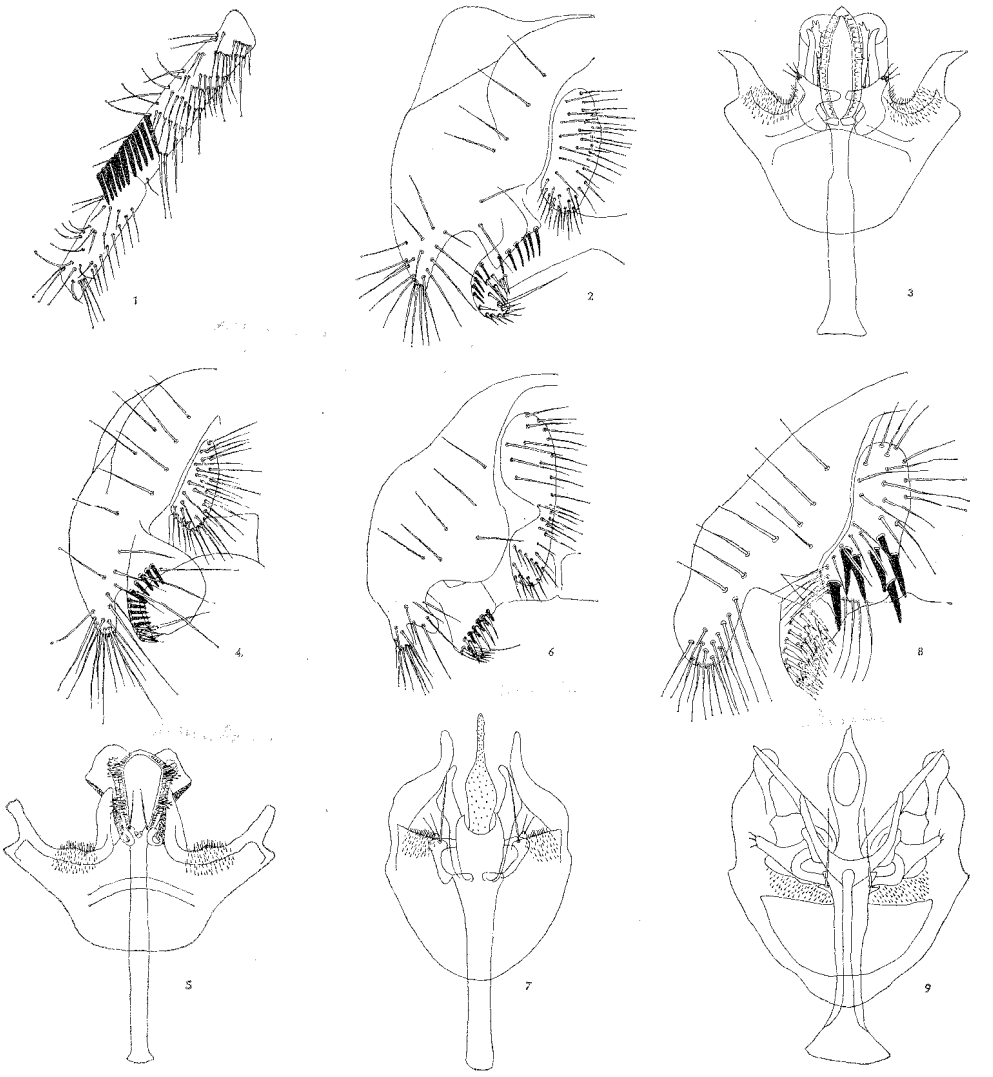


FIG. 1, 2, 3: *D. melanogaster*, sex-comb and ♂ genitalia; 4, 5. *simulans*, ♂ genitalia; 6, 7: *yakuba*, ♂ genitalia; 8, 9: *teissieri*, ♂ genitalia.

4. Drosophila teissieri

D. teissieri Tsacas 1971. Bull. Soc. ent. France 76: 35. *Type locality*: Mount Selinda, Rhodesia.

Sex-comb: Similar to those of the remaining *melanogaster* subgroup species.

Periphallic organs: Fig. 8. Anal plate with about half a dozen greatly enlarged black teeth on lower portion; numerous teeth on clasper. *Phallic organs*: Fig. 9.

Distribution: Widespread in central and western AFRICA (Tsacas, 1971).

5. Undescribed species

Tsacas (personal communication) has detected a fifth species, close to *teissieri* in the structure of the male genitalia, from Africa.

At least the first four species included in the *melanogaster* subgroup are sibling species in the generally understood sense, being separable one from another only by detailed examination of the male genitalia, although within the subgroup *melanogaster* and *simulans* constitute a pair of extremely similar species while these two are distinguished from *yakuba* and *teissieri* by somewhat more conspicuous differences in the male genitalia.

II. THE TAKAHASHII SUBGROUP.—Hsu 1949, Univ. Texas. Publ. 4920: 122.

Pale to medium-brown flies, male abdomens black distally; last segment of female abdomen brown or black. Wings clear in female, in male clear, apically dusky or with black patches. Sex-comb of male in short transverse rows of rounded black bristles on the first two tarsal segments. Genital arch narrow dorsally, broad laterally, with dorsolateral expansion; toe elongate, with numerous small and a few much larger bristles. Anal plate small, with numerous bristles, smaller below. Primary clasper only present, with a ventrolateral comb of long rounded black teeth, a few teeth dorsolaterally, and several medial bristles. Aedeagus non-bifid, bare, slender. Anterior parameres large, long, apically black, pointed. Posterior parameres large, with larger or smaller basal branches. Submedian spines on caudal margin of novasternum large and close. Basal apodeme of aedeagus somewhat longer than fragma.

1. Drosophila takahashii

D. takahashii Sturtevant 1927. Philippine J. Sci. 32: 371. *Type locality*: Taihoku, Taiwan.

General features: As described by Kikkawa and Peng (1938); Okada (1956); and Sturtevant (1927).

Sex-comb: Fig. 10; cf. also Table 3.

Periphallic organs: Fig. 11. *Phallic organs*: Fig. 12.

Distribution:

BORNEO—Okada (1964a) ♂♂ only.
PHILIPPINES—Bock (unpublished).

TABLE 3

Numbers of rows (a–d) and teeth per row (means and ranges) in the sex-combs of five species within the *takahashii* subgroup; 50 forelegs counted for each species; Taiwanese strain of *takahashii* used

	takahashii		*lutea*		*paralutea*		*trilutea*		*prostipennis*	
Metatarsus	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
a)	0.1	0–2	0.1	0–1	..	..	..	..	0.1	0–2
b)	3.5	2–5	3.2	2–4	1.1	0–3	1.6	0–3	1.9	1–4
c)	4.4	3–6	4.1	3–6	3.3	2–4	3.8	3–5	2.4	2–4
Second tarsal segment										
a)	..	..	..	..	0.1	0–1	..	..	0.1	0–1
b)	..	..	..	..	0.5	0–2	..	..	0.7	0–2
c)	1.1	1–2	1.4	1–2	1.3	1–3	1.2	1–2	1.2	1–3
d)	3.3	2–4	3.2	2–4	2.3	2–3	3.0	2–4	1.4	1–2

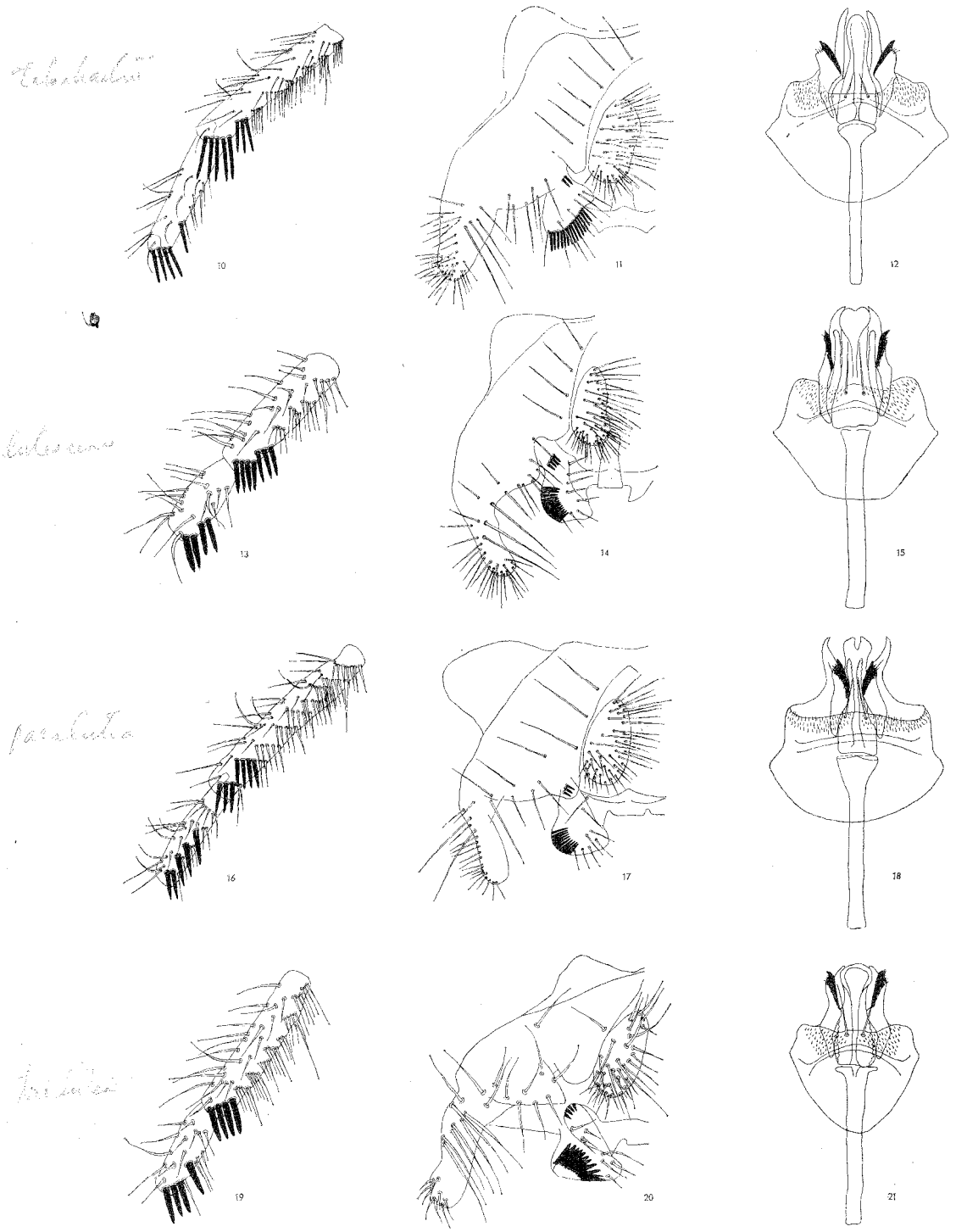


FIG. 10, 11, 12: *D. takahashii*, sex-comb and ♂ genitalia; 13, 14, 15: *lutea*, sex-comb and ♂ genitalia; 16, 17, 18: *paralutea*, sex-comb and ♂ genitalia; 19, 20, 21: *trilutea*, sex-comb and ♂ genitalia.

THAILAND—Texas stock 3250.5.
INDIA—Gupta and Ray-Chaudhuri (1970a, 1970c); Parshad and Paika (1964); Vaidya and Godpole (1971).
NEPAL—Okada (1955, 1966a).
CHINA—Kikkawa and Peng (1938); Peng (1937); Tan, Hsu and Sheng (1949).
MANCHURIA—Kikkawa and Peng (1938).
KOREA—Kim and Paik (1963); Lee (1966b); Paik (1957).
JAPAN—Okada (1956, 1964b, 1965); Takada and Wakahama (1967).
TAIWAN—Kikkawa and Peng (1938); Sturtevant (1927).

2. Drosophila pseudotakahashii

D. pseudotakahashii Mather 1957. Univ. Tex. Publ. 5721: 222. *Type locality*: Southeast Queensland, Australia.

General features: Described by Mather (1955) (*"takahashii"*).

Male genitalia: Not figured. Described by Mather (1957) as very similar to those of *takahashii*.

Distribution: Southeast Queensland, Australia (Mather, 1955).

Mather (1957) found incomplete sexual isolation between *takahashii* and *pseudotakahashii* in one direction (when *takahashii* was the male parent), coupled further with the interesting finding that offspring, where obtained, did not follow the pattern usual in interspecific crosses of producing a significant excess of the homogamic sex (Haldane's Law). Hybrid males were, however, sterile. Polytene chromosome pairing in the hybrid larvae was also observed to be poor—a characteristic of interspecific hybrids.

3. Drosophila lutea

D. lutea Kikkawa and Peng 1938. Jap. J. Zool. 7: 533. *Type locality*: Japan.

General features: As described by Kikkawa and Peng (1938) and Okada (1956).

Sex-comb: Fig. 13; cf. also Table 3.

Periphallic organs: Fig. 14. *Phallic organs*: Fig. 15.

Distribution (Map 1):

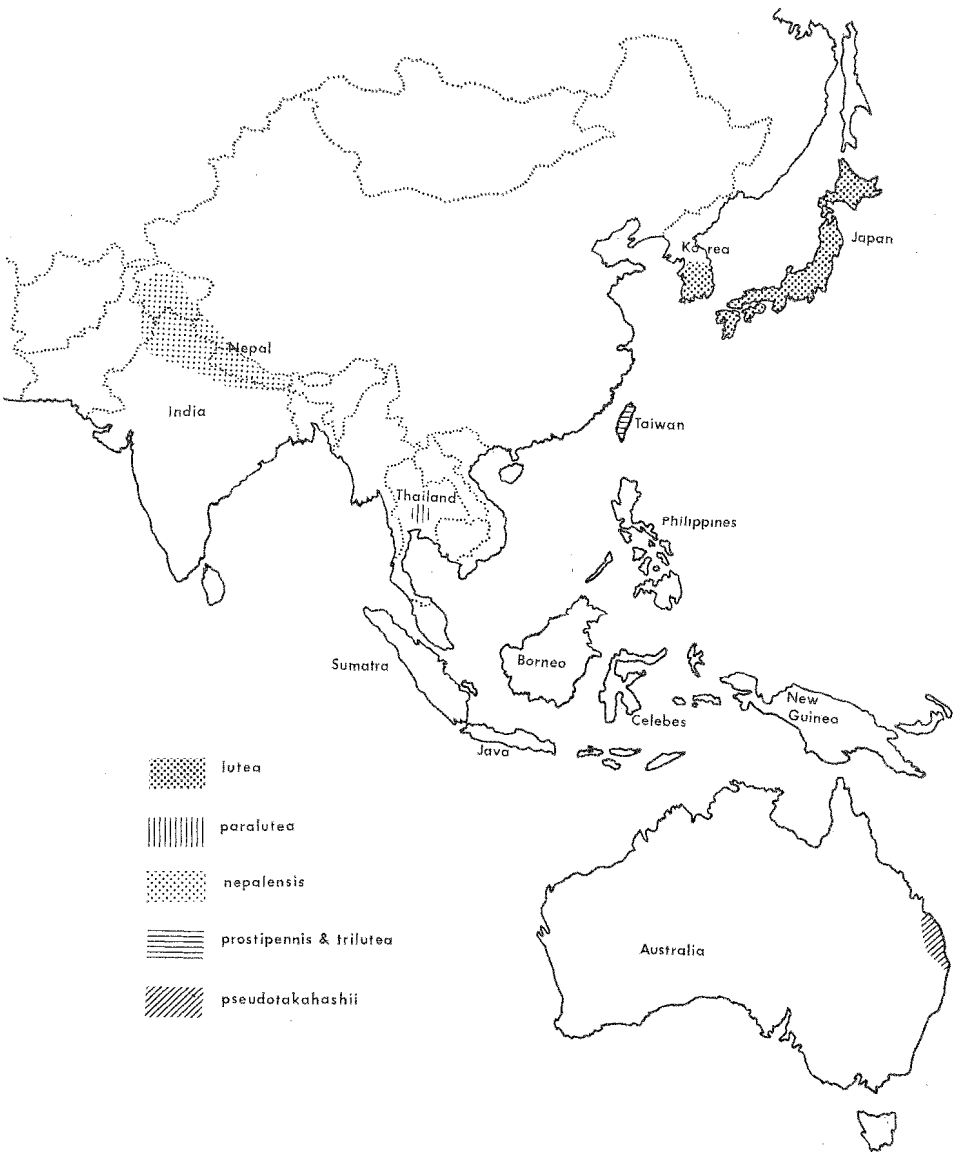
KOREA—Chung (1956); Kang, Chung and Lee (1958, 1959); Kim (1963); Kim and Paik (1963); Lee (1964a, 1966a, 1966b); Paik (1957); Takada and Lee (1958).
JAPAN—Kaneko (1960); Kikkawa and Peng (1938); Makino *et al.* (1952); Makino *et al.* (1955); Makino *et al.* (1963); Makino *et al.* (1964); Makino *et al.* (1965); Makino, Momma and Kaneko (1966); Momma (1957); Momma and Kaneko (1967); Okada (1956, 1966b); Takada (1957); Wakahama (1966).

4. Drosophila (Sophophora) paralutea SP. NOV. Bock and Wheeler

Type culture: Khao Yai, Thailand; collected by Dr. V. Baimai, March 1971. Texas stock 3250.7.

Body length: ♂ 2.2 mm.; ♀ 2.9 mm.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front pale brown. Orbital bristles in the ratio 3:1:3. Carina prominent, strongly convex. Ocelli orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.



Thorax, ♂ *and* ♀: Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6 Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 16; cf. also Table 3) in short transverse rows of stout black bristles; 2 distal metatarsal rows, and 3–4 rows on the second tarsal segment.

Wings, ♂ *and* ♀: Transparent. Approximate indices: Costal index 2.5; 4V index 2.2; 4C index 1.1; 5X index 2.2. Third costal section with heavy setation on basal half or slightly less. Wing lengths: ♂ 1.9 m.m.; ♀ 2.2 m.m.

Abdomen, ♂ *and* ♀: Tergites of female yellowish with thin apical black bands; last tergite completely black. First four tergites of male yellowish with

thin apical black bands; remaining two tergites shiny black dorsally, yellowish laterally.

Periphallic organs (Fig. 17): Black. Genital arch broad laterally, narrow dorsally. Toe elongate, finger-like, with a few very large bristles above and numerous fine bristles laterally. Primary clasper only present, with 3–5 short black teeth dorsolaterally, a ventrolateral comb of about 10 long slender rounded black teeth, and 7–8 medial bristles. Anal plate small, oval, with numerous bristles, longer above, shorter below.

Phallic organs (Fig. 18): Aedeagus slender, not hirsute or ornamented, apically broadened, slightly notched. Anterior parameres large, crescentic, articulated to aedeagus, apically black, pointed, subapically with a few tiny lateral sensilla. Posterior parameres long, with basal branches almost as long as main branches: basal branches strongly sclerotized, marginally serrate.

Egg guide: Brown, with about 15 teeth and a subterminal hair. Basal isthmus 0.35 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0 Rectal index 1.7. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.2 total length; anterior and posterior tubules of equal length.

Internal genitalia, ♂: Testes pale yellow, with 3 outer and 2 small inner coils. Accessory glands large. Ejaculatory bulb small, globular.

Internal genitalia, ♀: Spermathecae brown. Parovaria as large as spermathecae. Ventral receptacle tightly coiled.

Egg filaments: 2 long slender filaments, slightly flattened in apical quarter.

Pupae: Anterior spiracles with about 6 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y.

Distribution: Known only from the type locality in THAILAND (Map 1).

Preliminary attempts at intercrossing *lutea* and *paralutea* have indicated that some cross-inseminations may be obtained when *lutea* is the female parent in the cross.

5. Drosophila (Sophophora) trilutea SP. NOV. Bock and Wheeler

Type culture: Ali-Shan, Taiwan; collected by L. Throckmorton and F. J. Lin, summer 1967. Texas stock 3066.9.

Body length: ♂ 2.3 m.m.; ♀ 3.0 m.m.

Head, ♂ and ♀: Arista with 4–5 branches above, 3 below, plus the terminal fork. Front pale brown, pollinose. Orbital bristles in the ratio 5:2:5. Carina strongly convex. Ocelli orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax, ♂ and ♀: Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4–6 rows between dorsocentrals. Anterior scutellars strongly convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.7. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 19; cf. also Table 3) in 3–4 short transverse rows of stout black bristles; 1–2 metatarsal rows, and 2 rows on the second tarsal segment.

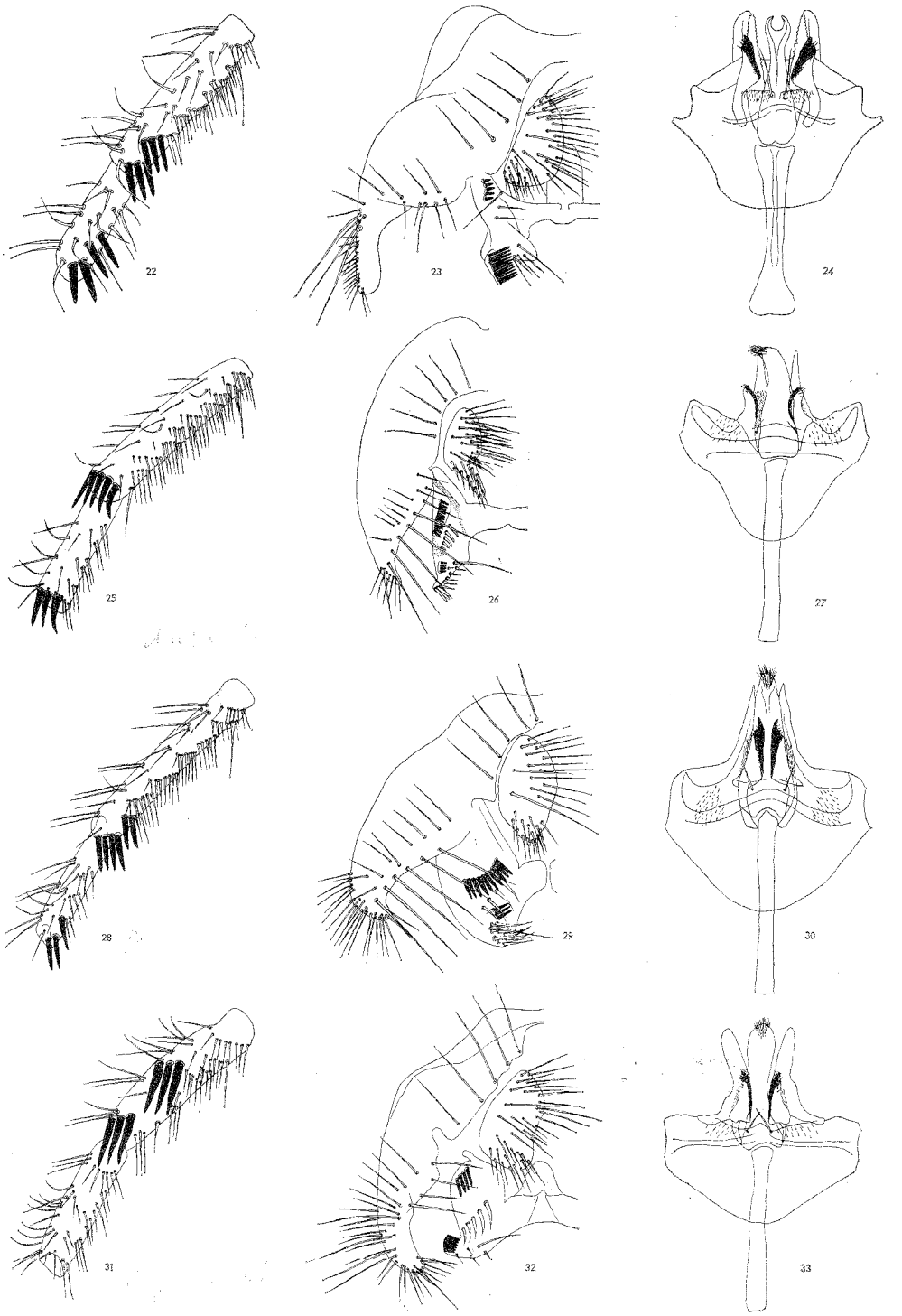


FIG. 22, 23, 24: *D. prostipennis*, sex-comb and ♂ genitalia; 25, 26, 27: *suzukii*, sex-comb and ♂ genitalia; 28, 29, 30: *pulchrella*, sex-comb and ♂ genitalia; 31, 32, 33: *rajasekari*, sex-comb and ♂ genitalia.

Wings, ♂ and ♀: Female wings clear. Male wing (Fig. 156B) slightly dusky between costa and second longitudinal vein or slightly beyond in older specimens. Approximate indices: Costal index 2.6; 4V index 2.0; 4C index 1.0; 5X index 2.0. Third costal section with heavy setation on basal third. Wing lengths: ♂ 2.2 m.m.; ♀ 2.7 m.m.

Abdomen, ♂ and ♀: Tergites of female yellowish with thin apical black bands. First 3 tergites of male similar to those of female, remaining tergites shiny black.

Periphallic organs (Fig. 20): Black. Genital arch broad laterally, narrow dorsally. Toe elongate, narrow, with 3 large and numerous small bristles. Anal plate oval, with numerous bristles. Primary clasper only present, large dorsally with a row of 4–7 short black teeth, ventrolaterally with a comb of 11–12 long black rounded teeth, medially with about 10 bristles. Decasternum with rectangular median process.

Phallic organs (Fig. 21): Aedeagus pale brown, apically rounded, not bifid, ornamented or hirsute. Anterior parameres large, distally pointed, black, with 3–4 minute subapical sensilla, proximally articulated to aedeagus. Posterior parameres large; basal branch of posterior paramere long, basally broad with serrate margin, apically pointed with straight margin (cf. *lutea, paralutea, prostipennis*).

Egg guide: Brown, with about 16 teeth and a subterminal hair. Basal isthmus 0.45 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.5. Malpighian tubules 2 anterior, free, common trunk 0.25 total length; 2 posterior, free, common trunk 0.1 total length; anterior half length of posterior.

Internal genitalia, ♂: Testes small, pale yellow, with 3 outer and 2–3 inner coils. Accessory glands larger than testes. Ejaculatory bulb small, globular.

Internal genitalia, ♀: Spermathecae bell-shaped, strongly sclerotized. Parovaria ovoid, larger than spermathecae. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, slightly flattened apically.

Pupae: Anterior spiracles with about 7 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short heterochromatic Y.

Distribution: Known only from the type locality in TAIWAN.

6. Drosophila (Sophophora) prostipennis SP. NOV., F. J. Lin

Type culture: Wulai, Taiwan; collected by L. Throckmorton and F. J. Lin, April 1968. Texas stock 3146.7.

Body length: ♂ 2.5 m.m.; ♀ 3.0 m.m.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front slightly whitish. Orbital bristles in the ratio 2:1:2. Carina prominent, convex. Ocelli orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax, ♂ and ♀: Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 irregular rows between dorsocentrals. Anterior scutellars strongly convergent. Ratio anterior/posterior dorsocentrals 0.7. Sterno-index 0.7. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 22; cf. also

Table 3) in 2 distal metatarsal rows of stout black bristles, 2 4 (usually 3) rows on the second tarsal segment.

Wings, ♂ and ♀: Female wing transparent. Male wing (Fig. 156C) gradually becoming dusky apically between the costal and third longitudinal veins, the color intensifying with age; small triangular unpigmented patch sometimes present between apex of first longitudinal vein and second longitudinal vein. Approximate indices: Costal index 2.7; 4V index 2.2; 4C index 1.1; 5X index 1.7. Third costal section with heavy setation on basal 0.4. Wing lengths: ♂ 2.2 mm.; ♀ 2.6 mm.

Abdomen, ♂ and ♀: Tergites of female with thin apical black bands. First two tergites of male with thin apical black bands; third with broad apical black band; remaining tergites shiny black dorsally, pale brown laterally narrowing posteriorly.

Periphallic organs (Fig. 23): Genital arch broad laterally, narrowed dorsally, black above, lighter below. Toe elongated, narrow, laterally and ventrally with numerous small bristles, dorsolaterally with 3 very large bristles. Primary clasper only present, large, dorsolaterally with a row of 4–5 short black teeth, ventrolaterally with a comb of 10–12 long rounded black teeth, medially with about 9 bristles one of which is elongated. Anal plate oval, black, with numerous bristles, long above, shorter below. Median lobe of decasternum rectangular.

Phallic organs (Fig. 24): Aedeagus slender, broader basally, not hirsute, apically rounded and notched. Anterior parameres large, apically pointed and black, subapically with 3 tiny lateral sensilla. Posterior parameres large, with long marginally serrate basal branches.

Egg guide: Brown, with 15–16 teeth and a large subterminal hair. Basal isthmus 0.4 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.7. Malpighian tubules 2 anterior, free, common trunk 0.3 total length; 2 posterior, free, common trunk 0.1 total length; anterior one third length of posterior.

Internal genitalia, ♂: Testes small, yellow, with 2–3 outer and 3 inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae brown, hemispherical. Parovaria very large. Ventral receptacle long, tightly coiled.

Egg filaments: 2 slender filaments, slightly flattened apically.

Pupae: Anterior spiracles with about 8 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short heterochromatic Y.

Distribution: Known only from the type locality in TAIWAN.

7. Drosophila nepalensis

D. nepalensis Okada 1955. Flora and Fauna Nepal Himalaya 1: 388. *Type locality*: Nepal.

General features: Described by Okada (1955).

Sex-comb and male genitalia: Figured by Okada (1955).

Distribution (Map 1):

INDIA—Gupta and Ray-Chaudhuri (1970c); Parshad and Duggal (1965, 1966); Parshad and Paika (1964).
NEPAL—Okada (1955, 1966a).

The *takahashii* subgroup is morphologically one of the most uniform subgroups in the *melanogaster* species group. The structure of the clasper varies little from one species to another and the sex-combs in all species are of the same basic type, i.e., transverse rows on the first two tarsal segments. The phallic organs of all species are also very similar, although species may be distinguished in some cases by the structure of the basal branch of the posterior paramere; thus *takahashii* and *pseudotakahashii* have very short basal branches; *lutea, paralutea, prostipennis* and *nepalensis* have long serrate branches, while *trilutea* has a branch which is apically pointed and not serrate. *D. nepalensis* male wings possess apical black patches (cf. *suzukii* and *elegans* subgroups); the male wings of *prostipennis* are diffusely darkened apically; male wings of the remaining species are clear with the exception of the slight darkening in *trilutea* male wings. In spite of the considerable morphological uniformity of the *takahashii* subgroup, each species may be characterized and identified by a combination of the following characteristics—coloration of male wings; number of sex-comb rows and bristles on the metatarsus and second tarsal segment; and structure of the basal branch of the posterior paramere.

III. THE SUZUKII SUBGROUP.—Hsu 1949. Univ. Tex. Publ. 4920: 122.

Pale to dark brown flies; abdomen of male black distally except in *immacularis* and *unipectinata*. Sex-comb of male in transverse rows of larger or smaller teeth on the metatarsus and second tarsal segment, oblique on the metatarsus (*rajasekari*), longitudinal (*unipectinata*), or absent (*tristipennis* and *lucipennis*). Wings clear in female, with or without apical black patches in male. Anal plate of periphallic organs with lower bristles differentiated to a larger or smaller extent in length and/or thickness from upper bristles. Primary clasper only present, large, with several sets of distinctly different teeth (lateral comb of stout black teeth on clasper of several species situated in sclerotized prominence somewhat separated from clasper). Aedeagus long, slender, non-bifid or composed of sclerotized lateral portions with membranous connection; apically hirsute or bare. Anterior parameres large, in most species *takahashii*-like, elongate, apically black, pointed. Posterior parameres large, without basal branches.

1. Drosophila suzukii

D. suzukii (Matsumura) 1931. = *Leucophenga suzukii* Matsumura 1931. Illus. Ins. Japan Empire: 366. *Type locality*: Japan.

General features: As described by Kikkawa and Peng (1938); Okada (1956); and Parshad and Paika (1964). Male wing: Fig. 156D.

Sex-comb: Fig. 25.

Periphallic organs: Fig. 26. *Phallic organs*: Fig. 27.

Distribution:

INDIA—Gupta and Ray-Chaudhuri (1970c); Parshad and Duggal (1965, 1966); Parshad and Paika (1964).
CHINA—Kikkawa and Peng (1938); Peng (1937); Tan, Hsu and Sheng (1949).
KOREA—Chung (1955, 1958); Chung and Rho (1959); Kang, Chung and Lee (1958, 1959); Kang and Moon (1968); Kim (1963); Kim and Paik (1963); Lee (1964a, 1966a, 1966b); Paik (1957); Takada and Lee (1958).
JAPAN—Kaneko and Shima (1960, 1962); Kaneko, Shima and Momma (1962); Kikkawa and Peng (1938); Makino *et al.* (1952); Makino *et al.* (1955); Makino *et al.* (1963); Makino *et al.* (1964); Makino *et al.* (1965); Makino *et al.* (1966); Makino and Takada (1959); Momma (1957); Momma and Kaneko (1967); Okada (1956, 1964b, 1965, 1966b); Takada (1957, 1958, 1960); Wakahama (1966).

Parshad and Paika (1964) established a separate subspecies (*suzukii indicus*) for the Indian populations of this species, which differ from the Japanese (type) form in a number of minor details (facial setation, average number of bristles in the sex-comb, costal index, disposition of teeth on the clasper, shape of decasternum, and number of teeth in the egg guide). The Japanese, Korean and Chinese populations should be designated *suzukii suzukii*. To what extent development of sexual isolation between these two forms has accompanied morphological divergence apparently remains to be determined.

2. Drosophila pulchrella

D. pulchrella Tan, Hsu and Sheng 1949. Univ. Tex. Publ. 4920: 198. *Type locality*: Meitan, China.

General features: As described by Okada (1956) and Tan, Hsu and Sheng (1949).

Sex-comb: Fig. 28.

Periphallic organs: Fig. 29. *Phallic organs*: Fig. 30.

Distribution:

INDIA—Gupta and Ray-Chaudhuri (1970c); Parshad and Duggal (1965, 1966).
NEPAL—Okada (1966a).
CHINA—Tan, Hsu and Sheng (1949).
JAPAN—(Oki Is.)—Wakahama (1966).
TAIWAN—Okada (1968) (identification based on a single female).

3. Drosophila unipectinata

D. unipectinata Duda 1924. Arch. Naturgesch. 90(A3): 215, 246. *Type locality*: Taiwan.

General features: Described by Duda (1924b) and Okada (1956).

Sex-comb: Longitudinal along entire length of metatarsus only (Duda, 1924b; Okada, 1956).

Periphallic organs: Figured by Okada (1956). *Phallic organs*: Figured by Okada (1954, 1956).

Distribution:

KOREA—Kang, Chung and Lee (1958); Lee (1966b).
JAPAN—Okada (1956).
TAIWAN—Duda (1924a, 1924b).

4. Drosophila tristipennis

D. tristipennis Duda 1924. Arch. Naturgesch. 90(A3): 215, 247. *Type locality*: Taiwan.

General features: Described by Duda (1924b) and Okada (1966a).

Sex-comb: absent.

Male genitalia: Figured by Okada (1966a).

Distribution:

INDIA—Sturtevant (1927).
NEPAL—Okada (1966a).
TAIWAN—Duda (1923, 1924a, 1924b); Sturtevant (1927).

5. Drosophila immacularis

D. immacularis Okada 1966. Bull. Brit. Mus. (Natur. Hist.) Entomol. Suppl. 6: 97. *Type locality*: Taplejung District, east Nepal.

General features: Described by Okada (1966a).

Sex-comb: Two transverse rows, on the distal border of the metatarsus and the distal border of the second tarsal segment (Okada, 1966a) (cf. *suzukii*).

Male genitalia: Figured by Okada (1966a).

Distribution: NEPAL (Okada, 1966a).

6. Drosophila rajasekari

D. rajasekari Reddy and Krishnamurthy 1968. Proc. Indian Acad. Sci. 68: 202. *Type locality*: Mysore, India.

= *raychaudhurii* Gupta 1969. Proc. Zool. Soc. (Calcutta) 22: 54. NEW SYN.

General features: As described by Gupta (1969) and Reddy and Krishnamurthy (1968).

Sex-comb: Fig. 31. The number of teeth in each row is variable.

Periphallic organs: Fig. 32. *Phallic organs*: Fig. 33.

Distribution:

CAMBODIA—Texas stock 3057.8.
INDIA—Gupta (1969); Gupta and Ray-Chaudhuri (1970c); Reddy and Krishnamurthy (1968); Vaidya and Godpole (1971) [as *biarmipes*].
THAILAND—Texas stock 3116.8.

7. Drosophila (Sophophora) lucipennis SP. NOV. F. J. Lin

Type Culture: Chi-Tou, Taiwan; collected by L. Throckmorton and F. J. Lin, summer 1967. Texas stock 3068.3.

Body length: ♂ 2.3 m.m.; ♀ 2.9 m.m

Head, ♂ and ♀: Arista with 4 branches above, 2 below, plus the terminal fork. Front brown in female, whitish in male. Orbital bristles in the ratio 9:4:9. Carina narrow, strongly ridged. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Brown dorsally, slightly dusky laterally. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6–8 rows between dorsocentrals. Anterior scutellars strongly convergent. Ratio anterior/posterior dorsocentrals 0.5.

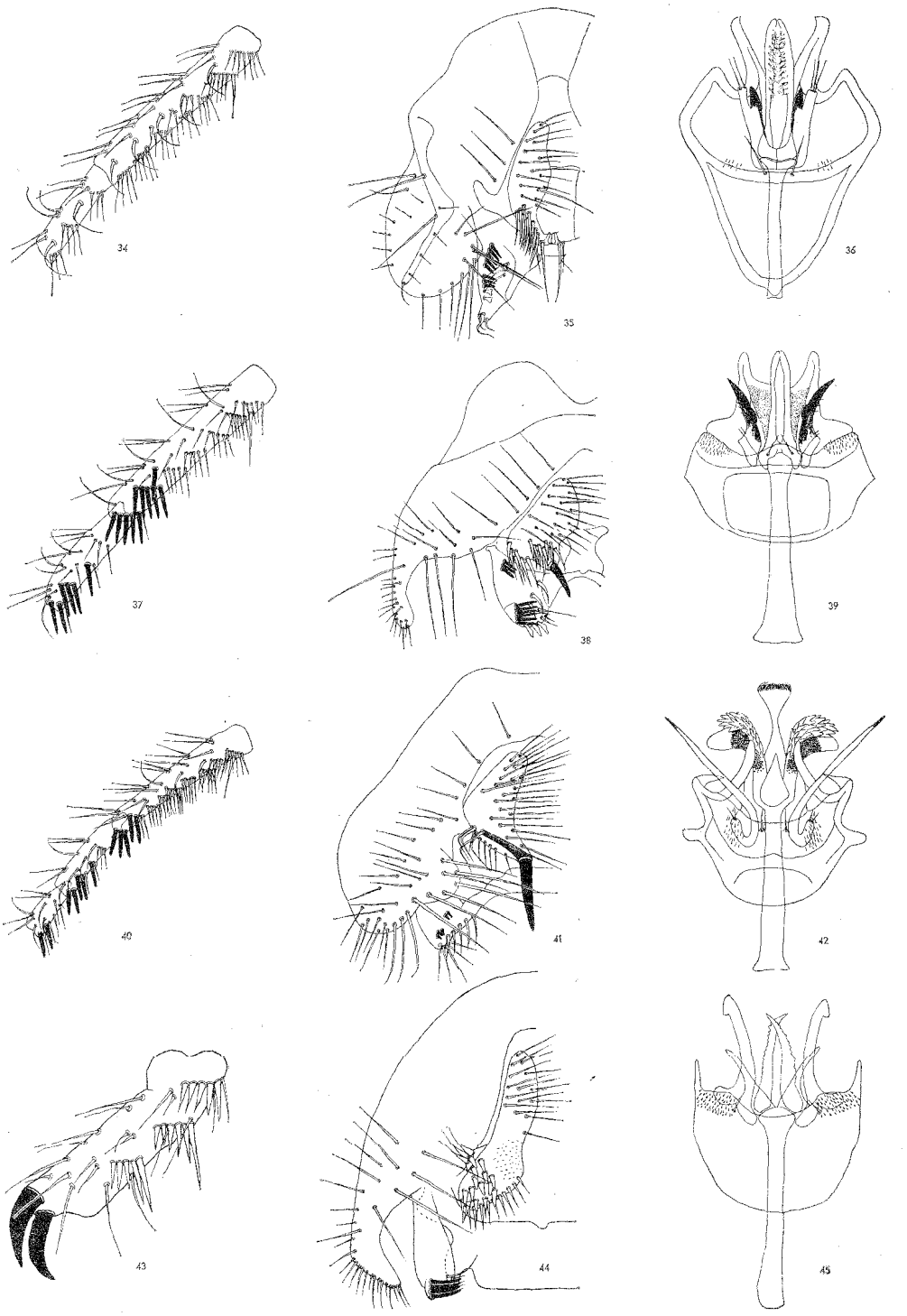


FIG. 34, 35, 36: *D. lucipennis*, first two tarsal segments of ♂ foreleg and ♂ genitalia; 37, 38, 39: *mimetica*, sex-comb and ♂ genitalia; 40, 41, 42: *elegans*, sex-comb and ♂ genitalia; 43, 44, 45: *denticulata*, sex-comb and ♂ genitalia.

Sterno-index 0.8. Preapical bristles on all tibiae; apicals on first and second tibiae. No sex-comb; male foreleg (Fig. 34) with recurved setae.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.2; 4V index 1.5; 4C index 1.4; 5X index 2.3. Third costal section with heavy setation on basal half or slightly less. Wing lengths: ♂ 2.0 m.m.; ♀ 2.4 m.m.

Abdomen, ♂ and ♀: Tergites of female with distinct apical dark bands, and brownish longitudinal mid-dorsal stripe, faint anteriorly, darker and broader posteriorly. Tergites of male dusky anteriorly, gradually darkening posteriorly to shiny black; brownish longitudinal mid-dorsal stripe evident anteriorly. Sternites of male black, faint anteriorly, dark posteriorly.

Periphallic organs (Fig. 35): Genital arch black, very broad laterally, slightly narrower dorsally. Toe very large, broadly rounded, laterally with short fine peripheral bristles, medially with large peripheral bristles. Genital arch with a very slender inner process reaching or almost reaching ventromedial border of toe, this process with 4 fine bristles along its length, 2 large basal bristles, and 1 distal apically recurved bristle. Primary clasper only present, with 4 sets of teeth —a lateral set of black rounded bristles in two groups of 5–6 above and 3–4 below; 2 short apically expanded spade-like teeth below the above; laterally with a row of 3–4 fine curved bristles; and ventrally with a cluster of 3–4 curved teeth, one of which is larger than the others and strongly recurved or S-shaped. Anal plate small, slender, dorsally with about 16 bristles, ventrally narrow, elongate, with a cluster of about 10 thicker bristles and apically with 1 very large bristle. Ventral lobes of anal plates slightly expanded apically and apparently fused in mid-line. Median lobe of decasternum large, rectangular.

Phallic organs (Fig. 36): Aedeagus slender, with very lightly sclerotized caudal feathery process. Anterior parameres large, medially contiguous proximally, apically bilobed—medial lobe black, pointed; lateral lobe apically truncate, with 2–4 long hairy sensilla. Posterior parameres large, not ornamented.

Egg guide: Pale brown, with about 16 teeth and a subterminal hair. Basal isthmus 0.35 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.0. Rectal index 1.4. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes bright yellow, small, with 2 outer and 2 inner coils. Accessory glands long and slender. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae small, strongly sclerotized, bell-shaped, very dark. Parovaria minute. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 7 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a small rod-shaped Y.

Distribution: TAIWAN.

8. Drosophila (Sophophora) mimetica SP. NOV. Bock and Wheeler

Type culture: From an area about 20 miles north of Kuala Lumpur, Malaya; collected by Dr. M. Wasserman, early 1962. Texas stock 3033.11.

Body length: ♂ 2.0 m.m.; ♀ 2.5 m.m.

Head, ♂ and ♀: Arista with 4–5 branches above, 4 below, plus the terminal fork. Front pale brown. Orbital bristles in the ratio 3:1:3. Carina strongly ridged. Ocelli pale orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax, ♂ and ♀: Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 37) in transverse rows of stout black bristles—2 lower metatarsal rows each of 4–5 bristles (sometimes an additional bristle above these rows); and 3 rows on the second tarsal segment of 1 bristle (upper row), and 2–3 bristles each (middle and lower rows).

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.9; 4V index 2.4; 4C index 1.4; 5X index 2.0. Third costal section with heavy setation on basal half or slightly more. Wing lengths: ♂ 1.7 m.m.; ♀ 2.2 m.m.

Abdomen, ♂ and ♀: Tergites of female with narrow apical black bands. First four tergites of male with narrow apical black bands; remainder of male abdomen shiny black dorsally, pale brown laterally.

Periphallic organs (Fig. 38): Genital arch dusky above; broad laterally, with median dorsal constriction. Toe elongate, narrow, with about 12 small lateral bristles. Lower portion of genital arch (above toe) with large bristles. Primary clasper only present, large, broadly triangular, with 6 sets of teeth—dorsolaterally with 2–3 long thin apically rounded black bristles; ventrolaterally with a comb of 6–7 similar bristles; dorsomedially with a row of 3–4 well-spaced, large, pointed, dusky, ventrally recurved teeth; medial to the lowermost of these 1 elongate fine hair; ventromedially 1–2 thin black dorsally recurved teeth; and between these and the ventrolateral comb (on lower border of clasper) 3 dusky teeth, broad basally, lower half of each tooth produced apically into a point. Anal plate with long fine bristles above, ventrolaterally with about 7 strong bristles, and with ventromedial lobe bearing 1 very large curved black tooth and a cluster of smaller bristles.

Phallic organs (Fig. 39): Aedeagus pale brown, bare, apically rounded; basal apodeme long. Anterior parameres large, crescentic, apically pointed, distally black, with small thin medial lobe in middle portion; sensilla laterally in 2 sets on middle and lower parts of parameres. Posterior parameres large, apically rounded, basally very broad with fine nodular ornamentation.

Egg guide: Brown, with about 16 teeth, proximally somewhat irregularly arranged. Basal isthmus 0.4 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.5. Malpighian tubules large, pale yellow; 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior subequal in length.

Internal genitalia, ♂: Testes small, pale yellow, with 3 large outer and 2–3 small inner coils. Accessory glands very large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae hemispherical, strongly sclerotized. Parovaria same size as spermathecae. Ventral receptacle long, coiled.

Egg filaments: 2 filaments, expanded and flattened in apical quarter.

Pupae: Anterior spiracles with about 8 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a pair of dots, a rod-shaped X-chromosome, and a short rod-shaped Y.

Distribution: Known only from the type locality in MALAYA.

Three of the species of the *suzukii* subgroup (*suzukii, pulchrella, rajasekari*) are characterized by the presence of an apical black patch in the male wing (Fig. 156D, E, and F respectively); in *tristipennis* the male wing possesses a narrow apical black crescent extending from the costa to about a third of the way between the fourth and fifth longitudinal veins (figured by Okada, 1966a); the male wings of *unipectinata, immacularis, lucipennis* and *mimetica* are without black patches.

The structure of the aedeagus is somewhat variable throughout the *suzukii* subgroup. In *suzukii, pulchrella* and *rajasekari* the aedeagus is fused and apically hirsute; in *lucipennis* and *mimetica* fused and apically bare (with caudal feathery process in the former species); in *immacularis* bifid and subapically hirsute; and in *tristipennis* and *unipectinata*, bifid and laterally serrate (apically bare in *tristipennis*, slightly hirsute in *unipectinata*).

The sex-combs in the *suzukii* subgroup present the largest range of forms encountered within a subgroup of the *melanogaster* species group. The sex-comb is absent in *tristipennis* and *lucipennis*; longitudinal on the metatarsus only in *unipectinata*; in 2 oblique metatarsal rows in *rajasekari*; and in transverse rows on the first 2 tarsal segments in the remaining species (1 apical row on each segment in *suzukii* and *immacularis*, several rows on each segment in *pulchrella* and *mimetica*). As pointed out by Okada (1964a), the presence of a few short, thick, hooked medial bristles on the distal portion of the mid-tibia and the proximal portion of the mid-metatarsus in males is also a general characteristic of the *suzukii, takahashii, ficusphila* and *eugracilis* subgroups with the two exceptions noted below; *suzukii, pulchrella, immacularis* and *rajasekari* possess the bristles on both tibia and metatarsus; in *tristipennis* and *lucipennis* the bristles are present on the tibia only; *mimetica*, however, lacks hooked medial bristles on the male mid-tibia and metatarsus, as also does *unipectinata* (Okada, 1964a). Similar bristles were noted within the *takahashii* subgroup by Okada (1946a) in *takahashii, lutea* and *nepalensis*; they are also present (on both tibia and metatarsus) in *paralutea, trilutea* and *prostipennis*; *pseudotakahashii* was unavailable for the present study.

The geographic range of the *suzukii* subgroup as a whole is somewhat restricted. Known species range from India and Nepal in the west to Japan, Taiwan and the Malayan peninsula in the east. The ranges of a number of species overlap broadly so that several *suzukii* subgroup species are sympatric in many areas within the above geographic limits. Representatives of the subgroup are unknown from the major Southeast Asian islands (Borneo, Philippines, etc.) east of the Malayan peninsula.

IV. THE ELEGANS SUBGROUP.—new subgroup

This subgroup is established for the single Philippine species *D. elegans*, described below, which bears some superficial resemblance to several of the

members of the *suzukii* subgroup but differs substantially in the structure of the male genitalia.

The principal gross distinguishing features of the species are (in males): wings rather plump, with apical black patches; forelegs slender, sex-comb in transverse rows on the first 3 tarsal segments; mid-tibiae without hooked medial bristles; testes deep orange, conspicuous through ventral abdominal wall; Malpighian tubules of both sexes orange, also visible through ventral abdominal wall. Anal plate crescentic, with single lower very large black medial tooth. Anterior parameres very long and slender, medially recurved. Posterior parameres large, with small medial finger-like branches. Aedeagus with subapical constriction, apically broadly flattened and hirsute.

I. Drosophila (Sophophora) elegans SP. NOV. Bock and Wheeler

Type culture: Baguio City, Luzon, Philippines; collected by L. Throckmorton and F. J. Lin, July 1968. Texas stock 3140.2.

Body length: ♂ 2.5 m.m.; ♀ 2.7 m.m.

Head, ♂ *and* ♀: Arista with 3 branches above, 2–3 below, plus a large terminal fork. Front pale, whitish. Occiput brown. Orbital bristles in the ratio 3:1:3. Carina convex. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ *and* ♀: Brown. Acrostichal hairs in 8 regular rows in front of dorsocentral bristles, irregularly arranged between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.7. Sterno-index 0.7. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 40) in transverse rows on the first 3 tarsal segments; metatarsal portion consisting of 2 distal rows of 1–2 (upper) and 2–3 (lower) teeth; portion on second tarsal segment consisting of 2–3 rows of (from above down) 0–1, 1–2, and 1–2 teeth; and portion on third tarsal segment consisting of 2 teeth, one above the other.

Wings, ♂ *and* ♀: Female wings clear. Male wing (Fig. 156H) with apical black patch. Approximate indices: Costal index 2.8; 4V index 2.1; 4C index 1.0; 5X index 2.1. Third costal section with heavy setation on basal 0.4 Wing lengths: ♂ 2.0 m.m.; ♀ 2.1 m.m.

Abdomen, ♂ *and* ♀: Tergites of female yellowish with broad black apical bands, especially pronounced in last segment. Tergites of male dark brown with slightly darker apical bands; male abdomen darker posteriorly. Sternites of male dark.

Periphallic organs (Fig. 41): Genital arch black, broad laterally and dorsally with slight mid-dorsal constriction; lower part of genital arch bilobed, lateral lobe (toe) larger, medial lobe covering base of clasper. Lower portion of genital arch with numerous bristles, larger along undermargin. Primary clasper only present, with 3 sets of teeth—a row of stout bristles along medial margin of clasper; a cluster of bristles close to lower part of medial margin; and 2 groups of 2–3 short black rounded teeth in middle region of clasper. Anal plate black, with concave medial margin. 1 very large black ventromedial tooth, a few strongly curved ventrolateral teeth, and the usual long bristles. Decasternum slender, strongly sclerotized.

Phallic organs (Fig. 42): Aedeagus slender, lightly sclerotized, constricted in mid region, apically expanded, truncate and hirsute. Anterior parameres very long, heavily sclerotized, curved towards and articulated with aedeagus, dorsally black at tip, ventral lobe with 2–4 hairy sensilla. Posterior parameres large, with numerous finger-like ornamentations medially. Caudal margin of novasternum concave, with a pair of small submedian spines.

Egg guide: Brown, with 10–11 teeth and a long subterminal hair. Basal isthmus 0.5 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.6. Malpighian tubules dark yellow; 2 anterior, free, common trunk 0.15 total length; 2 posterior, free, common trunk 0.1 total length; posterior 1.5 times length of anterior.

Internal genitalia, ♂: Testes orange, with 3–4 outer and 3 swollen inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae small, hemispherical, heavily sclerotized. Parovaria large. Ventral receptacle long, coiled.

Egg filaments: 2 vestigial filaments.

Pupae: Anterior spiracles with about 8 branches.

Chromosomes: Male metaphase plate consists of 4 pairs of rods, a rod-shaped X-chromosome, and a short J-shaped Y-chromosome.

Distribution: LUZON, PHILIPPINES.

V. THE DENTICULATA SUBGROUP.—new subgroup

This subgroup is established for the single species described below, which in general facies seems best included in the *melanogaster* group although not in any of the existing subgroups.

Males and females of *denticulata* are yellowish with distinct abdominal bands. The males are distinguished by the unique sexcomb, consisting of 2 (or 3) very large claw-like teeth on the distal border of the metatarsus, and also by the structure of the periphallic organs, especially the anal plate which possesses several different sets of teeth including a cluster of 3–4 bristles in a small lateral conical projection. The phallic organs are also unique in having very lightly sclerotized anterior parameres but long heavily sclerotized posterior parameres.

1. Drosophila (Sophophora) denticulata SP. NOV. Bock and Wheeler.

Type culture: Popondetta, New Guinea; collected by Dr. M. Wasserman, August 1961. Texas stock 3029.1.

Body length: ♂ 2.2 m.m.; ♀ 2.6 m.m.

Head, ♂ and ♀: Arista with 4–5 branches above, 3 below, plus the terminal fork. Front pale brown, pollinose. Orbital bristles in the ratio 5:2:5. Carina narrow, strongly ridged. Ocelli orange; eyes red. Greatest width of cheek 0.14 greatest diameter of eye.

Thorax, ♂ and ♀: Dorsum brown. Pleura with a broad dark brown longitudinal stripe with diffuse margins. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4–6 rows between dorsocentrals. Anterior scutellars slightly convergent; posterior scutellars crossed at right angles. Ratio anterior/posterior dorsocentrals

0.5. Sterno-index 0.5–0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 43) consisting only of 2 (or 3) very large claw-like black teeth on the distal border of the fore-metatarsus; fore femur of male unusually plump, densely pubescent, with a posteromedial row of about 9 long bristles. Mid-tibiae of male without small hooked bristles.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.2; 4V index 2.1; 4C index 1.2; 5X index 2.1. Third costal section with heavy setation on basal half. Wing lengths: ♂ 1.8 m.m.; ♀ 2.2 m.m.

Abdomen, ♂ and ♀: Tergites 2–4 of female yellowish with dull black apical bands, broader in middle; fifth tergite with narrow black apical band of uniform width; remainder of female abdomen yellowish. Tergites 2–4 of male abdomen yellowish with dark apical bands, the first 2 slightly broader in middle; remainder of male abdomen yellowish.

Periphallic organs (Fig. 44): Yellowish. Genital arch broad laterally, slightly constricted dorsally; toe narrow, curved medially, with numerous bristles along lateral and lower margins. Anal plate large, elongate, dorsally tapering, with long thin bristles dorsally; slightly broader ventrally; ventral portion with short thick teeth, pointed below, rounded above; lateral margin of anal plate with small conical projection just above lower teeth, bearing 3–4 pointed basally thickened bristles; middle portion of anal plate with microtrichia medially. Primary clasper only present, with 2 lower sets of teeth—a lateral comb of 4 long black bristles, and a few small bristles medially (the uppermost longer than the others). Decasternum rectangular, with lower lateral finger-like processes.

Phallic organs (Fig. 45): Aedeagus bifid, apically pointed, bare, laterally finely serrate. Anterior parameres very faintly sclerotized, apically very narrow, without sensilla. Posterior parameres strongly sclerotized, long and slender, apically rounded, subapically slightly hooked, basally bilobed. Caudal margin of novasternum with shallow concavity and a small pair of widely separated submedian spines.

Egg guide: Brown, with about 18 teeth (somewhat irregularly arranged proximally) and a long subterminal hair. Basal isthmus completely unsclerotized, membranous.

Internal structures, ♂ and ♀: Intestinal coiling index 1.0. Rectal index 1.3. Malphighian tubules 2 anterior, free, common trunk less than 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior longer than posterior.

Internal genitalia, ♂: Testes yellow, with 3–4 outer coils ending in an uncoiled arm, and 1 swollen inner coil. Accessory glands short, thick. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae large, strongly sclerotized, bell-shaped. Parovaria small. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long filaments, very slightly flattened in apical third.

Pupae: Anterior spiracles with about 13 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a slightly longer rod-shaped Y-chromosome with a spherical expansion at one end.

Distribution:

CAIRNS, NORTH AUSTRALIA—Bock (unpublished).
NEW GUINEA—Texas stock 3021.9.
PHILIPPINES—Bock (unpublished).

VI. The eugracilis Subgroup.—new subgroup

Duda (1924a) erected the genus *Tanygastrella* on the basis of two species found in Southeast Asia, viz., *gracilis* (Java), and *hypopygialis* (Sumatra), both described by Duda in the same paper. The attributes of these species which Duda then considered sufficient to distinguish them from *Drosophila* at the generic level were "wing indentation (i.e., costal break) in front of the first longitudinal vein only a little deeper than in *Drosophila*; abdomen noticeably small and long".

The original description of *Tanygastrella gracilis* was based on a single male. Duda (1926) subsequently obtained additional specimens from Sumatra and provided an expanded description of this species, at the same time noting "that the genus *Tanygastrella* is retainable at most as a subgenus of *Drosophila*". Duda also observed that the females of *gracilis* were not recognizable amongst the mixture of *ananassae*, *bipectinata*, etc., females in the Museum collection on which his descriptions were based, thus imputing a rather close relationship amongst all of these (*melanogaster* group) species.

As has already been mentioned, Okada (1964a) drew attention to the resemblance between *gracilis* and members of the *takahashii*, *suzukii* and *ficusphila* subgroups of the *melanogaster* group in the possession by these species of small hooked bristles on the midtibiae and metatarsi of male flies; *gracilis* also possesses a sex-comb (albeit consisting of only 2 bristles), and male genitalia typical in many respects of *melanogaster* group flies. Okada suggested that *gracilis* thus seems best included in the *melanogaster* species group.

The *Drosophila* (*Tanygastrella*) *gracilis* of Duda unquestionably resembles the large number of *melanogaster* group species now known in many fundamental respects, both in external and internal morphology. We are therefore of the opinion that this species should now be included in the *melanogaster* species group of the subgenus *Sophophora*; *Tanygastrella* thus becomes a synonym of *Drosophila* and of *Sophophora*. Unfortunately the specific name "*gracilis*" was already preoccupied in the genus *Drosophila* when Duda made use of it, having been used by Walker in 1853 (Basden, 1961; it had formerly been assumed that the "*gracilis*" of Walker was described in the genus *Scaptomyza*, whereas it was actually described in *Drosophila*). We are therefore renaming Duda's fly "*D. eugracilis*".

1. **Drosophila (Sophophora) eugracilis** NOM. NOV. Bock and Wheeler

Tanygastrella gracilis Duda 1924. Arch. Naturgesch. 90(A3):253.
Drosophila (*Tanygastrella*) *gracilis* Duda 1926. Suppl. Entomologica 14:99.
Type locality: Java.
Not = *Drosophila gracilis* Walker 1853. Ins. Brit. Dipt. 2: 239.
General features: External morphology as described by Duda (1924a, 1926) and Okada (1964a).

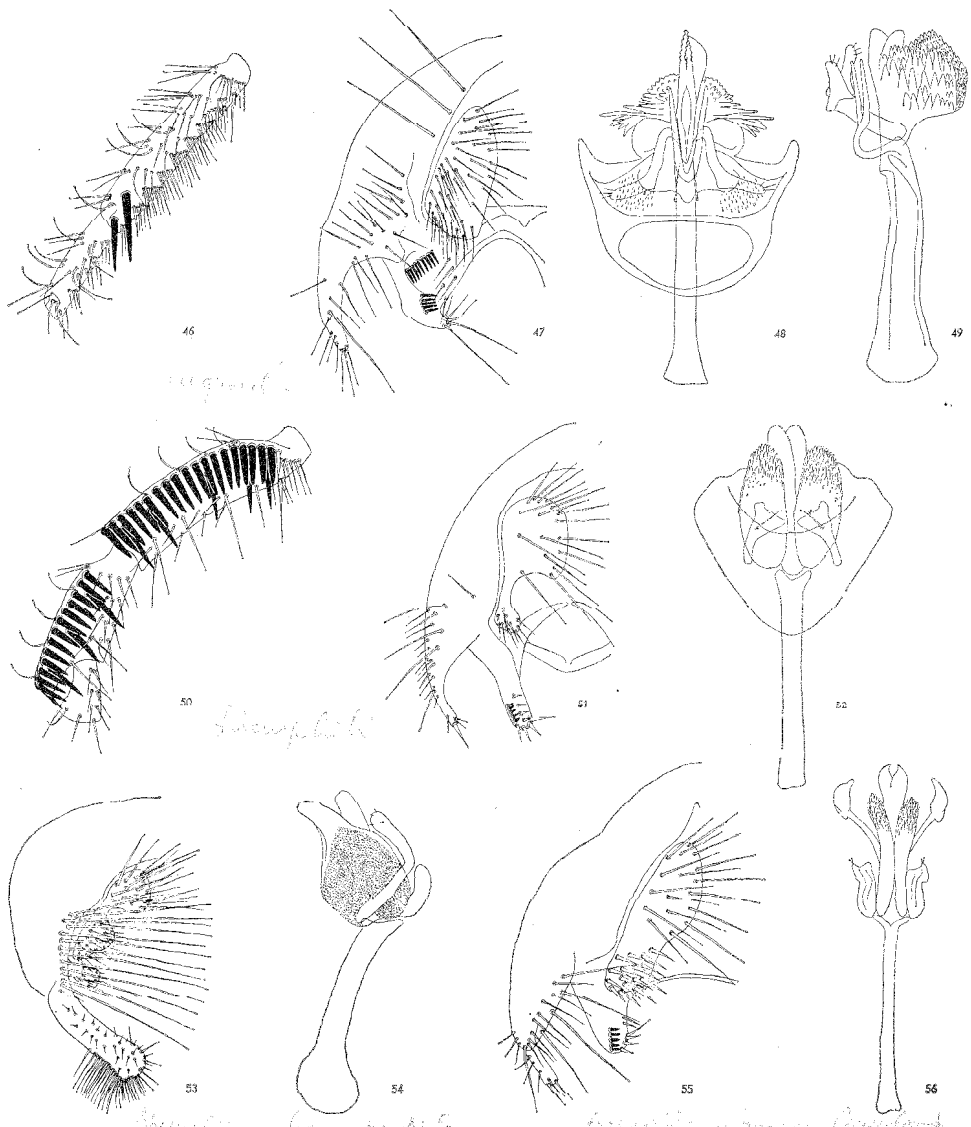


FIG. 46, 47, 48, 49: *D. eugracilis*, first two tarsal segments of ♂ foreleg and ♂ genitalia (49: lateral aspect of aedeagus and parameres); 50, 51, 52: *ficusphila*, sex-comb and ♂ genitalia; 53, 54: *ficusphila* subgp. sp. from New Guinea, ♂ genitalia; 55, 56: *ficusphila* subgp., sp. from Queensland, ♂ genitalia.

Sex-comb (Fig. 46): Consisting only of 2 very strong distal metatarsal bristles. Male forelegs with characteristic recurved setae.

Periphallic organs: Fig. 47. *Phallic organs*: Figs. 48, 49.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.3. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 4 outer and 2–3 swollen inner coils. Accessory glands large. Ejaculatory bulb oblong, globular.

Internal genitalia, ♀: Spermathecae moderately heavily sclerotized, small, conical. Parovaria spherical, as large as spermathecae. Ventral receptacle long, tightly coiled.

Egg guide: Lightly sclerotized, with about 14 teeth and a subterminal hair. Basal isthmus very lightly sclerotized, 0.3 length of lobe.

Egg filaments: 2 long slender filaments, not flattened apically.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a short rod-shaped X-chromosome, and a larger thick heterochromatic rod-shaped Y-chromosome slightly swollen at one end.

Distribution:

AUSTRALIA (northeast)—Bock (unpublished).
NEW GUINEA—Bock (unpublished).
BORNEO—Okada (1964a).
PHILIPPINES—Bock (unpublished).
JAVA—Duda (1924a).
SUMATRA—Duda (1926).
CAMBODIA—Texas stock 3057.5.
THAILAND—Texas stock 3250.13.
INDIA—Gupta and Ray-Chaudhuri (1970b); Singh (1970).

Within the *melanogaster* group, *eugracilis* is close to the *suzukii* subgroup in possession of hooked bristles on the male midlegs and in the structure of the periphallic organs (single clasper with several sets of teeth; bristles on anal plate shorter below than above). There are, however, substantial differences between *eugracilis* and the members of the *suzukii* subgroup in the structure of the phallic organs and in the male forelegs. *D. eugracilis* is therefore accorded a separate subgroup within the *melanogaster* group. The status of *hypopygialis*, Duda's second species of *Tanygastrella*, is discussed below in the Section "Questionable Species".

VII. The ficusphila Subgroup.—Okada 1954. Kontyu 22:43.

Dark flies with distinct black bands on abdominal tergites. Sex-comb of male longitudinal along entire lengths of fore-metatarsus and second tarsal segment, the latter produced apically into a prominent protuberance; sex-comb consisting of two types of teeth—an entire row of blunt close teeth, and a few irregularly spaced longer pointed teeth deep to the former (cf. Fig. 50). Wings clear. Genital arch narrow dorsally and laterally; toe elongate and narrow; setation on genital arch confined entirely to lower portion. Primary clasper only present, narrow. Anal plate elongate, narrow, with larger or smaller medial constriction in middle or lower region separating longer bristles above from shorter, sometimes thicker bristles below. Aedeagus long, slender, bare; basal apodeme considerably longer than fragma.

1. Drosophila ficusphila

D. ficusphila Kikkawa and Peng 1938. Jap. J. Zool. 7:531. *Type locality*: Central Honshu, Japan.

General features: Described by Kikkawa and Peng (1938) and Okada (1956).

Sex-comb: Fig. 50.

Periphallic organs: Fig. 51. *Phallic organs*: Fig. 52; cf. Okada (1954).
Distribution:

KOREA—Lee (1964a, 1966a, 1966b); Takada and Lee (1958).
JAPAN—Kikkawa and Peng (1938); Okada (1956, 1964b, 1965, 1966b); Takada and Wakahama (1967); Wakahama (1966).
TAIWAN—Texas stock 3075.8.
INDIA (Andaman Is.)—Gupta and Ray-Chaudhuri (1970b).

2. Undescribed species from Goroka, New Guinea.

The male genitalia of a single male (collected by Dr. H.L. Carson) of the *ficusphila* subgroup in the Genetics Foundation pinned collection of New Guinea material are shown in Figs. 53 and 54. The species is an undescribed member of the subgroup. The genital arch is distinguished by a set of extremely long bristles in its middle region; the toe is strongly developed, with scattered very small bristles, and lower lateral marginal bristles tightly clustered together. The clasper is exceptionally small, with a few small bristles. The aedeagus possesses a caudally recurved protuberance. Anterior parameres are long and curved, while posterior parameres are very large and basally expanded.

3. Undescribed species from Australia.

A further undescribed member of the *ficusphila* subgroup is known from Deeral, northern Queensland, Australia. Male genitalia are depicted in Figs. 55 and 56 (specimen courtesy of Mr. E.B. Basden of Edinburgh). The anal plate of this species is exceptionally large, with lower teeth strongly differentiated from the upper teeth. The anterior parameres are large and somewhat irregularly shaped; posterior parameres are bilobed, with medial lobulate process and lateral branch ending in an apically pointed expansion.

VIII. THE NIPPONICA SUBGROUP.—Okada 1954. Kontyu 22: 43.

This small, apparently rather homogeneous subgroup comprises three species known only from Japan and Korea. The principal diagnostic features of the subgroup (males) are a longitudinal sex-comb on the first two tarsal segments; anal plate with a single very large tooth ventromedially in addition to the usual bristles; primary clasper only present, with a row of stout teeth along its medial margin; and aedeagus branched or serrate.

1. Drosophila nipponica

D. nipponica Kikkawa and Peng 1938. Jap. J. Zool. 7:531. *Type locality*: Ayabe, Honshu, Japan.
General features: Described by Kikkawa and Peng (1938) and Okada (1956).
Periphallic organs: Figured by Okada (1956). *Phallic organs*: Figured by Okada (1954).
Distribution:

KOREA—Chung (1958); Lee (1964a, 1966a, 1966b); Makino *et al.* (1957); Takada and Lee (1958).

JAPAN—Kaneko and Shima (1962); Kaneko, Shima and Momma (1962); Kikkawa and Peng (1938); Makino *et al.* (1955); Makino *et al.* (1963); Makino *et al.* (1964); Momma (1957); Momma and Kaneko (1967); Okada (1956); Takada (1958); Wakahama (1966).

2. Drosophila magnipectinata

D. magnipectinata Okada 1956. Systematic Study of Drosophilidae and Allied Families of Japan: 113. *Type locality*: Sapporo, Hokkaido, Japan.

= "Sp from Sapporo" Okada 1954. Kontyu 22: 39.

General features: Described by Okada (1956).

Sex-comb and male genitalia: Figured by Okada (1956).

Distribution:

KOREA—Kang, Chung and Lee (1959); Kim and Paik (1957); Lee (1964a, 1966a, 1966b); Paik (1957).

JAPAN (Hokkaido)—Kaneko and Shima (1962); Makino *et al.* (1955); Makino *et al.* (1963); Makino *et al.* (1965); Momma (1957); Okada (1956); Takada (1957); Takada *et al.* (1953) ("*megalopectinata*").

Okada (1956) included a description of a female "sp. like *magnipectinata*" following his description of *magnipectinata*. This species was subsequently rediscovered and fully described by Takada and Okada (1960) as *D. mommai*. Okada (1966a) included three new species from Nepal in the "*mommai* group" within the subgenus *Sophophora*. This group was characterized as follows: "Male fore-leg without sex-comb. Mesonotum highly convex. Anterior reclinate orbital minute. Only one prominent oral. Anterior paramere of phallic organs large, hairy, usually with a longitudinal row of sensilla. Aedeagus hairy, often with a pair of basal elongate processes."

3. Drosophila clarofinis

D. clarofinis Lee 1959. Korean J. Zool. 2:43. *Type locality*: Kongju, South Korea.

General features: External morphology described by Lee (1959).

Sex-comb and periphallic organs: Figured by Lee (1959).

Phallic organs: Not described or figured.

Distribution: KOREA (Lee, 1959, 1964a, 1966b).

IX. THE ANANASSAE SUBGROUP.—Hsu 1949. Univ. Tex. Publ. 4920:122.

Pale to dark flies; male abdomens black distally in some species. Sex-comb in transverse rows on the first two or three tarsal segments of male foreleg, or one or two longitudinal or oblique metatarsal rows with one or a few additional teeth on the second tarsal segment. Wings clear. Primary and secondary claspers present (except *varians*). Primary clasper with two sets of teeth—a medial row or cluster of pointed teeth (one somewhat longer than the others), and a lateral row of blunt black teeth (in most species in 2 groups; dorsal row on clasper of *varians*). Secondary clasper small, elongate, with a very large black medial tooth and a few tiny additional ventral or lateral hairs. Aedeagus bifid, apically hooked and bare, or non-bifid and hirsute.

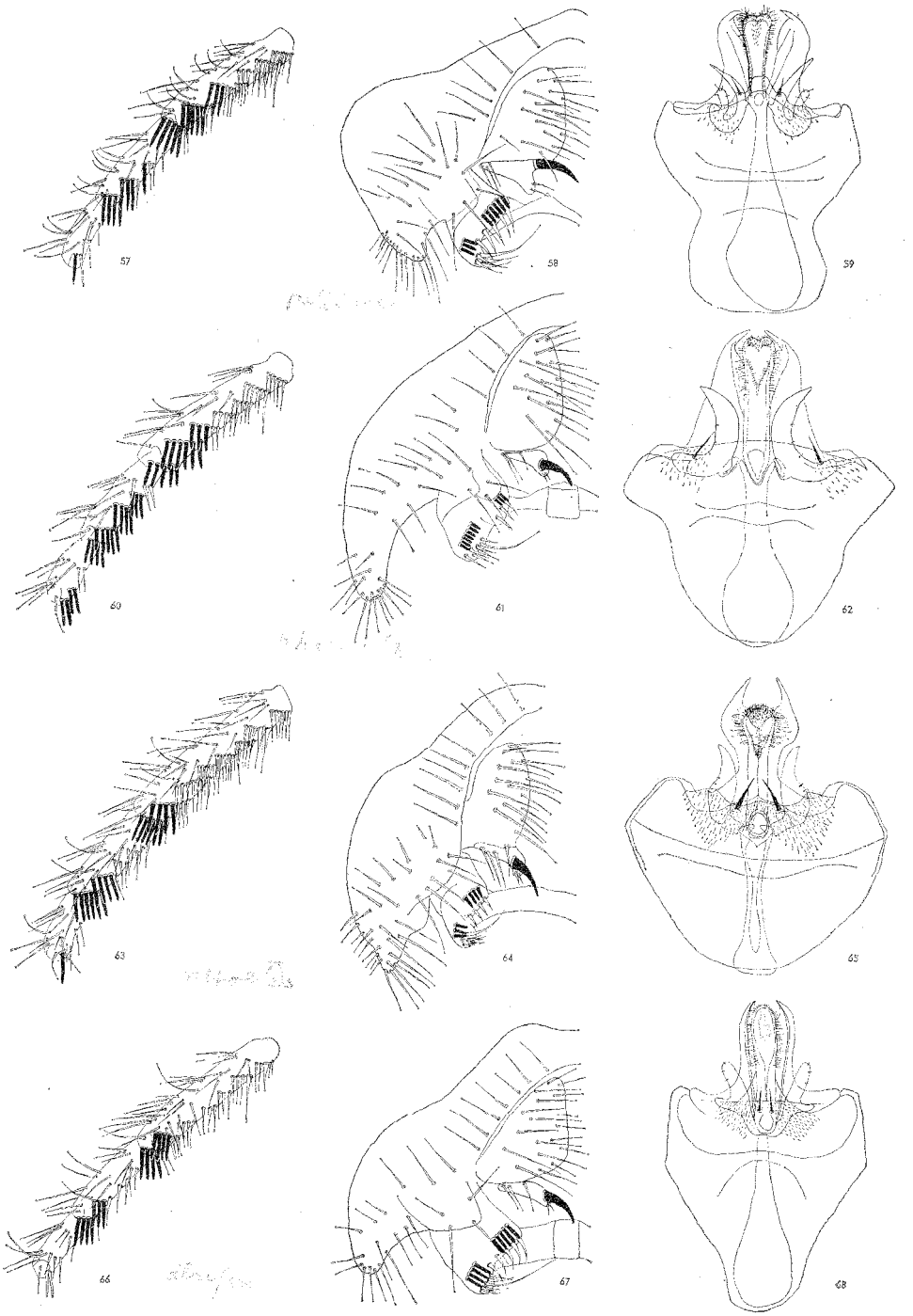


FIG. 57, 58, 59: *D. pallidosa*, sex-comb and ♂ genitalia; 60, 61, 62: *phaeopleura*, sex-comb and ♂ genitalia; 63, 64, 65: *nesoetes*, sex-comb and ♂ genitalia; 66, 67, 68: *atripex*, sex-comb and ♂ genitalia.

1. Drosophila ananassae

D. ananassae Doleschall 1858. Nat. Tijd. Ned. Ind. 17:128. *Type locality*: Ambon Is., Indonesia.

= *imparata* Walker 1859. Proc. Linn. Soc. Lond. 3:126 (de Meijere, 1908).

= *similis* Lamb 1914. Trans. Linn. Soc. Lond. II 16:347 (preoccupied).

= *errans* Malloch 1933. Bull. Bishop Museum 114:21, nom. nov. for *similis* Lamb.

= *caribea* Sturtevant 1916. Ann. Entomol. Soc. Amer. 9:335 (Kikkawa, 1935).

General features: As described by Kikkawa and Peng (1938); Patterson (1943); Sturtevant (1916).

Sex-comb: Transverse rows on the first 2 tarsal segments; (5) metatarsal rows of (from above down) 2–3, 2–4, 4–6, 5–7, and 5–8 teeth; and 3–4 rows on the second tarsal segment of (from above down) 0–2, 3–4, 3–5, and 3–5 teeth; a further tooth generally present apically on the third tarsal segment.

Periphallic organs: Figured by Hsu (1949); Kikkawa and Peng (1938); Malogolowkin (1948); and Wheeler and Takada (1964). *Phallic organs*: Figured by Malogolowkin (1948); Okada (1954); and Wheeler and Takada (1964).

The periphallic and phallic organs of *ananassae* and *pallidosa* (Figs. 58, 59) are virtually indistinguishable.

Chromosomes: Metaphase chromosomes figured by Kaneshiro and Wheeler (1970). Salivary chromosomes figured in Stone *et al.* (1957), further discussed by Futch (1966).

Distribution:

AUSTRALIA—eastern: Barker (personal communication).
FIJI—Bezzi (1928); Harrison (1954).
SAMOA—Futch (1966); Harrison (1954); Malloch (1934a); Wheeler and Kambysellis (1966).
GUAM—Bohart and Gressitt (1951).
POLYNESIA+MELANESIA—Curran (1936).
MARQUESAS IS.—Malloch (1933, 1934b).
HAWAII—Hardy (1952); Momma (1968); Zimmerman (1943).
MICRONESIA—Pipkin (1952); Wheeler and Takada (1964).
NEW GUINEA—Futch (1966).
EAST INDIES (Indonesia)—Duda (1923).
BORNEO—Okada (1964a).
PHILIPPINES—Texas stock 3135.1.
AMBON IS.—Doleschall (1858).
JAVA—Sturtevant (1927).
SUMATRA—de Meijere (1908); Duda (1926); Sturtevant (1927).
INDIA—Gupta and Ray-Chaudhuri (1970b, 1970c); Parshad and Duggal (1965, 1966); Parshad and Paika (1964); Rahman and Singh (1969); Singh (1970); Vaidya and Godpole (1971).
SEYCHELLES—Lamb (1914) ("*similis*").
CHINA—Kikkawa and Peng (1938); Peng (1937); Tan, Hsu and Sheng (1949).
JAPAN (Honshu and Ogasawara Is.)—Kikkawa and Peng (1938).
TAIWAN—Duda (1923, 1924a, 1924b); Kikkawa and Peng (1938); Sturtevant (1927).
EUROPE—Basden (1953b, 1954); Monclus (1964); Prevosti (1953).
AFRICA—Burla (1954b); Tsacas (1967b); Tallantire and Burugo (1971).
NORTH AMERICA—Kikkawa (1935); Patterson (1943); Patterson and Mainland (1944); Patterson and Wagner (1943); Sturtevant (1916) ("*caribea*").

CENTRAL AMERICA—Duda (1925a); Heed (1956, 1957); Hunter and Newball (1961); Patterson and Mainland (1944); Townsend and Wheeler (1955).
SOUTH AMERICA—Brncic (1957a); Cova-Garcia and Suarez (1962); Dobzhansky and Pavan (1943); Duda (1925a, 1925b); Frota-Pessoa (1952); Malogolowkin (1951); Mourão *et al.* (1965); Pavan and da Cunha (1947); Sturtevant (1916) ("*caribea*").

D. ananassae has been recorded from all six biogeographic zones, although it is conspicuously absent from some areas. Its range in North America extends only as far northward as southern Texas, Florida and the intermediate states of the U.S.A. The species appears to be rare in Australia, although it is abundant in New Guinea and many Pacific islands. Records for the African continent are scant but *ananassae* appears to be widespread there.

Futch (1966) demonstrated that several of the populations of *ananassae* have attained varying degrees of sexual isolation from one another: the "light" and "dark" forms of the Fiji-Samoa area were, in addition, shown to be completely reproductively isolated in nature and the "light" form is therefore here accorded specific status (*q.v.*). A range of intensities of abdominal coloration is also known in *ananassae*, from very dark in the Fiji-Samoa area to very pale in Micronesia. Futch further demonstrated a high sexual isolation between the New Guinea strains which he used in his investigation and the Pacific dark strain, suggesting that the New Guinea populations represented a separate species. The evolutionary position within *ananassae* is certainly complex; varying degrees of sexual isolation exist between the various populations of New Guinea and the neighboring British Solomon Islands (Bock, unpublished). We do not believe that a new species should be recognized among the New Guinea populations of *ananassae* unless further work done to clarify the relative evolutionary status of the various populations in this area, and the relationships of these populations to others of *ananassae*, indicates that this is clearly warranted.

2. Drosophila (Sophophora) pallidosa SP. NOV. Bock and Wheeler

Type culture: Fiji; collected by M. R. Wheeler, Summer 1966. Texas stock 3044:12.
= "light" form of "*ananassae*."
Body length: ♂ 2.2 mm; ♀ 2.5 mm.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front pale brown, pollinose. Orbital bristles in the ratio 5:2:5. Carina broad, convex. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.5. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 57) in transverse rows of (from above down) 0–2, 2–3, 5–6, and 4–7 teeth; 3 rows on the second tarsal segment of (from above down) 1, 3–4, and 3–4 teeth; and an additional tooth apically on the third tarsal segment.

Wings, ♂ *and* ♀: Transparent. Approximate indices: Costal index 1.7; 4V

index 2.2; 4C index 1.5; 5X index 2.2. Third costal section with heavy setation on basal half. Wing lengths: ♂ 1.8 mm; ♀ 2.0 mm.

Abdomen, ♂ and ♀: Tergites of both sexes pale brown with dark posterior bands of uniform width, fainter posteriorly.

Periphallic organs (Fig. 58): Genital arch broad laterally, narrow dorsally; toe with about a dozen large bristles. Primary and secondary claspers present. Primary clasper large, with 5–6 large medial teeth, a ventromedial cluster of teeth (one greatly elongated, curved towards decasternum), and lateral to these a row of rounded black teeth in 2 sets of 5–7 (above) and 3–4 (below). Secondary clasper small, with a very large curved black medial tooth and a few small hairs. Decasternum narrow, with median dorsal protuberance.

Phallic organs (Fig. 59): Aedeagus brown, non-bifid, hirsute. Anterior parameres strongly recurved, articulated to aedeagus, dorsally pointed, at opposite end rounded with 4 minute sensilla. Posterior parameres large, sheathing aedeagus. Caudal margin of novasternum with prominent median convexity and short stout submedian spines.

Egg guide: Brown, with about 14 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.5. Malpighian tubules 2 anterior, free, common trunk less than 0.1 total length; 2 posterior, free, common trunk less than 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3–4 outer and 2–3 small inner coils. Accessory glands strongly recurved. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae elongate, strongly sclerotized. Parovaria small. Ventral receptacle very long, tightly coiled.

Egg filaments: 2 filaments, expanded and flattened in apical third.

Pupae: Anterior spiracles with branches tightly clustered.

Chromosomes: Discussed by Futch (1966).

Distribution: FIJI and SAMOA (Texas collections).

Although the genus *Drosophila* abounds in pairs or groups of exceedingly similar species, there are few that cannot be separated by detailed examination of the male genitalia and in this respect *ananassae* and *pallidosa* are exceptional. Stone *et al.* (1966), discussing these species, made the following generalization. "If given no choice of mate, they cross and the F_1 and F_2 show no, or minor, residual isolation. This complete initial isolation is, therefore, sexual (behavioral) and dependent on no other isolating factors for its success." Futch (1966), in addition to finding evidence of complete ethological isolation between *ananassae* and *pallidosa* in nature, noted differences in inversion patterns between the two species. Johnson *et al.* (1966) investigated isozyme polymorphisms and found that *ananassae* and *pallidosa* have attained different polymorphic balances for a number of enzyme systems. According to Narise (1966), *ananassae* and *pallidosa* show differences in migratory activity (dependent on strains used and relative composition of the experimental populations) under competitive conditions. One morphological difference (apart from coloration) between the two species may serve as a criterion for separation of males, i.e. the reduced number of rows

in the sex-comb of *pallidosa* in comparison with *ananassae*. To the extent that one may judge remoteness of common ancestry from degrees of similarity between species (especially in the male genitalia), the phylogenetic separation of *ananassae* and *pallidosa* must have been one of the most recent events of speciation in the *melanogaster* group.

3. **Drosophila (Sophophora) phaeopleura** SP. NOV. Bock and Wheeler

= sp. 5 of Kaneshiro and Wheeler 1970. Drosophila Information Service 45:143.

Type culture: Fiji; collected by M. R. Wheeler, summer 1966. Texas stock 3044.4.

Body length: ♂ 2.1 mm; ♀ 2.4 mm.

Head, ♂ and ♀: Arista with 4–5 branches above, 3 below, plus the terminal fork. Orbital bristles in the ratio 5:2:5. Carina prominent, convex, dorsally with very narrow ridge. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.5. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 60) in transverse rows of stout black bristles; 3–4 metatarsal rows of (from above down) 0–4, 2–5, 5–6, and 4–6 teeth; 3–4 rows on the second tarsal segment of (from above down) 0–4, 3–5, 5–6, and 4–6 teeth; and 2 rows on the third tarsal segment (upper 1–3, lower 1–2 teeth).

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.6; 4V index 2.7; 4C index 1.7; 5X index 2.3. Third costal section with heavy setation on basal 0.5–0.6. Wing lengths: ♂ 1.9 mm; ♀ 2.0 mm.

Abdomen, ♂ and ♀: Tergites of both sexes brown (darkening considerably with age to dusky), with darker posterior bands of uniform width, fainter posteriorly.

Periphallic organs (Fig. 61): Genital arch narrow dorsally and ventrally; toe elongate, with about 14 bristles. Primary and secondary claspers present. Primary clasper large, with 2 sets of teeth—a medial row of 3 strong pointed upper teeth and a cluster of about 7 lower pointed teeth (one greatly elongated, curved towards decasternum); and a lateral row of thicker blunt black teeth in 2 portions, an upper of 3 and a lower of 7 teeth. Secondary clasper small, with a very large curved black medial tooth, 2 minute medial hairs, and 3 small lateral bristles. Decasternum large, tapering laterally.

Phallic organs (Fig. 62): Aedeagus brown, non-bifid, strongly hirsute, apically with median indentation. Anterior parameres very large, crescentic, articulated to aedeagus, laterally with 4 well-spaced minute sensilla. Posterior parameres large, broad basally, strongly tapering apically, extending past tip of aedeagus. Submedian spines on caudal margin of novasternum widely separated.

Egg guide: Brown, with about 12 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.5. Malpighian tubules yellow; 2 anterior, free, common trunk 0.1 total length; 2

posterior, free, common trunk 0.15 total length; anterior and posterior subequal in length.

Internal genitalia, ♂: Testes yellow, with 3 large outer and 2–3 small inner coils. Accessory glands large, curved. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae elongate, brown, strongly sclerotized. Parovaria about half size of spermathecae. Ventral receptacle long, tightly coiled.

Egg filaments: 2 slender filaments, flattened in apical third.

Pupae: Anterior spiracles with about 15 branches.

Chromosomes: Metaphase chromosomes figured by Kaneshiro and Wheeler (1970). Polytene chromosomes consist of 4 long autosomal arms and 2 shorter X-chromosome arms embedded in a large chromocentre.

Distribution: FIJI (Texas collections): Viti Levu and Vanua Levu.

D. phaeopleura is a third member of the *ananassae* cluster, apparently restricted in distribution to Fiji and hence sympatric there with both *ananassae* and *pallidosa*. In general coloration, *phaeopleura* is practically indistinguishable from the sympatric *ananassae* (i.e., the darkly pigmented form of the species), but males of *phaeopleura* may be distinguished from males of *ananassae* by the more extensive development of the sex-comb on the third tarsal segment of *phaeopleura* and especially by the distinct differences between the phallic organs of the two species, and by the slightly darker pleurae.

4. **Drosophila (Sophophora) nesoetes** SP. NOV. Bock and Wheeeler

Type culture: Palau, Caroline Is., Micronesia; collected by Dr. H. L. Carson, January 1968. Texas stock 3069.3.

=="sp. 3" of Kaneshiro and Wheeler 1970. Drosophila Information Service 45.143.

Body length: ♂ 2.4 mm; ♀ 2.6 mm.

Head, ♂ and ♀: Arista with 4–5 branches above, 3–4 below, plus the terminal fork. Orbital bristles in the ratio 3:1:3. Carina slightly convex. Ocelli orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 8 rows also between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.5. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 63) in transverse rows of stout black bristles; 2–3 metatarsal rows of (from above down) 0–1, 4–6, and 6–7 teeth; 2–3 rows on the second tarsal segment of (from above down) 0–1, 4–5, and 5–7 teeth; and a further bristle on the distal border of the third tarsal segment.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.5; 4V index 2.4; 4C index 1.7; 5X index 2.0. Third costal section with heavy setation on basal 0.6. Wing lengths: ♂ 1.9 mm; ♀ 2.0 mm.

Abdomen, ♂ and ♀: Tergites of both sexes pale brown with thin posterior dark bands; male abdomen slightly darker posteriorly. Abdomen of both sexes unusually plump.

Periphallic organs (Fig. 64): Genital arch broad laterally, narrow dorsally; toe acutely rounded, with numerous bristles. Primary and secondary claspers present. Primary clasper large, with 2 sets of teeth—a medial row of 4 upper and

7–8 lower teeth (one of the lower teeth greatly elongated, curved towards decasternum); and a lateral row of about 7 stout blunt black teeth in 2 sets of about 4 above and 3 below. Secondary clasper small, with a very large curved black medial tooth, 2 tiny medial hairs, and 3 larger lateral hairs; secondary clasper apparently fused to anal plate. Decasternum elongate-quadrate.

Phallic organs (Fig. 65): Aedeagus brown, non-bifid, apically flattened and expanded with 2 lateral projections, strongly hirsute. Anterior parameres very large, crescentic, with 3 minute lateral sensilla in middle region. Posterior parameres large, proximally fused, distally curved and pointed, extending past tip of aedeagus. Submedian spines on caudal margin of novasternum large.

Egg guide: Brown, with 14–15 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.4. Malpighian tubules yellow; 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior subequal in length.

Internal genitalia, ♂: Testes yellow, with 3 large outer and 2 small inner coils. Accessory glands large, curved. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae ovoid, strongly sclerotized. Parovaria tiny, about a quarter size of spermathecae. Ventral receptacle long and tightly coiled.

Egg filaments: 2 slender filaments, flattened in apical fifth.

Pupae: Anterior spiracles with about 10 branches.

Chromosomes: Metaphase chromosomes figured by Kaneshiro and Wheeler (1970). Polytene chromosomes consist of 4 long autosomal arms and 2 shorter X-chromosome arms embedded in a large chromocentre.

Distribution: PALAU.

As a fourth member of the *ananassae* cluster, *nesoetes* is known only from Palau in Micronesia where it is sympatric with the usual light form of *ananassae* and from which it may be distinguished in the male sex by the lesser development of the sex-comb in *nesoetes* and by the marked differences in the phallic organs between the two species.

5. **Drosophila (Sophophora) atripex** SP. NOV. Bock and Wheeler

Type culture: Laguna, Luzon, Philippines; collected by M. Delfinado, April 1967.

= "sp. 2" of Kaneshiro and Wheeler 1970. Drosophila Information Service 45:143.

Body length: ♂ 2.3 mm; ♀ 2.5 mm.

Head, ♂ and ♀: Arista with 4–5 branches above, 3 below, plus the terminal fork. Orbital bristles in the ratio 2:1:2. Carina slightly convex, dorsally very narrow. Ocelli orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae.

Sex-comb of male (Fig. 66) in 2 transverse rows on the second tarsal segment (upper 3–5, lower also 3–5 teeth).

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.6; 4V index 2.4; 4C index 1.6; 5X index 2.1. Third costal section with heavy setation on basal half. Wing lengths: ♂ 1.8 mm; ♀ 2.0 mm.

Abdomen, ♂ and ♀: Tergites of female yellow-brown with dark apical bands. Tergites 2 and 3 of male similar to those of female; remainder of male abdomen shiny black.

Periphallic organs (Fig. 67): Genital arch narrow dorsally, broader laterally, with rounded process covering base of primary clasper; toe with about 9 bristles. Primary and secondary claspers present. Primary clasper large, with 2 sets of teeth—a medial row of 11–12 teeth, pointed, distally slightly curved, one lower tooth greatly elongated towards decasternum; and a lateral row of 9–10 teeth in 2 sets of 4–5 teeth each, black, straight, blunt. Secondary clasper small, elongate-ovoid, with a very large curved black medial tooth and 5 tiny additional hairs. Anal plate small. Decasternum quadrate.

Phallic organs (Fig. 68): Aedeagus brown, non-bifid, apically strongly hirsute. Anterior parameres large, with dorsal and ventral lobes, articulated to aedeagus, with 3 minute apical sensilla on dorsal lobe. Posterior parameres large, apically pointed, extending past tip of aedeagus. Submedian spines on caudal margin of novasternum close.

Egg guide: Brown, with about 13 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.0. Rectal index 1.4. Malpighian tubules yellow; 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior subequal in length.

Internal genitalia, ♂: Testes yellow, with 3 large outer and 2–3 small inner coils. Accessory glands long, slender. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae small, lightly sclerotized. Parovaria relatively large. Ventral receptacle long, tightly coiled.

Egg filaments: 2 slender filaments, slightly flattened in apical third.

Pupae: Anterior spiracles with about 11 branches.

Chromosomes: Metaphase chromosomes figured by Kaneshiro and Wheeler (1970). Polytene chromosomes consist of 4 long autosomal arms and 2 shorter X-chromosome arms embedded in a large chromocentre.

Distribution: BORNEO and PHILIPPINES (Texas collections; Bock, unpublished). THAILAND (Texas stock 3256.9).

6. **Drosophila (Sophophora) varians** SP. NOV. Bock and Wheeler

Type culture: Los Baños, Luzon, Philippines; collected by Dr. L. Throckmorton, July 1968. Texas stock 3146.53.

= "sp. 4" of Kaneshiro and Wheeler 1970. Drosophila Information Service 45: 143.

Body length: ♂ 2.1 m.m.; ♀ 2.5 m.m.

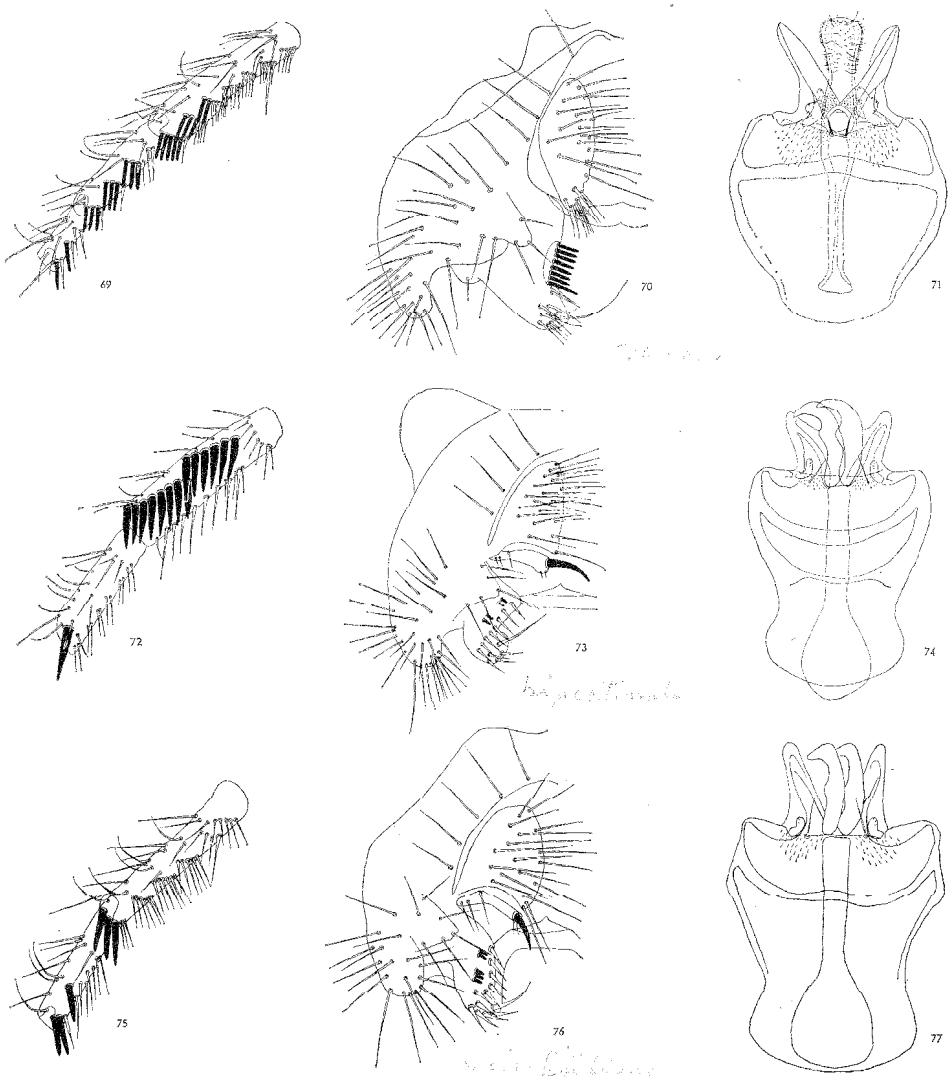


FIG. 69, 70, 71: *D. varians*, sex-comb and ♂ genitalia; 72, 73, 74: *bipectinata*, sex-comb and ♂ genitalia; 75, 76, 77: *malerkotliana*, sex-comb and ♂ genitalia.

Head, ♂ *and* ♀: Arista with 5 branches above, 3 below, plus the terminal fork. Orbital bristles in the ratio 3:1:3. Carina convex. Ocelli orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax, ♂ *and* ♀: Dusky brown dorsally, blackish laterally. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.7. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 69) in transverse rows of stout black bristles; 3 metatarsal rows of (from above down) 1–3, 2–4, and 4–5 teeth; 3–4 rows on the second tarsal segment of (from above down) 0–1, 3–4, 3–5, and 3–4 teeth; and 2 rows on the third tarsal segment (upper 1, lower 1–2 teeth).

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.6; 4V index 2.2; 4C index 1.5; 5X index 2.0. Third costal section with heavy setation on basal half. Wing lengths: ♂ 1.8 m.m.; ♀ 2.1 m.m.

Abdomen, ♂ and ♀: Tergites of female and first 5 tergites of male dusky brown, with broad apical black bands. Male abdomen apically black. Dusky coloration intensifies considerably with age.

Periphallic organs (Fig. 70): Genital arch very narrow dorsally, broad laterally, with rounded process partially covering base of clasper; toe with numerous large bristles. Primary clasper only present, large, with teeth in 2 sets; and upper row of 8–9 large rounded black teeth (the lowermost longer than the others), and a lower set of 10–12 finer pointed teeth (one greatly elongated, curved towards decasternum). Anal plate small, with a cluster of hairs about the lower tip. Decasternum small, with median dorsal point and median ventral notch.

Phallic organs (Fig. 71): Aedeagus brown, non-bifid, apically hirsute. Anterior parameres small, trilobed, articulated to aedeagus, with minute sensilla on lateral and dorsal lobes. Posterior parameres large, divergent, basally ornamented with minute spherules, apically rounded, reaching level of tip of aedeagus. Submedian spines on caudal margin of novasternum close.

Egg guide: Brown, with about 13 teeth and a subterminal hair. Basal isthmus 0.25 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.5. Rectal index 1.5. Malpighian tubules yellow; 2 anterior, free, common trunk 0.2 total length; 2 posterior, free, common trunk 0.2 total length; anterior and posterior subequal in length.

Internal genitalia, ♂: Testes dark yellow, with 4 large outer coils one of which is greatly swollen, and 1–2 tiny inner coils. Accessory glands very large. Ejaculatory bulb large, globular.

Internal genitalia, ♀: Spermathecae small, lightly sclerotized. Parovaria about two thirds size of spermathecae. Ventral receptacle extremely long, tightly coiled.

Egg filaments: 2 slender filaments, flattened in apical quarter.

Pupae: Anterior spiracles with about 12 branches.

Chromosomes: Metaphase chromosomes figured by Kaneshiro and Wheeler (1970). Polytene chromosomes consist of 4 long autosomal arms and 2 shorter X-chromosome arms embedded in a large chromocentre.

Distribution: LUZON, PHILIPPINES.

Two "species complexes" may be recognized within the *ananassae* subgroup (Bock, 1971a; Kaneshiro and Wheeler, 1970): the *ananassae* complex (aedeagus non-bifid, apically hirsute), and the *bipectinata* complex (aedeagus bifid, bare, apically hooked). The above 6 species constitute the *ananassae* complex, the next 4 the *bipectinata* complex. The position of *andamanensis*, the final species in this subgroup, is less clear. The aedeagus of *andamanensis* resembles that of the *ananassae* complex species in being non-bifid and apically hirsute, although the small anterior parameres resemble those of the *bipectinata* complex species. The sex-comb of *andamanensis* is closest to that of *bipectinata* and *parabipectina*. In the absence of further information (e.g. whether *andamanensis* may be crossed

with any other species in the subgroup), *andamanensis* is not assigned to either species complex.

On purely morphological grounds, the inclusion of *varians* in the *ananassae* subgroup might be questioned. The species lacks the single-toothed secondary clasper characteristic of all other members of the subgroup, and the anal plate shows some of the differentiation of the lowermost bristles characteristic of the species of the *suzukii* subgroup. We are obliged, nevertheless, to include *varians* in the *ananassae* subgroup on grounds of chromosomal homology. Each of the other members of the *ananassae* subgroup (except *andamanensis*) has been examined and found to possess the same polytene chromosome complement of 4 long autosomal arms and 2 shorter X-chromosome arms plus a large chromocentre. *D. varians* possesses exactly the same polytene chromosome complement, and the free ends of this species' chromosomes are identical to those of the other members of the subgroup. (A polytene chromosome map of *ananassae* is given in Stone *et al.*, 1957). Beyond the free ends, a number of chromosomal rearrangements evidently distinguish *varians* from the other species in the subgroup, and the other species from one another. Unfortunately it has not proved possible to obtain interspecific crosses between *varians* and any of the other members of the *ananassae* complex, or indeed between any two members of this complex with the exception of *ananassae* and *pallidosa* (cf. Futch, 1966). If hybrid larvae could be obtained, the extent to which chromosomal rearrangements distinguish one member of the *ananassae* complex from another would doubtless be considerably clearer; such an analysis has been possible in the species of the *bipectinata* complex (Bock, 1971b).

The phylogenetic relationships of the species of the *bipectinata* complex are discussed in detail by Yang, Wheeler and Bock (this Bulletin).

7. Drosophila bipectinata

D. bipectinata Duda 1923. Ann. Mus. Nat. Hung. 20:52. *Type locality*: "India: Matheran 800 m."

= *szentivanii* Mather and Dobzhansky 1962. Pac. Insects 4:247.

= "sp. 6" of Kaneshiro and Wheeler 1970. Drosophila Information Service 45:143.

General features: As described by Duda (1923); Kikkawa and Peng (1938); and Mather and Dobzhansky (1962).

Sex-comb: Fig. 72.

Periphallic organs: Fig. 73. *Phallic organs*: Fig. 74.

Chromosomes: Metaphase chromosomes figured by Kaneshiro and Wheeler (1970). Polytene chromosomes discussed by Bock (1971b).

Distribution:

SAMOA—Wheeler and Kambysellis (1966).
FIJI—Texas collections.
MICRONESIA (Palau)—Pipkin (1952).
NEW GUINEA—Bock (1971a); Mather and Dobzhansky (1962).
PHILIPPINES—Bock (1971a).
BORNEO—Bock (1971a).
THAILAND—Texas stock 3250.12.

INDIA—Duda (1923); Gupta and Ray-Chaudhuri (1970a, 1970b, 1970c); Rahman and Singh (1969); Singh (1970).
NEPAL—Okada (1955, 1966a).
JAPAN—Kikkawa and Peng (1938); Makino and Kanehisa (1951); Okada (1964b, 1965); Takada and Wakahama (1967).
TAIWAN—Kikkawa and Peng (1938).

8. Drosophila parabipectinata

D. parabipectinata Bock 1971. Univ. Tex. Publ. 7103:277. *Type locality*: Sabah, Borneo.

= "sp. 7" of Kaneshiro and Wheeler 1970. Drosophila Information Service 45:143.

General features: As described by Bock (1971a).

Sex-comb and male genitalia: Figured by Bock (1971a).

Chromosomes: Metaphase chromosomes figured by Kaneshiro and Wheeler (1970). Polytene chromosomes discussed by Bock (1971b).

Distribution:

BORNEO—Bock (1971a).
PHILIPPINES—Bock (1971a).
THAILAND—Bock (1971a).
CAMBODIA—Texas stock 3057.6.

9. Drosophila malerkotliana

D. malerkotliana Parshad and Paika 1964. Res. Bull. Panjab Univ. 15:235. *Type locality*: Chandigarh, Pinjore and Malerkotla, India.

= "*Drosophila* (*Sophophora*) sp." of Okada 1964. Nature and Life in Southeast Asia 3:449.

= "sp. 10" and "sp. 11" of Kaneshiro and Wheeler 1970. Drosophila Information Service 45:143.

General features: As described by Okada (1964a) and Parshad and Paika (1964).

Sex-comb: Fig. 75; 1 or 2 additional bristles may be present above the row on the metatarsal border; the number of bristles in each row is somewhat variable.

Periphallic organs: Fig. 76. *Phallic organs*: Fig. 77.

Distribution:

BORNEO—Bock (1971a).
PHILIPPINES—Bock (1971a).
THAILAND—Bock (1971a).
MALAYA—Texas stock 3033.14.
INDIA—Gupta and Ray-Chaudhuri (1970a, 1970b, 1970c); Parshad and Paika (1964); Rahman and Singh (1969); Singh (1970); Vaidya and Godpole (1971).

Two subspecies may be recognized in *malerkotliana* on the basis of male abdominal pigmentation. In specimens from mainland Asia, the distal portion of the male abdomen is shiny black; in specimens from Borneo and the Philippines, the entire male abdomen is pale brown (sex-combs and male genitalia are the same in both subspecies). Bock (1971a) designated the former subspecies *malerkotliana malerkotliana*, the latter *malerkotliana pallida* (type locality Borneo). The name

"*pallida*" is preoccupied in the genus *Drosophila* and should not have been used; the pale subspecies is accordingly renamed *malerkotliana pallens*, NOM. NOV.

10. Drosophila pseudoananassae

D. pseudoananassae Bock 1971. Univ. Tex. Publ. 7103:274. *Type locality*: Cairns, Australia.

= *Drosophila ananassae* of Mather 1955. Aust. J. Zool. 3:569.

= "sp. 8" and "sp. 9" of Kaneshiro and Wheeler 1970. Drosophila Information Service 45:143.

General features: As described by Bock (1971a).

Sex-comb and male genitalia: Figured by Bock (1971a).

Distribution:

AUSTRALIA (northeast)—Bock (1971a).
NEW GUINEA—Bock (1971a).
BORNEO—Bock (1971a).
PHILIPPINES—Bock (1971a).
MALAYA—Texas stock 3033.13.
THAILAND—Texas stock 3251.8.

As in *malerkotliana*, two subspecies may be recognized in *pseudoananassae*. In specimens from north Australia, New Guinea and the Philippines, male abdomens are pale brown; in specimens from Borneo and mainland Asia, male abdomens are shiny black distally (sex-combs and male genitalia are the same in both subspecies). Bock (1971a) designated the former subspecies *pseudoananassae pseudoananassae*, the latter, *pseudoananassae nigra*. The name "*nigra*" is preoccupied and the latter subspecies is accordingly renamed *pseudoananassae nigrens*, NOM. NOV.

11. Drosophila andamanensis

D. andamanensis Gupta and Ray-Chaudhuri 1970. Orient. Insects 4:171. *Type locality*: Andaman Is.

General features: Described by Gupta and Ray-Chaudhuri (1970b).

Sex-comb and male genitalia: Figured by Gupta and Ray-Chaudhuri (1970b). The sex-comb consists of a longitudinal row of teeth along the metatarsus and a single tooth apically on the second tarsal segment.

Distribution: ANDAMAN and NICOBAR ISLANDS (Gupta and Ray-Chaudhuri, 1970b).

As noted above, the affinities of *andamanensis* within the *ananassae* subgroup are not clear. The highly restricted geographic distribution of this species does, however, resemble the situations in *pallidosa*, *nesoetes* and *phaeopleura*, each species being known only from one or a few small islands.

X. The montium Subgroup.—Hsu 1949, Univ. Tex. Publ. 4920:121.

Medium to dark brown flies, usually with relatively slender, shiny, yellowish abdominal tergites with distinct apical bands; male abdomen distally black in some species. With the few exceptions noted, sex-combs of males longitudinal

along entire lengths of metatarsus and second tarsal segment. Male wings clear. Genital arch not constricted dorsally, Anal plate small, with long bristles, the lowermost few in some species shorter and thicker. Primary and secondary setigerous claspers present; secondary clasper fused to anal plate or free, with one or more very large curved black medial teeth (except *baimaii*), and a few small hairs. Aedeagus bare or hirsute, not bifid or apically branched. Anterior parameres generally large, broad, in most species not elongate, black or pointed. Spermathecae in most species vestigial, or unsclerotized and apparently nonfunctional (i.e., spermatozoa in inseminated females evident in ventral receptacle only).

The *montium* subgroup is by far the largest in the *melanogaster* species group, accounting for close to half of all known species. In a few cases, several species within the subgroup have been shown by sexual isolation or chromosomal studies to be very closely related; the members of each such complex are so indicated and treated together below. In the case of *D. kikkawai*, strong morphological resemblances also suggest close phylogenetic affinities between this species and the several others indicated; these species are also treated together. Many of the species in the *montium* subgroup, however, are, apart from sharing the general characteristics diagnostic of the subgroup as a whole, not obviously particularly closely related to any of the remaining species. The African species are considered together for convenience.

The most extensively studied complex in the *montium* subgroup from the point of view of speciation and incipient speciation is that consisting of the three species *serrata, birchii* and *dominicana. D. serrata* was described by Malloch (1927) from Queensland, Australia. Dobzhansky and Mather (1961) detected a very similar form from New Guinea and northern Australia, partially overlapping in distribution with *serrata;* the new form was designated a subspecies of *serrata, D. serrata birchii.* Ayala (1965a), on the basis of extensive tests of sexual isolation between these two forms and a third (very closely resembling *birchii*) known only from Madang on the north coast of New Guinea, accorded full specific status to *birchii*, and to the Madang fly which was described as *D. dominicana* (Ayala, 1965b). Baimai (1970a) studied incipient speciation within *birchii*, confirming Ayala's earlier conclusion that the populations of this species from Rabaul (New Britain), from mainland New Guinea, and from northern Australia constitute subdivisions of the species showing partial reproductive isolation from one another. Incipient speciation has therefore proceeded within *birchii*, but has not reached a level sufficient to regard the populations as distinct species. Baimai (1970b) also found that several of the at least 40 polytene chromosome inversions in *birchii* are restricted to specific geographic areas.

1. Drosophila serrata

D. serrata Malloch 1927. Proc. Linnean Soc. N.S.W. 52: 6. *Type locality*: Eidsvolt, Queensland, Australia.

General features: External morphology briefly described by Malloch (1927); coloration discussed by Dobzhansky and Mather (1961); additional descriptive information given by Mather (1955), and as below. Mather (1955) described

FIG. 78, 79, 80: *D. serrata*, sex-comb and ♂ genitalia; 81, 82: *birchii*, ♂ genitalia; 83, 84: *auraria*, ♂ genitalia; 85, 86: *biauraria*, ♂ genitalia; 87, 88: *triauraria*, ♂ genitalia; 89, 90: *quadraria*, ♂ genitalia.

the anterior scutellar bristles of *serrata* as divergent; these bristles are convergent in specimens examined in the present study.

Sex-comb (Fig. 78): Teeth on upper portion of metatarsus and on entire second tarsal segment fine, densely packed, contiguous.

Periphallic organs: Fig. 79. *Phallic organs*: Fig. 80.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.7. Malpighian tubules 2 anterior, free, common trunk less than 0.1 total length; 2 posterior, free, common trunk less than 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3–4 outer and a few tiny inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae relatively large, spherical, but completely unsclerotized and apparently non-functional. Parovaria ovoid, about half as large as spermathecae. Ventral receptacle exceptionally long, tightly coiled.

Egg filaments: 2 slender filaments, not flattened apically.

Egg guide: Brown, with about 16 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Distribution:

AUSTRALIA (eastern and northern)—Ayala (1965a); Dobzhansky and Mather (1961); Malloch (1927); Mather (1955).
NEW GUINEA—Ayala (1965a).

2. Drosophila birchii

D. birchii Dobzhansky and Mather 1961. Evolution 15: 462. *Type locality*: Crystal Cascades, northern Australia.

D. serrata birchii Dobzhansky and Mather 1961. Evolution 15: 462.

D. birchii, Ayala 1965. Evolution 19: 538–545.

General features: Principal differences in external morphology between *serrata* and *birchii* (coloration, periphallic organs) discussed by Dobzhansky and Mather (1961). Additional descriptive information as below.

Sex-comb: Similar to that of *serrata*, with densely packed contiguous fine teeth in upper portion of metatarsal comb and entire portion of second tarsal segment.

Periphallic organs: Fig. 81. *Phallic organs*: Fig. 82.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.5. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 4–5 outer and a few tiny inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae large but completely unsclerotized and apparently non-functional. Parovaria half size of spermathecae. Ventral receptacle very long, tightly coiled.

Egg filaments: 2 slender filaments, not flattened apically.

Egg guide: Brown, with about 15 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Distribution:

AUSTRALIA (northeastern)—Ayala (1965a); Baimai (1970a); Dobzhansky and Mather (1961).
NEW GUINEA—Ayala (1965a); Baimai (1970a); Dobzhansky and Mather (1961).

3. Drosophila dominicana

D. dominicana Ayala 1965. Pac. Insects 7: 620. *Type locality*: Madang, New Guinea. (without figure)

General features and ♂ genitalia: Described and figured by Ayala (1965a, 1965b) and compared with those of *serrata* and *birchii*; very closely resembles *birchii* but almost totally sexually isolated from both *serrata* and *birchii*.

Distribution: Known only from MADANG, NEW GUINEA (Ayala, 1965a, 1965b).

A further complex of very interesting species is the *auraria* cluster of Japan, Korea, China, and Taiwan. The most widespread of these species is *D. auraria*, described by Peng (1937) from China, and subsequently found to be widespread in Japan and Korea. Moriwaki, Okada and Kurokawa (1952) reported the existence of an additional two forms from Japan, very closely resembling *auraria;* the three forms were designated "*auraria* Type A" (= the *auraria* of Peng), "*auraria* Type B", and "*auraria* Type C". Takada and Makino (1952) and Takada (1954) noted that "Type A" and "Type B" possessed substantially different distributions by altitude, the former occurring at low altitudes, the latter at high altitudes.

The results of an extensive investigation of the distributions, abundance, and ecological preferences of these forms, of sexual isolation between and within them, and of some morphological comparisons, are summarized in a series of papers by Kurokawa (1956a, 1956b, 1959, 1960, 1962, 1963, 1967a, 1967b). Sexual isolation within each "type" is low to very low. Some pairwise crosses may be obtained amongst all three forms in the laboratory, but sexual isolation in each case is very strong; all such crosses proceed more easily in one direction than the other. The three forms do not interbreed in nature where they occur sympatrically in zones of overlap of their preferred habitats; "Type A" is largely associated with low altitude human habitations; "Type B" occurs in mountainous regions; the distribution of "Type C" is somewhat intermediate between that of "Type A" and that of "Type B". The principal morphological differences between the three forms lie in the phallic organs, although lack of sixth sternite setation distinguishes "Type B" from types "A" and "C". Okada (1954) has figured the phallic organs of the three forms; considerable differences between them are evident in the structures of the aedeagus, the caudal margin of the novasternum, and to a lesser extent, the anterior parameres.

It is quite evident that the three "types" of "*D. auraria*", all now known from Japan and Korea, "Type A" in addition from China, are biological species, and they are therefore accorded specific status in this paper. We have, in addition, a fourth, heretofore unknown member of this complex from Taiwan. The relationship of this species to the former three as determined by sexual isolation tests remains to be investigated.

4. Drosophila auraria

D. auraria Peng 1937. Annot. Zool. Jap. 16: 23. *Type locality*: Nanchang, China.
= "*auraria* Type A" of various authors.

General features: As described by Kikkawa and Peng (1938); Okada (1956); and Peng (1937).

Periphallic organs: Fig. 83. *Phallic organs*: Fig. 84.

Distribution:

CHINA—Kikkawa and Peng (1938); Peng (1937); Tan, Hsu and Sheng (1949).
MANCHURIA—Kikkawa and Peng (1938)
KOREA—Chung (1958); Chung and Rho (1959); Kang and Moon (1968, 1969); Kurokawa (1967a); Lee (1963, 1964b, 1966a); Takada and Lee (1958).
JAPAN—Kaneko (1960); Kaneko and Shima (1960, 1962); Kurokawa (1967a); Makino *et al.* (1952); Makino *et al.* (1963); Makino *et al.* (1964); Makino *et al.* (1965); Makino *et al.* (1966); Makino and Takada (1959); Momma and Kaneko (1967); Okada (1966b); Shima (1968); Takada (1957, 1958, 1960); Takada and Makino (1952); Wakahama (1966).

Lee (1963, 1964b) noted a polymorphism for the coloration of the abdomen in Korean *auraria* females; "light" and "dark" forms were noted, the difference found to be controlled by a single pair of alleles, "dark" being dominant.

5. Drosophila (Sophophora) biauraria SP. NOV. Bock and Wheeler

= "*auraria* Type B" of various authors.

Type culture: Ka-ari, South Korea; courtesy of Dr. Taek Jun Lee, Chungang University, Seoul, South Korea. Texas stock 3255.1.

Body length: ♂ 2.5 m.m.; ♀ 3.0 m.m.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front whitish pollinose, whiter in males. Orbital bristles in the ratio 3:1:3. Carina small, not prominent, convex. Ocelli orange; eyes red. Greatest width of cheek 0.13 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 irregular rows between dorsocentrals. Anterior scutellars parallel; posterior scutellars crossed almost at right angles. Ratio anterior/posterior dorsocentrals 0.7. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb with about 25 teeth, smaller above, larger below, the lowermost 2 displaced from the axis of the remaining teeth; comb on second tarsal segment with about 19 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 3.0; 4V index 2.5; 4C index 1.0; 5X index 2.3. Third costal section with heavy setation on basal half. Wing lengths: ♂ 2.2 m.m.; ♀ 2.6 m.m.

Abdomen, ♂ and ♀: Tergites of female yellowish with apical black bands. First 5 tergites of male yellowish with apical black bands; remainder of male abdomen black dorsally, yellowish laterally.

Periphallic organs (Fig. 85): Genital arch broad dorsally and laterally, black above level of lower margin of anal plate, yellow below; toe small, with a few long bristles; narrow triangular process covering base of primary clasper. Pri-

mary and secondary claspers present. Primary clasper with a lateral row of about 7 small pointed teeth and a medial cluster of larger teeth, one thin and elongate. Secondary clasper large, with 3 large curved black medial teeth and several fine hairs ventrally and laterally. Anal plate black, with very long bristles. Median lobe of decasternum bicornute.

Phallic organs (Fig. 86): Yellow. Aedeagus hirsute, apically broadened, subapically with pointed lateral expansions. Anterior parameres large, apically with a few tiny sensilla. Posterior parameres very small, medially fused. Caudal margin of novasternum with notched median lobe bearing small submedian spines.

Egg guide: Brown, with about 17 teeth and a long subterminal hair. Basal isthmus 0.25 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.6. Malpighian tubules yellow; 2 anterior, free, common trunk less than 0.1 total length; 2 posterior, free, common trunk less than 0.1 total length; anterior and posterior equal in length.

Internal genitalia, ♂: Testes yellow, with 3–4 outer coils and an uncoiled arm, and 3 thickened inner coils. Accessory glands large, curved. Ejaculatory bulb globular, almost spherical.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria minute. Ventral receptacle long, coiled.

Egg filaments: 2 slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 7 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y-chromosome.

Distribution:

KOREA—Chung (1958); Chung and Rho (1959); Kang and Moon (1968, 1969); Kurokawa (1967a); Lee (1966a); Takada and Lee (1958).

JAPAN—Kaneko and Shima (1960, 1962); Kurokawa (1967a); Makino *et al.* (1963); Makino *et al.* (1964); Makino *et al.* (1965); Momma and Kaneko (1967); Okada (1966b); Shima (1958); Takada (1957, 1958, 1960); Takada and Makino (1952); Wakahama (1966).

6. **Drosophila (Sophophora) triauraria** SP. NOV. Bock and Wheeler

— "*auraria* Type C" of various authors.

Type culture: Tokyo, Japan; courtesy Dr. H. Kurokawa, Tokyo Metropolitan University. Texas stock 1736.1.

Body length: ♂ 2.5 m.m.; ♀ 2.8 m.m.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front strongly silvery in males, slightly silvery in females. Orbital bristles in the ratio 3:1:3. Carina small, narrow, ridged; broader in females. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Anterior scutellars parallel; posterior scutellars crossed at right angles. Ratio anterior/posterior dorsocentrals 0.7. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 31 teeth, smaller above,

larger below, the lowermost 2 displaced from the axis of the remaining teeth; comb on second tarsal segment with about 19 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.8; 4V index 2.5; 4C index 1.6; 5X index 1.7. Third costal section with heavy setation on basal half. Wing lengths: ♂ 2.3 mm; ♀ 2.6 mm.

Abdomen, ♂ and ♀: Tergites of female yellowish with apical black bands. First 5 tergites of male yellowish with apical black bands; remainder of male abdomen shiny black dorsally, yellowish laterally.

Periphallic organs (Fig. 87); Genital arch broad dorsally and laterally; black above level of lower margin of anal plate, yellow below; toe with 3 long bristles and about 6 shorter bristles; narrow triangular process covering base of primary clasper. Primary and secondary claspers present. Primary clasper with a lateral row of about 7 pointed teeth and a ventromedial cluster of larger teeth with a few longer medial bristles. Secondary clasper with 3 very large curved black teeth and several small ventral and lateral bristles. Anal plate black, with long bristles above and a few shorter thicker bristles below. Median lobe of decasternum bicornute.

Phallic organs (Fig. 88): Yellow. Aedeagus broad, apically broadly rounded, hirsute, laterally with pointed expansions. Anterior parameres large, triangular, apically pointed, subapically with minute sensilla. Posterior parameres small, horn-like, medially fused. Caudal margin of novasternum with prominent bilobed median process, without submedian spines.

Egg guide: Brown, with about 18 teeth and a subterminal hair. Basal isthmus 0.2 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.5. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior subequal in length; posterior tubules apically thickened.

Internal genitalia, ♂: Testes pale yellow, with 3–4 outer and 1–2 swollen inner coils. Accessory glands relatively small. Ejaculatory bulb small, globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria small. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 8 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y-chromosome.

Distribution:

KOREA—Chung (1958); Chung and Rho (1959); Kang and Moon (1968, 1969); Kurokawa 1967a); Kim (1963); Lee (1966a).

JAPAN—Kaneko and Shima (1962); Kurokawa (1967a); Makino *et al.* (1963); Makino *et al.* (1964); Makino *et al.* (1965); Makino and Takada (1959); Momma and Kaneko (1967); Okada (1966b); Takada (1960).

7. Drosophila (Sophophora) quadraria SP. NOV. Bock and Wheeler

Type culture: Chi-Tou, Taiwan. Texas stock 3075.1.

Body length: ♂ 2.5 mm; ♀ 3.2 mm.

Head, ♂ and ♀: Arista with 4–5 branches above, 3 below, plus the terminal

fork. Front pale brown pollinose, silvery in males. Orbital bristles in the ratio 3:1:3. Carina convex. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Anterior scutellars parallel or slightly convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 25 teeth, smaller above, larger below, the lowermost 2 slightly displaced from the axis of the remaining teeth; comb on second tarsal segment consisting of about 18 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.5; 4V index 1.8; 4C index 1.4; 5X index 2.2. Third costal section with heavy setation on basal half. Wing lengths: ♂ 2.2 mm; ♀ 2.6 mm.

Abdomen, ♂ and ♀: Tergites of female yellowish with apical black bands; band on sixth tergite distinctly broader in middle. First 5 tergites of male yellowish with apical black bands; remainder of male abdomen shiny black dorsally, yellowish laterally.

Periphallic organs (Fig. 89): Genital arch broad laterally, slightly narrower dorsally; black above level of lower margin of anal plate, yellow below; toe acutely rounded, with a few long and several shorter bristles; narrow triangular process covering base of primary clasper. Primary and secondary claspers present. Primary clasper with a lateral row of about 10 pointed black teeth and a ventromedial cluster of about 10 larger teeth, one thinner, elongate. Secondary clasper large, oval, with 3 large curved black medial teeth and several small bristles ventrally and laterally. Anal plate black, with long bristles above and 3 thick lower bristles, larger medially. Median lobe of decasternum bicornute.

Phallic organs (Fig. 90): Aedeagus brown, slender, distally spade-like, laterally hirsute, apically bare. Anterior parameres large, brown, apically pointed, with 3 tiny sensilla in middle region. Posterior parameres smaller than anterior parameres. Ventral fragma quadrate. Caudal margin of novasternum with median process, strongly sclerotized, dusky (remainder of phallic organs brown), apically notched, without submedian spines.

Egg guide: Brown, with about 16 teeth and a subterminal hair. Basal isthmus 0.15 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.8. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3–4 large outer and 2–3 small inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria small. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 9 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y-chromosome.

Distribution: Known only from the type locality in TAIWAN.

The following 2 species are known only from New Guinea and are morphologically very close, although completely sexually isolated (Baimai, 1970c).

8. Drosophila mayri

D. mayri Mather and Dobzhansky 1962. Pac. Insects 4:245. *Type locality*: Bulolo, New Guinea.

General features: As described by Mather and Dobzhansky (1962).

Periphallic organs: Fig. 91. *Phallic organs*: Fig. 92.

Distribution: NEW GUINEA (Mather and Dobzhansky, 1962).

9. Drosophila pseudomayri

D. pseudomayri Baimai 1970. Pac. Insects 12:22. *Type locality*: Bulolo, New Guinea.

General features: Described by Baimai (1970c).

Male genitalia: Figured by Baimai (1970c).

Distribution: NEW GUINEA (Baimai, 1970c).

The best-known species in the *montium* subgroup, as well as being the most widespread and probably the most studied, is *kikkawai*. *D. kikkawai* ranges across the Southeast Asian region from India to Japan and Korea in the north and to Australia and various Pacific islands in the east; the species is also widespread in South America. The confusion in the identification of *kikkawai* has already been mentioned. De Meijere (1916) described *D. montium* from Java and deposited type specimens in the Amsterdam Museum. Duda (1924b, 1926, 1940) subsequently identified "*D. montium*" from various regions in Southeast Asia and Africa. It is probable that most or all of the specimens Duda thus identified were not the *montium* described by de Meijere but (in the case of the Southeast Asian flies) the *kikkawai* subsequently described by Burla (1954a), or (in the case of the African flies) a member of the *seguyi* complex. The lateral view of the hypopygium drawn by Duda (1926) for "*montium*" from Sumatra is indeed very suggestive of *kikkawai*; the description given by Duda (1940) for "*montium*" in his African material is not sufficient to permit specific determination. (No records of the occurrence of *kikkawai* in Africa have been published; cf., however, sp. 13 below).

10. Drosophila kikkawai

D. kikkawai Burla 1954. Rev. Brasil. Biol. 14:47. *Type locality*: Brazil.

General features: As described by Burla (1954a); Kikkawa and Peng (1938) ("*montium*"); Okada (1956); and Wheeler and Takada (1964).

Periphallic organs: Fig. 93. *Phallic organs*: Fig. 94.

Distribution (Records prior to 1954 are for "*montium*"):

SAMOA—Harrison (1954); Malloch (1934a); Wheeler and Kambysellis (1966).
FIJI—Harrison (1954).
HAWAII—Hardy (1952); Momma (1968); Zimmerman (1943).
MICRONESIA—Wheeler and Takada (1964).
NEW GUINEA—Bock (unpublished).

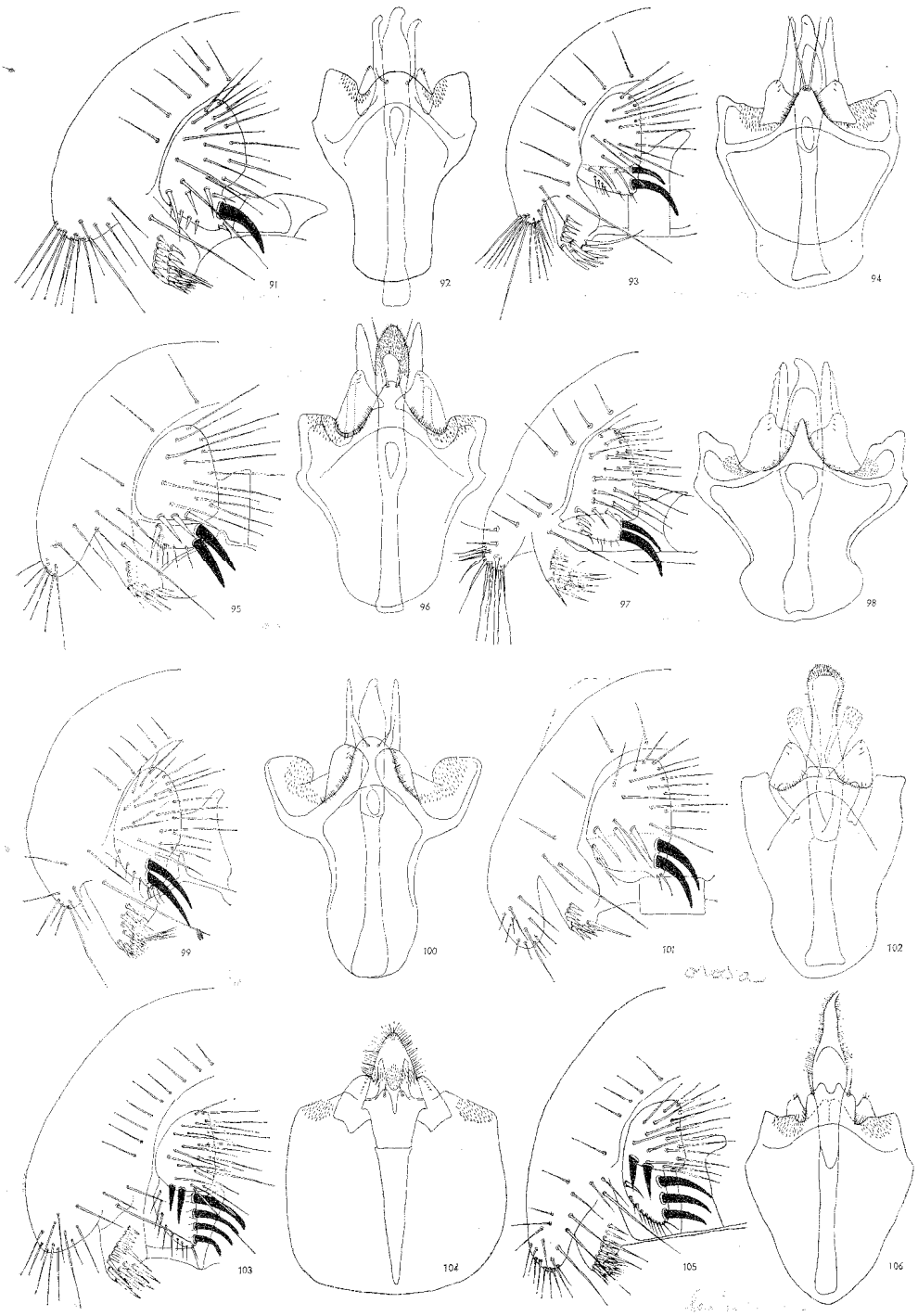


FIG. 91, 92: *D. mayri*, ♂ genitalia; 93, 94: *kikkawai*, ♂ genitalia; 95, 96: *lini*, ♂ genitalia; 97, 98: *pennae*, ♂ genitalia; 99, 100: *barbarae*, ♂ genitalia; 101, 102: *orosa*, ♂ genitalia; 103, 104: *rufa*, ♂ genitalia; 105, 106: *lacteicornis*, ♂ genitalia.

BORNEO—Okada (1964a).
PHILIPPINES—Bock (unpublished).
SUMATRA—Okada (1964a).
VIETNAM—Okada (1964a).
MALAYA—Texas stock 3047.3.
THAILAND—Texas stock 3250.10.
INDIA—Gupta and Ray-Chaudhuri (1970a, 1970c); Parshad and Duggal (1965, 1966); Parshad and Paika (1964); Rahman and Singh (1969); Sturtevant (1927); Vaidya and Godpole (1971).
NEPAL—Okada (1955, 1966a).
CHINA—Burla (1956).
KOREA—Kang, Chung and Lee (1959); Lee (1966b).
JAPAN—Kikkawa and Peng (1938); Okada (1956, 1965); Takada and Wakahama (1967).
TAIWAN—Duda (1923, 1924a, 1924b) (*kikkawai* ?); Kikkawa and Peng (1938).
SOUTH AMERICA—Burla (1956); Freire-Maia (1949, 1953, 1955a); Mourão *et al.* (1965); Pavan and da Cunha (1947); Hunter (1964).

D. kikkawai has been shown to possess variation both for the color of the last abdominal tergite and for the metaphase chromosome configuration. The last abdominal tergite may be either black or yellow. Since both phenotypes may occur in the same population (the color variation being controlled by a single allelic difference), the phenomenon is a polymorphism rather than a racial difference (Freire-Maia, 1949, 1953, 1955; Wheeler, 1949b). Of considerable interest are the findings of Baimai (1969, 1970d) regarding karyotype variation in, and the preliminary findings regarding sexual isolation between, several strains of *kikkawai* (identified in error as "*D. montium*"). Baimai reported the presence of four, possibly five, different karyotypes in Southeast Asian strains of *kikkawai*; there appears, further, to be complete sexual isolation between the Kota Kinabalu strain and two other strains within the island of Borneo. An extensive study of sexual isolation between as many strains as possible of the widespread *kikkawai* is needed to clarify the situation; this "species" may in fact consist of several morphologically very similar or identical, if karyotypically different, reproductively isolated groups of populations. Burla (1956) mentioned differences in male genitalia between Brazilian and Oriental specimens.

Several other species resemble *kikkawai* closely in the structure of the male genitalia. These species together with *kikkawai* appear to constitute one phylogenetic branch within the *montium* subgroup; they are therefore considered together below. The species most closely resembling *kikkawai* is *D. lini* sp. nov.; the periphallic organs of *lini* possess larger dorsal bristles on the medial margins of the secondary claspers than do those of *kikkawai*, and the aedeagus of *lini* is apically broader than that of *kikkawai* in addition to being hirsute; otherwise, as comparison of Figs. 93, 95, 94 and 96 shows, the two species are exceedingly similar in the structure of the male genitalia.

11. Drosophila (Sophophora) lini SP. NOV. Bock and Wheeler

Type culture: Yun-Shui, Taiwan; collected by L. Throckmorton and F. J. Lin, June 1968. Texas stock 3146.1.

Body length: ♂ 2.6 mm.; ♀ 3.0 mm.

Head, ♂ and ♀: Arista with 4–5 branches above, 3–4 below, plus the terminal

fork. Front whitish. Orbital bristles in the ratio 3:1:3. Carina convex, somewhat broader in females. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Anterior scutellars parallel; posterior scutellars crossed at right angles. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 21 teeth, smaller above, the lowermost 2 slightly displaced from the axis of the remaining teeth; comb on second tarsal segment consisting of about 16 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.6; 4V index 2.8; 4C index 1.4; 5X index 2.0. Third costal section with heavy setation on basal half. Wing lengths: ♂ 2.2 mm.; ♀ 2.6 mm.

Abdomen, ♂ and ♀: Tergites of female yellowish with very distinct apical black bands. First 5 tergites of male similar to those of female; remainder of male abdomen black dorsally.

Periphallic organs (Fig. 95): Genital arch broad laterally and dorsally, black dorsally; toe broadly rounded with 1 long bristle and 5–6 shorter bristles; medial process of genital arch covering base of primary clasper with a very long bristle. Anal plate black, with very long bristles. Primary and secondary claspers present. Primary clasper with a row of 3–4 curved pointed black teeth above and a cluster of 7–8 longer black teeth below. Secondary clasper oval, sclerotized and attached to anal plate via membranous connection; secondary clasper with 2 very large black medial teeth equal in size, 3 lower and 3 larger lateral bristles.

Phallic organs (Fig. 96): Aedeagus long, slender, apically pointed, finely hirsute. Anterior parameres large, broad, with 3 minute apical sensilla. Caudal margin of novasternum strongly convex, with a pair of long, close submedian spines.

Egg guide: Dark brown, with about 16 teeth and a subterminal hair. Basal isthmus 0.15 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.5. Rectal index 1.5. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes pale yellow, with 4 outer and 3–4 inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae relatively large but completely unsclerotized and apparently non-functional. Parovaria minute. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 11 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, a short Y-chromosome, plus a pair of very short rods.

Distribution: Known only from the type locality in TAIWAN.

The following New Guinea species is also very close to *kikkawai*, differing mainly in being of darker coloration and in lacking the long submedian spines

on the caudal margin of the novasternum which distinguish both *kikkawai* and *lini*. The periphallic organs of all 3 species are very similar.

12. Drosophila (Sophophora) pennae SP. NOV. Bock and Wheeler

Type culture: Goroka, New Guinea; collected by Dr. H. L. Carson, October 1961. Texas stock 3028.1.

Body length: ♂ 2.3 mm.; ♀ 2.8 mm.

Head, ♂ and ♀: Arista with 4 branches above, 2–3 below, plus the terminal fork. Front brown, slightly pollinose. Orbital bristles in the ratio 3:1:3, but in many specimens of the type (and only) culture the posterior reclinate orbital is greatly underdeveloped or absent, while in a few specimens the proclinate and anterior reclinate orbitals are underdeveloped; presumably a genetic aberration in the type culture. Carina convex. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Dark brown, almost black in old specimens. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4–6 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.7. Sternoindex 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Femora dark brown, almost black in old specimens. Sex-comb of male in longitudinal rows along the entire lengths of the metatarsus and second tarsal segment; metatarsal comb consisting of about 30 teeth, shorter above, the lowermost 2 displaced from the (curved) axis of the remaining teeth; comb on second tarsal segment consisting of about 21 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.9; 4V index 2.8; 4C index 1.6; 5X index 2.3. Third costal section with heavy setation on basal 0.6. Wing lengths: ♂ 2.1 mm; ♀ 2.4 mm.

Abdomen, ♂ and ♀: Tergites of male yellowish with broad apical dull black bands, broader in middle. Tergites of female entirely dull black.

Periphallic organs (Fig. 97): Genital arch broad dorsally and laterally, black mid dorsally, yellowish laterally; toe with about 10 long bristles. Primary and secondary claspers present. Primary clasper large, with a row of 5–6 teeth above and a cluster of about 7 longer teeth about the centromedial margin, the upper 2 longer and thinner. Secondary clasper oval, with 2 very large curved black medial teeth (the upper smaller than the lower), and a few small hairs. Anal plate black, with long bristles. Median process of decasternum bicornute.

Phallic organs (Fig. 98): Brown. Aedeagus slender, non-bifid, bare, apically tapered and slightly curved. Anterior parameres large, broad, with minute apical sensilla. Posterior parameres long, slender, reaching tip of aedeagus. Caudal margin of novasternum with long, narrow, very strongly sclerotized median convexity and long hairs; submedian spines absent.

Egg guide: Dark brown, with about 17 teeth and a subterminal hair. Basal isthmus 0.25 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.5. Rectal index 1.5. Malpighian tubules yellow; 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 or less total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3 large outer coils and an uncoiled arm, and 3 small inner coils. Accessory glands large. Ejaculatory bulb small, globular.

Internal genitalia, ♀: Spermathecae minute, completely unsclerotized. Parovaria small. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 9 black branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a long rod-shaped X-chromosome, and a short Y.

Distribution: NEW GUINEA.

13. Species like *kikkawai* from Africa

Tsacas (1971) figured the male genitalia of a species from Cameroun, Africa, which very closely resembles *kikkawai*, especially in the setation of the secondary clasper (large medial bristle below, smaller bristle above). There is, however, a conspicuous difference in the structure of the caudal margin of the novasternum of the phallic organs between the Cameroun species and *kikkawai;* in *kikkawai* (Fig. 94) the caudal margin of the novasternum is strongly convex and narrow, with a pair of very long spines; in the Cameroun species the caudal margin of the novasternum is convex but broadly rounded, with smaller spines (cf. *barbarae*, Fig. 100).

The following 3 species somewhat resemble *kikkawai* in the structure of the periphallic organs, although the phallic organs are quite distinctly different in one or more respects.

14. Drosophila (Sophophora) barbarae SP. NOV. Bock and Wheeler

Type culture: Bon Chakkrarat, Thailand; collected by D. E. Hardy and M. Delfinado, March 1968. Texas stock 3116.10.

Body length: ♂ 2.0 m.m.; ♀ 2.3 m.m.

Head, ♂ *and* ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front pale brown. Orbital bristles in the ratio 3:1:3. Carina prominent, convex. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ *and* ♀: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 18 teeth, smaller above, lowermost 2 displaced from the axis of the remaining teeth; comb on second tarsal segment consisting of about 13 uniform teeth.

Wings, ♂ *and* ♀: Transparent. Approximate indices: Costal index 1.6; 4V index 2.8; 4C index 1.8; 5X index 2.7. Third costal section with heavy setation on basal half. Wing lengths; ♂ 1.7 mm; ♀ 2.0 mm.

Abdomen, ♂ *and* ♀: Tergites of both sexes yellowish. First 5 tergites of female and first 4 of male with dark apical bands; remaining tergites in both sexes unbanded.

Periphallic organs (Fig. 99). Genital arch yellow, broad dorsally and laterally; toe small, with a large bristle and about 10 smaller bristles. Primary and secondary claspers present. Primary clasper yellow, with about 10 irregularly arranged lateral teeth, a cluster of similar teeth about the ventromedial border, and 4–5 longer medial bristles above the latter. Secondary clasper large, dark yellow, fused to anal plate, with 2 very large equal curved black medial teeth and a row of small bristles along the ventral border. Anal plate black (conspicuous in living specimens) with numerous long bristles. Median lobe of decasternum broad, bicornute.

Phallic organs (Fig. 100): Yellow. Aedeagus very similar to that of *kikkawai*; slender, bare, apically recurved. Anterior parameres large, basally very broad, with minute apical sensilla. Posterior parameres long, lightly sclerotized, with straight margins. Caudal margin of novasternum with strong broad median convexity and a pair of short close submedian spines.

Egg guide: Brown, with about 17 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.8. Malpighian tubules yellow; 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3–4 outer and 1–2 inner coils. Accessory glands large, swollen. Ejaculatory bulb large, globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria very small. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, slightly flattened apically.

Pupae: Anterior spiracles with about 11 black branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y.

Distribution:

BORNEO Bock (unpublished).
MALAYA—Texas stock 3033.3.
PHILIPPINES—Bock (unpublished).
THAILAND—Texas stock 3116.10.

15. Drosophila truncata

D. truncata Okada 1964. Nature and Life in Southeast Asia 3:455. *Type locality*: Amo, Brunei, Borneo.

General features: Described by Okada (1964a).

Male genitalia: Figured by Okada (1964a). A difference was noted in the structure of the caudal margin of the novasternum between specimens from Borneo and those from India.

Distribution: Known from BORNEO and INDIA (Okada, 1964a).

This species is very similar to the preceding (*barbarae*) but differs in the coloration of the anal plate (pale yellow in *truncata*, black in *barbarae*), and in the margins of the aedeagus and posterior parameres (serrate in *truncata*, not serrate in *barbarae*).

16. Drosophila (Sophophora) orosa SP. NOV. Bock and Wheeler

Type culture: Khao Yai, Thailand; collected by Dr. V. Baimai, March 1971. Texas stock 3250.17.

Body length: ♂ 2.4 mm; ♀ 3.0 mm.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front pale brown, slightly pollinose. Orbital bristles in the ratio 3:1:3. Carina strongly ridged, broader below. Ocelli dark orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4–6 irregular rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 16 fine contiguous teeth above, about 9 larger separated teeth below, plus a further 2 on the distal metatarsal border displaced from the axis of the remaining teeth; comb on second tarsal segment consisting of about 15 teeth gradually decreasing in size from above down, plus an additional stouter slightly curved tooth on the distal border.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.3; 4V index 2.9; 4C index 1.6; 5X index 2.8. Third costal section with heavy setation on basal 0.4. Wing lengths: 1.8 mm; ♀ 2.0 mm.

Abdomen, ♂ and ♀: Tergites of female with broad apical black bands, broader in middle, on first 4 tergites of male with broad apical black bands; remainder of male abdomen faintly banded.

Periphallic organs (Fig. 101): Yellow. Genital arch broad dorsally and laterally; toe broadly rounded, with 1–2 long and 6–8 small bristles. Primary and secondary claspers present. Primary clasper small, medially rounded, with a peripheral row of about 12 stout black teeth and 1 considerably larger tooth. Secondary clasper large, fused to anal plate, with 2 very large curved black medial teeth, 2 tiny medial bristles below these, and 3 large lateral bristles. Anal plate with stouter bristles below. Median lobe of decasternum shallow.

Phallic organs (Fig. 102): Aedeagus slender, subapically slightly constricted, apically with fine marginal hairs. Anterior parameres large, broadly triangular, apically with minute sensilla, proximally with slender processes articulating with aedeagus. Posterior parameres club-shaped, distally ornamented with tiny spherules. Caudal margin of novasternum with median convexity, laterally with fine long hairs; submedian spines very weakly developed, absent in some specimens.

Egg guide: Brown, with about 16 teeth, a large subterminal hair, and 2–3 minute terminal hairs. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.7. Malpighian tubules 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3 outer coils the outermost of which is substantially larger than the others, and 1–2 tiny inner coils. Accessory glands short, thick. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria small. Ventral receptacle long, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 9 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y.

Distribution: Known only from the type locality in THAILAND.

Among the following species, relationships with one another and with the preceding species are in most cases not obvious; these species are arranged mainly according to geographic distribution, the African forms considered last.

17. Drosophila rufa

D. rufa Kikkawa and Peng 1938. Jap. J. Zool. 7:529. *Type locality*: Honshu and Kyushu, Japan.

General features: As described by Kikkawa and Peng (1938) and Okada (1956). Oshima and Taira (1953) noted a color polymorphism (light or dark) in the last abdominal tergite of females.

Periphallic organs: Fig. 103. *Phallic organs*: Fig. 104.

Distribution:

INDIA—Gupta and Ray-Chaudhuri (1970c); Parshad and Duggal (1965, 1966); Parshad and Paika (1964).
CHINA—Tan, Hsu and Sheng (1949).
KOREA—Kim (1963); Lee (1966b).
JAPAN—Kikkawa and Peng (1938); Makino and Kanehisa (1951); Makino *et al.* (1952); Makino *et al.* (1955); Momma (1957); Okada (1956, 1966b); Wakahama (1966).

18. Drosophila asahinai

D. asahinai Okada 1964. Kontyu 32:111. *Type locality*: Kametsu, Amami Is. Japan.

General features: Described by Okada (1964b).

Male genitalia: Figured by Okada (1964b).

Distribution: AMAMI IS., JAPAN (Okada, 1964b).

19. Drosophila lacteicornis

D. lacteicornis Okada 1965. Kontyu 33:347. *Type locality*: Ishigaki, Okinawa Is.

General features: As described by Okada (1965).

Periphallic organs: Fig. 105. *Phallic organs*: Fig. 106.

Distribution: OKINAWA (Okada, 1965).

20. Drosophila punjabiensis

D. punjabiensis Parshad and Paika 1964. Res. Bull. Panjab Univ. 15:241. *Type locality*: Kulu Valley and Chandigarh, India.

General features: As described by Parshad and Paika (1964).

Periphallic organs: Fig. 107. *Phallic organs*: Fig. 108.

Distribution:

MALAYA—Texas stock 3033.4.
INDIA—Parshad and Paika (1964).

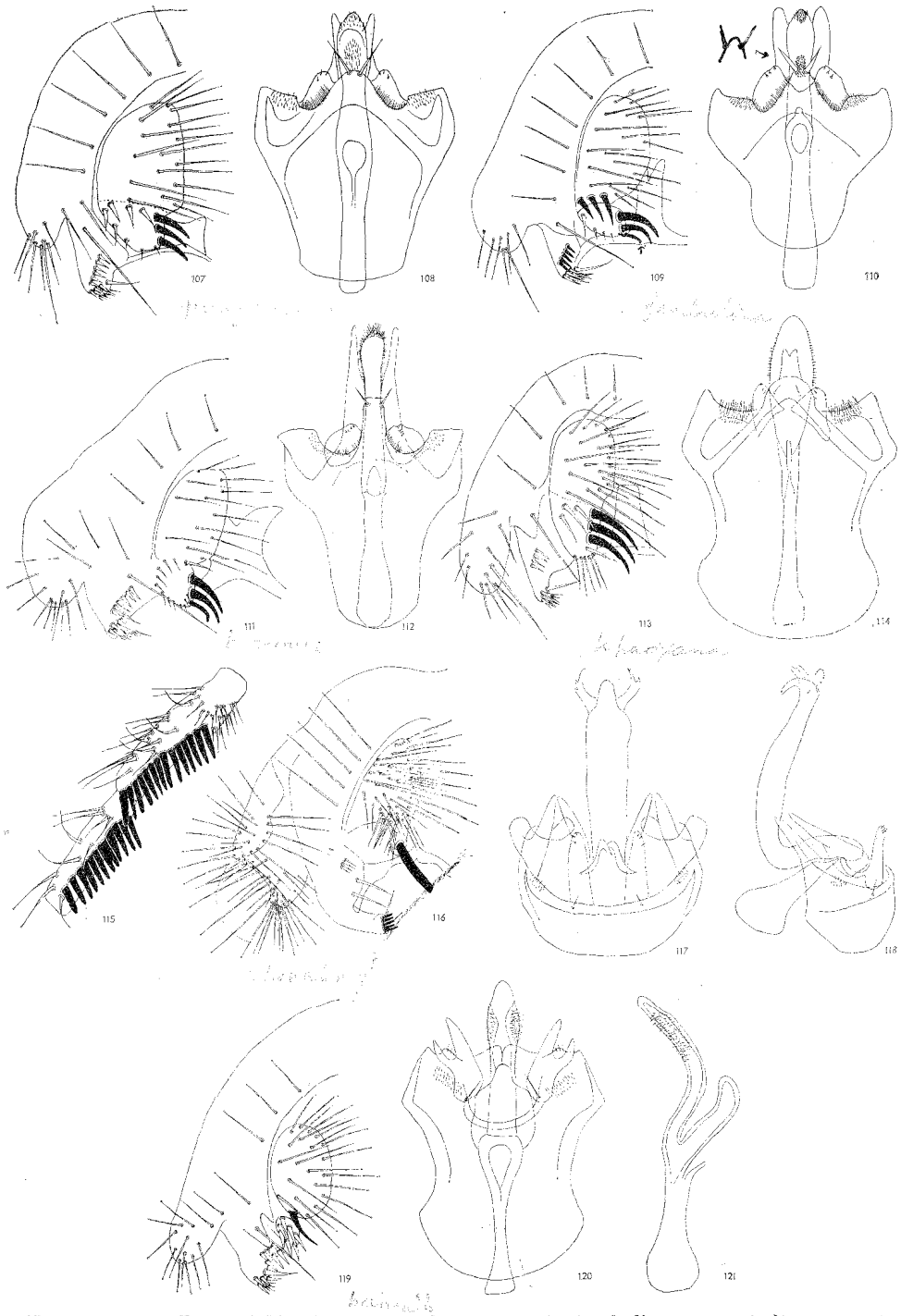


FIG. 107, 108: *D. punjabiensis*, ♂ genitalia; 109, 110: *jambulina*, ♂ genitalia; 111, 112: *bicornuta*, ♂ genitalia; 113, 114: *khaoyana*, ♂ genitalia; 115, 116, 117, 118: *rhopaloa*, sex-comb and ♂ genitalia (118: lateral aspect of phallic organs); 119, 120, 121: *baimaii*, ♂ genitalia (121: lateral aspect of aedeagus).

21. Drosophila jambulina

D. jambulina Parshad and Paika 1964, Res. Bull. Panjab Univ. 15:240. *Type locality*: Chandigarh and Malerkotla, India.

General features: As described by Parshad and Paika (1964).

Periphallic organs: Fig. 109. *Phallic organs*: Fig. 110.

Distribution:

CAMBODIA—Texas stock 3120.5.

INDIA—Gupta and Ray-Chaudhuri (1970c); Parshad and Duggal (1965, 1966); Parshad and Paika (1964); Vaidya and Godpole (1971).

22. Drosophila (Sophophora) bicornuta SP. NOV. Bock and Wheeler

Type culture: Los Baños, Luzon, Philippines; collected by Dr. C. Kanapi. Texas stock 3126.1.

Body length: ♂ 2.2 mm; ♀ 2.6 mm.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front pale brown. Orbital bristles in the ratio 3:1:3. Carina strongly convex. Ocelli orange; eyes red. Greatest width of cheek 0.14 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 irregular rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 27 teeth, smaller above, the lowermost 2 slightly displaced from the axis of the remaining teeth; comb on second tarsal segment consisting of about 20 uniform, mostly contiguous teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.7; 4V index 2.7; 4C index, 1.7; 5X index 3.5. Third costal section with heavy setation on basal half. Wing lengths: ♂ 1.7 mm; ♀ 2.0 mm.

Abdomen, ♂ and ♀: First 5 tergites of female and first 4 of male yellowish with dark apical bands; fifth tergite of male with faint apical band; sixth tergite yellowish in male, black in female (darker in older specimens).

Periphallic organs (Fig. 111): Entirely yellow. Genital arch broad dorsally, broader laterally; toe small, with about 10 bristles. Primary and secondary claspers present. Primary clasper with a row of about 6 strong pointed teeth dorsally and a cluster of strong ventromedial teeth, 1 elongate and slightly curved. Secondary clasper fused to anal plate, with 2 very large curved black medial teeth above and 1 smaller similar tooth below, and a row of tiny bristles along the ventral and lateral borders becoming larger laterally. Anal plate with long bristles, a few of them thickened below. Median lobe of decasternum bicornute.

Phallic organs (Fig. 112): Yellow. Aedeagus long, slender, apically pointed, apically and subapically hirsute. Anterior parameres large, ovoid, with minute apical sensilla. Posterior parameres long, with straight margins. Caudal margin of novasternum with elongate median truncate process, apically bearing 2 short spines.

Egg guide: Brown, with about 13 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ *and* ♀: Intestinal coiling index 2.0. Rectal index 1.4. Malpighian tubules yellow; 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior subequal in length.

Internal genitalia, ♂: Testes long, yellow, with 4–5 outer and 1–2 swollen inner coils. Accessory glands relatively small. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria small. Ventral receptacle very long, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 11 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a pair of dots, a rod-shaped X-chromosome, and a short Y.

Distribution:

BORNEO—Bock (unpublished).
PHILIPPINES—Texas stock 3126.1.
THAILAND—Texas stock 3250.16.

23. Drosophila trapezifrons

D. trapezifrons Okada 1966. Bull. Brit. Mus. (Natur. Hist.) Entomol. Suppl. 6:93.
Type locality: East Nepal.

General features: Described by Okada (1966a).

Male genitalia: Figured by Okada (1966a).

Distribution: NEPAL (Okada, 1966a).

24. Drosophila (Sophophora) khaoyana SP. NOV. Bock and Wheeler

Type culture: Khao Yai, Thailand; collected by Dr. V. Baimai, March 1971. Texas stock 3250.15.

Body length: ♂ 2.4 m.m.; ♀ 3.1 m.m.

Head, ♂ *and* ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front brown. Orbital bristles in the ratio 5:2:5. Carina strongly ridged, broad below. Ocelli orange; eyes red. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax, ♂ *and* ♀: Dark brown, darker laterally. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4–6 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 21 teeth, smaller above, lowermost 2 slightly displaced from the axis of the remaining teeth; comb on second tarsal segment consisting of about 13 uniform teeth.

Wings, ♂ *and* ♀: Transparent. Approximate indices: Costal index 2.3; 4V index 2.5; 4C index 1.3; 5X index 2.2. Third costal section with heavy setation on basal half. Wing lengths: ♂ 2.0 m.m.; ♀ 2.3 m.m.

Abdomen, ♂ *and* ♀: Tergites of female yellowish with broad apical black bands; fifth tergite completely black dorsally; sixth tergite completely black. First 3 tergites of male yellowish with broad apical black bands; remainder of male abdomen shiny black.

Periphallic organs (Fig. 113): Black except primary clasper. Genital arch broad dorsally and laterally; toe broadly rounded, with about 10 bristles. Primary and secondary claspers present. Primary clasper broad, yellowish, with 2 sets of teeth—a lateral row of 4–5 teeth, and a lower cluster of about 9 teeth the uppermost of which is substantially longer than the others. Secondary clasper large, fused to anal plate, with 3 very large curved black medial teeth, 1 much smaller tooth below these, and a row of 5–6 long setae along the ventral border. Anal plate small, oval, with long bristles. Median lobe of decasternum roughly rectangular.

Phallic organs (Fig. 114): Aedeagus elongate-oval, brown, laterally with fine teeth, apically bare. Anterior parameres broadly triangular, with minute apical sensilla. Posterior parameres small, fused in mid-line. Caudal margin of novasternum broadly convex, with a pair of short stout submedian spines.

Egg guide: Brown, strongly sclerotized, with about 15 teeth and a large subterminal hair. Basal isthmus 0.2 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.5. Rectal index 1.8. Malpighian tubules 2 anterior, free, common trunk 0.3 total length; 2 posterior, free, common trunk 0.2 total length; anterior tubules substantially shorter than posterior.

Internal genitalia, ♂: Testes yellow, with 3 outer coils and 1 swollen inner coil. Accessory glands large, with several constrictions. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae small, unsclerotized and apparently nonfunctional. Parovaria small. Ventral receptacle thick, tightly coiled.

Egg filaments: 2 long slender filaments, not flattened apically.

Pupae: Anterior spiracles with about 10 black branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y.

Distribution: Known only from the type locality in THAILAND.

25. Drosophila (Sophophora) rhopaloa SP. NOV. Bock and Wheeler

Type culture: Khao Yai, Thailand; collected by Dr. V. Baimai, March 1971. Texas stock 3250.11.

Body length: ♂ 2.4 m.m.; ♀ 2.7 m.m.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front brown. Orbital bristles in the ratio 5:2:5. Carina prominent, convex, narrow. Ocelli dark orange; eyes red. Greatest width of cheek 0.16 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, irregularly arranged between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.7. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 115) longitudinal on the metatarsus and the second tarsal segment; metatarsal comb consisting of about 14 uniform teeth; comb on second tarsal segment consisting of about 11 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.4; 4V index 2.6; 4C index 1.3; 5X index 2.1. Third costal section with heavy setation on basal 0.4. Wing lengths: ♂ 2.2 m.m.; ♀ 2.5 m.m.

Abdomen, ♂ and ♀: Tergites of female yellowish with thin apical black bands. First 3 tergites of male with faint apical black bands; fourth tergite yellow anteriorly, black posteriorly and laterally; remainder of male abdomen shiny black dorsally, pale brown laterally.

Periphallic organs (Fig. 116): Dusky-yellow. Genital arch broad dorsally, broader laterally; toe small; lower portion of genital arch with numerous large bristles. Primary clasper large, with narrow process bearing 5 strong teeth, a large thick bristle, and a small bristle; 2 large bristles present above process on medial border of primary clasper, 3 small black teeth present towards top of clasper. Secondary clasper apparently represented by strongly sclerotized medial process fused to anal plate, with ventromedially directed finger-like process bearing apically a very large black tooth of almost uniform width, apically truncated; proximal portion of secondary clasper with large bristles. Anal plate with long bristles, thicker ventrally. Decasternum strongly sclerotized, very narrow, with median dorsal point.

Phallic organs (Figs. 117, 118): Aedeagus very long, brown, strongly curved, apically hooked, with faintly sclerotized apical wing-like processes, not ornamented or hirsute. Basal apodeme of aedeagus short, lightly sclerotized. Anterior parameres large, finger like, articulated to aedeagus, with minute apical sensilla. Posterior parameres long, brown, narrow, apically pointed. Ventral fragma broad but shallow, with a pair of small submedian spines, dorsolaterally produced into large finger-like processes resembling posterior parameres.

Egg guide: Pale brown, weakly sclerotized, with 15–16 dark slender teeth and a large subterminal hair. Basal isthmus 0.75 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.5. Rectal index 1.8. Malpighian tubules very well developed, pale yellow to white; 2 anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes small, pale yellow, with 3 outer and 2–3 inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae well-developed and strongly sclerotized. Parovaria well developed. Ventral receptacle long, thick, tightly coiled.

Egg filaments: 2 filaments, expanded and flattened in apical half.

Pupae: Anterior spiracles with 4–6 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a pair of dots, a rod-shaped X-chromosome, and a short Y.

Distribution: Known only from the type locality in THAILAND.

The *montium* subgroup, as here constituted, is considerably more heterogeneous than the other, smaller subgroups. The above species is not typical in its possession of well-developed and functional spermathecae and in several aspects of the morphology of the male genitalia. Several further species included in the *montium* subgroup are also atypical in one or more respects; comment is made on these species at the appropriate places below.

26. Drosophila (Sophophora) baimaii SP. NOV. Bock and Wheeler

Type culture: Khao Yai, Thailand; collected by Dr. V. Baimai, March 1971. Texas stock 3250.9.

Body length: ♂ 2.3 m.m.; ♀ 2.7 m.m.

Head, ♂ and ♀: Arista with 5 branches above, 3 below, plus the terminal fork. Front brown, slightly shiny. Orbital bristles in the ratio 3:1:3. Carina prominent, strongly convex. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Anterior scutellars slightly divergent. Ratio anterior/posterior dorsocentrals 0.7. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 27 teeth, smaller above, lowermost 2 displaced from axis of remaining teeth; comb on second tarsal segment consisting of about 19 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.0; 4V index 2.3; 4C index 1.3; 5X index 2.6. Third costal section with heavy setation on basal half. Wing lengths: male 2.0 m.m.; female 2.3 m.m.

Abdomen, ♂ and ♀: Tergites of female yellowish with very distinct apical black bands. First 5 tergites of male similar to those of female; sixth tergite black dorsally and ventrolaterally.

Periphallic organs (Fig. 119): Small. Genital arch black dorsally; broad dorsally and laterally, with small triangular process at base of primary clasper; toe broadly rounded, with about 8 bristles. Primary and secondary claspers present. Primary clasper with 3–5 large marginal teeth above, a cluster of about 9 marginal teeth (1 larger than the others) below, and 4–6 strong teeth dorsolaterally. Secondary clasper almost circular, with a cluster of 7–15 pointed teeth. Anal plate black, oval, with about 21 long bristles and ventrolaterally 1 large black curved tooth. Decasternum narrow, dorsally with median convexity.

Phallic organs (Figs. 120, 121): Aedeagus long and slender, brown, non-bifid, apically bare and rounded, subapically hirsute, with large broader hollow process. Anterior parameres very large, black, with large medial lobe, small lateral lobe, and intermediate process bearing 3 fine sensilla; anterior parameres faintly sclerotized ventrally, apparently articulated to aedeagus. Posterior parameres small, short, faintly sclerotized, medially contiguous and apparently fused. Caudal margin of novasternum concave, with a pair of widely separated spines.

Egg guide: Brown, with about 16 teeth and a long subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.0. Rectal index 1.7. Malpighian tubules yellow; 2 anterior, free, common trunk 0.2 total length; 2 posterior, free, common trunk 0.2 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3 large outer and 2 small inner coils. Accessory glands large. Ejaculatory bulb small, globular.

Internal genitalia, ♀: Spermathecae relatively large but completely unsclerotized and apparently non-functional. Parovaria same size as spermathecae. Ventral receptacle long, coiled.

Egg filaments: 2 long, slender filaments, slightly flattened in apical tenth.

Pupae: Anterior spiracles with about 9 strong black branches.

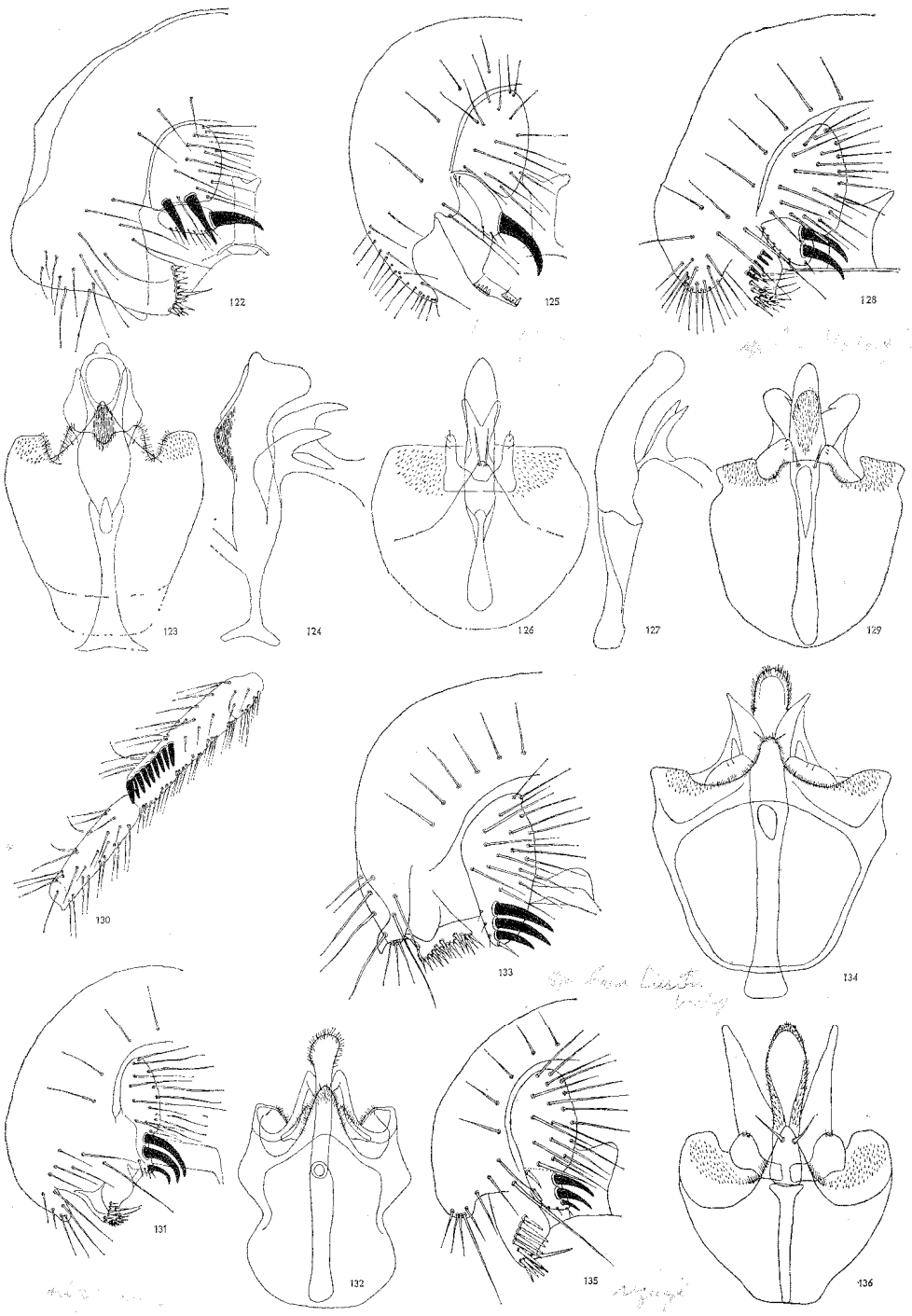


FIG. 122, 123, 124: *parvula*, ♂ genitalia (124: lateral aspect of aedeagus and posterior parameres); 125, 126, 127: *kanapiae*, ♂ genitalia (127: lateral aspect of aedeagus and posterior parameres); 128, 129: sp. from Madang, ♂ genitalia; 130, 131, 132: *nikananu*, sex-comb and ♂ genitalia; 133, 134: sp. from Lusitu Valley, Rhodesia, ♂ genitalia; 135, 136: *seguyi*, ♂ genitalia.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a short Y.

Distribution:

MALAYA—Texas stock 3033.9.
THAILAND—Texas stock 3250.14.

As mentioned in the introduction to the *montium* subgroup, *baimaii* is the only species the secondary clasper of which lacks one or more greatly enlarged medial bristles. The structure of the anterior parameres of *baimaii* is also somewhat exceptional, resembling those of the *takahashii* and *suzukii* subgroup species. The blind process of the *baimaii* aedeagus is unique in the *melanogaster* group except for the similar bifurcate process in *eugracilis*.

27. Drosophila (Sophophora) parvula SP. NOV. Bock and Wheeler

Type culture: From an area about 20 miles north of Kuala Lumpur, Malaya; collected by Dr. M. Wasserman, early 1962. Texas stock 3033.9.

Body length: ♂ 2.0 m.m.; ♀ 2.3 m.m.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front brown, slightly silvery. Orbital bristles in the ratio 4:1:4. Carina prominent, convex. Ocelli orange; eyes red. Greatest width of cheek 0.15 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Scutellar bristles long. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.4. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb with about 18 uniform teeth; comb on second tarsal segment with about 10 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: costal index 2.0; 4V index 2.2; 4C index 1.3; 5X index 2.2. Third costal section with heavy setation on basal half. Wing lengths: ♂ 1.9 m.m.; ♀ 2.0 m.m.

Abdomen, ♂ and ♀: Tergites of both sexes yellowish with apical black bands.

Peripheallic organs (Fig. 122): Genital arch very broad dorsally and laterally; toe broadly rounded, with about 12 bristles. Primary and secondary claspers present. Primary clasper large, broad, with about 13 teeth along the medial margin, 1 elongate. Secondary clasper large, oval, with 1 very large curved black medial tooth and 8–9 fine bristles along the ventral margin. Anal plate with 2 very large straight black teeth on ventral margin in addition to the usual bristles. Median lobe of decasternum slightly notched.

Phallic organs (Figs. 123, 124): Aedeagus pale brown, non-bifid, ornamented in middle portion with small elongate spherules. Anterior parameres large, contiguous, with numerous hairy sensilla along lateral margins; not articulated to aedeagus. Posterior parameres horn-like, ventrally attached to aedeagus, dorsally attached via a sclerotized ring to novasternum. Caudal margin of novasternum strongly convex, with a pair of very small widely separated spines.

Egg guide: Brown, with about 12 teeth and a subterminal hair; apical 5–6 teeth darker, stouter, rounded. Basal isthmus 0.25 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 1.0. Rectal index 1.5.

Malpighian tubules pale yellow; 2 anterior, free, common trunk 0.2 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior subequal in length.

Internal genitalia, ♂: Testes yellow, with 3 large outer and 3 inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria small. Ventral receptacle thick, long, tightly coiled.

Egg filaments: 2 long thin filaments, not flattened apically, slightly thicker basally.

Pupae: Anterior spiracles with about 11 branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a small densely heterochromatic Y.

Distribution:

MALAYA—Texas stock 3033.24.
THAILAND—Texas stock 3250.9.

The sex-comb of *parvula* is unusual within the *montium* subgroup in that the metatarsal teeth are of uniform size (cf. also *rhopaloa*). The unusual posterior parameres of *parvula* resemble those of the species below.

28. Drosophila (Sophophora) kanapiae SP. NOV. Bock and Wheeler

Type culture: Tagaytay, Luzon, Philippines; collected by L. Throckmorton and F. J. Lin, June 1968. Texas stock 3138.6.

Body length: ♂ 2.0 mm; ♀ 2.5 mm.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front pale brown. Orbital bristles in the ratio 5:2:5. Carina nose-like. Ocelli orange; eyes red. Greatest width of cheek 0.14 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.7. Sterno-index 0.7. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 29 teeth, smaller, finer and contiguous above, lowermost 2 not displaced; comb on second tarsal segment consisting of about 23 fine teeth very tightly crammed together except for lowermost 3–4.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 1.9; 4V index 2.7; 4C index 1.6; 5X index 2.6. Third costal section with heavy setation on basal 0.4. Wing lengths: 1.8 mm; ♀ 2.0 mm.

Abdomen, ♂ and ♀: Tergites of both sexes yellowish with apical black bands.

Periphallic organs (Fig. 125): Genital arch broad dorsally and laterally with small rounded process covering base of primary clasper; toe elongate, with about 12 bristles. Primary and secondary claspers present. Primary clasper basally broad, apically narrow and elongate; apical portion with 2 sets of teeth, each set containing a few small rounded teeth and at least 1 longer pointed tooth. Secondary clasper well-developed, ovoid, with 2 tiny lateral teeth, 3 tiny medial teeth, and 1 very large curved black medial tooth. Anal plate large. Median lobe of decasternum long, narrow, apically expanded, bicornute.

Phallic organs (Figs. 126, 127): Aedeagus brown, not bifid or hirsute. Anterior parameres large, finger-like, medially contiguous and apparently fused, not articulated to aedeagus, with fine sensilla on distal portion. Posterior parameres horn-like, medially fused, articulated to aedeagus. Caudal margin of novasternum convex, with a pair of large submedian spines. Basal apodeme of aedeagus short.

Egg guide: Brown, with about 13 teeth and a subterminal hair. Basal isthmus 0.25 length of lobe.

Internal structures, ♂ *and* ♀. Intestinal coiling index 2.0. Rectal index 1.6. Malpighian tubules yellow; 2 anterior, free, common trunk 0.15 total length; 2 posterior, free, common trunk 0.15 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3 large outer coils ending in a long swollen arm, and 3 small inner coils. Accessory glands large. Ejaculatory bulb globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria small. Ventral receptacle very long, tightly coiled.

Egg filaments: 2 long straight thin filaments, not flattened, widely divergent.

Pupae: Anterior spiracles with about 10 black branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a rod-shaped X-chromosome, and a small densely heterochromatic Y. The polytene chromosome complement consists of 5 long arms embedded in a chromocentre.

Distribution: PHILIPPINES (Texas stock 3138.6; Bock, unpublished).

29. Drosophila montium

D. montium de Meijere 1916. Tijd. Ent. 69:205. *Type locality*: Java.

General features: External morphology described by de Meijere (1916) and (more extensively) by Burla (1954a).

Male genitalia: Figured by Burla (1954a).

Distribution: Known only from the original types from JAVA (cf. discussions in other parts of this paper).

30. Drosophila pectinifera

D. pectinifera Wheeler and Takada 1964. Insects of Micronesia (B. P. Bishop Museum) 14:176. *Type locality*: Bonin Is., Micronesia.

General features: Described by Wheeler and Takada (1964).

Sex-comb and male genitalia: Figured by Wheeler and Takada (1964).

Distribution: BONIN IS., MICRONESIA (Wheeler and Takada, 1964).

31. Drosophila tanorum

D. tanorum Okada 1964. Nature and Life in Southeast Asia 3:452. *Type locality*: Amo, Brunei, Borneo.

General features: Described by Okada (1964a).

Male genitalia: Figured by Okada (1964a).

Distribution: BORNEO (Okada, 1964a).

As pointed out by Okada, the position of *tanorum* in the *melanogaster* species

group is somewhat exceptional. The sex-comb of this species does not consist of the 2 longitudinal rows usual in the *montium* subgroup, but rather a set of transverse rows on the metatarsus and second tarsal segment as found in the *takahashii* and some members of the *suzukii* and *ananassae* subgroups. The toe of the genital arch is also elongate and tapered, and the anterior parameres are long, pointed and black; the basal apodeme of the aedeagus is considerably longer than the (shallow)) ventral fragma. These latter characteristics are strongly reminiscent of several of the *takahashii* and *suzukii* subgroup species, especially *D. mimetica* sp. nov. which we have included in the *suzukii* subgroup. Okada included *tanorum* in the *montium* subgroup because of its "two pairs of setigerous claspers and compact rod-like aedeagus," although the "secondary clasper" is joined to the anal plate and could conceivably represent merely a differentiation of the lower teeth as occurs in the *suzukii* subgroup (cf. *mimetica* again, Fig. 38, where the lower teeth are strongly differentiated from the upper and partially lie in a projection from the anal plate. When the secondary clasper is firmly fused to the anal plate and sclerotized to precisely the same extent, the distinction between the two is indeed not obvious and whether the unit is recognized as anal plate with fused secondary clasper or anal plate with differentiated lower portion admittedly becomes somewhat arbitrary). We are provisionally leaving *tanorum* in the *montium* subgroup, but emphasize that further comparative studies on this species, particularly if a culture could be obtained, might require revision of this classification.

32. Drosophila mysorensis

D. mysorensis Reddy and Krishnamurthy 1970. J. Biol. Sci. 13:24. *Type locality*: Mysore and Mercara, India.

General features: Described by Reddy and Krishnamurthy (1970).

Sex-comb and male genitalia: Figured by Reddy and Krishnamurthy (1970).

Distribution: MYSORE and surrounding areas, INDIA (Reddy and Krishnamurthy, 1970).

The male genitalia of this species are somewhat reminiscent of those of *kikkawai*. The egg guide appears to be unusual in possession of a "brownish folded brushy structure" extending along its lumen.

33. Undescribed species from Madang, New Guinea

Figs. 128 and 129 depict the periphallic and phallic organs, respectively, of a species known only from Madang, New Guinea; the culture was lost before preserved material was obtained. The species is particularly distinguished by the fact that the last abdominal segment and the egg guides of the female are black; the male abdomen is not black apically.

34. Drosophila nikananu

D. nikananu Burla 1954. Rev. suisse Zool. 61:160. *Type locality*: Ivory Coast, Africa.

General features: As described by Burla (1954b).

Sex-comb: Fig. 130.

Periphallic organs: Fig. 131. *Phallic organs.* Fig. 132.

Distribution: IVORY COAST, AFRICA (Burla, 1954b).

The sex-combs of *nikananu* and of the following species are exceptional within the *montium* subgroup in being considerably smaller than the usual row of teeth extending the lengths of the first two tarsal segments (but cf. also *tanorum* above). The position of *nikananu* in the *montium* subgroup is confirmed by its possession of genitalia characteristic of this subgroup, and also by the vestigial spermathecae of *nikananu* females.

35. Undescribed species from Rhodesia, Africa

A single preserved male available for study from Lusitu Valley, Rhodesia has proved to be a sibling of *nikananu*. The sex-comb is similar to that of *nikananu*, i.e., a short longitudinal row of teeth on the distal half of the metatarsus. The genitalia are depicted in Figs. 133 and 134. Differences between the genitalia of this species and of *nikananu* are evident especially in the phallic organs.

♂♀ 36. Drosophila seguyi

D. seguyi Smart 1945. Proc. Roy. Entomol. Soc. Lond. (B) 14:56. *Type locality:* Kenya, Africa.

= *D. subobscura* Segúy 1938. Mem. Mus. Hist. nat. Paris 8:352 (homonym).

General features: The original description provided by Segúy (1938) is quite superficial. Burla (1954b) provided an expanded description of "*D. seguyi*" from the Ivory Coast, but Burla's species was later shown to be not identical with the *seguyi* type (see discussion below). An expanded description of *seguyi* proper is therefore here provided on the basis of a culture from Salisbury, Rhodesia, supplied by Dr. H. E. Paterson of the University of Western Australia.

Body length: ♂ 2.3 mm; ♀ 3.0 mm.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front whitish in males, brown in females. Orbital bristles in the ratio 2:1:2. Carina prominent, raised, slightly convex. Ocelli orange; eyes red. Greatest width of cheek 0.17 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 20 teeth, smaller above, lowermost 2 slightly displaced from axis of remaining teeth; comb on second tarsal segment consisting of about 17 uniform teeth.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.5; 4V index 2.9; 4C index 1.4; 5X index 3.3. Third costal section with heavy setation on basal half. Wing lengths: ♂ 2.1 mm; ♀ 2.4 mm.

Abdomen, ♂ and ♀: First 4 tergites of male yellowish with very distinct apical black bands; fifth tergite with broader band; sixth tergite shiny black. First 5 tergites of female yellowish with distinct apical black bands; sixth tergite brown or black.

Periphallic organs (Fig. 135): Black. Genital arch broad dorsally and laterally; toe small, with 1–2 large and a few smaller bristles. Primary and secondary claspers present. Primary clasper with a lateral row of about 4 pointed teeth and a ventromedial cluster of teeth, 1 elongated. Secondary clasper large, fused to anal plate, with 2 or 3 very large curved black medial teeth and a row of fine bristles about the ventral and lateral borders. Anal plate large, oval, with a few thick bristles ventrally in addition to the usual long bristles. Median lobe of decasternum bicornute.

Phallic organs (Fig. 136): Aedeagus long, slender, hirsute. Anterior parameres large, dorsolaterally expanded and rounded with minute apical sensilla, medially truncate. Posterior parameres large, same length as aedeagus, with very finely serrate margins. Caudal margin of novasternum with strong more darkly pigmented convexity, subapically with a pair of short thick spines.

Egg guide: Brown, with about 14 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.6. Malpighian tubules large, yellow; 2 anterior, free, common trunk 0.1 or less total length; 2 posterior, free, common trunk 0.1 or less total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, large, with 4 large outer and a few small inner coils. Accessory glands very large. Ejaculatory bulb small, globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria very small, Ventral receptacle exceptionally long, tightly coiled.

Egg filaments: 2 long slender filaments, very slightly expanded in apical seventh.

Pupae: Anterior spiracles very short, with about 10 black branches.

Distribution: AFRICA (widespread)—Paterson (1960); Paterson and Tsacas (1967); Tsacas (1967b).

Gupta and Ray-Chaudhuri (1970a) included "*seguyi*" in a list of Drosophilidae collected in Varanasi, India. The same authors (1970c) included "*seguyi*" in their key to Indian *Sophophora*, and briefly described some of the external morphology of their species. In view of the fact that the taxonomic position of "*Drosophila seguyi*" is considerably more complicated than was originally apparent, re-examination of the Indian material seems appropriate.

Burla (1954b) figured the periphallic organs and provided a general description of "*D. seguyi*" from the Ivory Coast, Africa; Burla (1954a), in comparing several species of the *montium* subgroup, also figured "*D. seguyi*" periphallic and phallic organs of Ivory Coast and Tanganyika material. It was established by Paterson (1960) and Paterson and Tsacas (1967) that the true *seguyi* is that species figured by Burla (1954a), Tanganyika material. The Ivory Coast species figured by Burla (1954b) was tentatively designated "sp. A" (see below). The two forms figured by Burla (1954a) as "*D. seguyi*" are in fact distinct species, differing substantially in the structure of the phallic organs; the Ivory Coast forms of the two 1954 papers are, in addition, different species, the 1954b form being the "sp. A" of Paterson and Tsacas, the 1954a form being an as yet undescribed species. A culture of this latter form is available for this project and the species is described below as "*D. tsacasi*".

37. Drosophila (Sophophora) tsacasi SP. NOV. Bock and Wheeler

Type culture: Ivory Coast, Africa; collected by Prof. H. Burla ca. 1954. Texas stock 2371.4.

= "*D. seguyi*" from Ivory Coast of Burla (1954a).

Body length: ♂ 2.3 mm; ♀ 2.9 mm.

Head, ♂ and ♀: Arista with 4 branches above, 3 below, plus the terminal fork. Front shiny white in males, pale brown in females. Orbital bristles in the ratio 5:2:5. Carina prominent, convex, somewhat larger in females. Ocelli orange; eyes red. Greatest width of cheek 0.12 greatest diameter of eye.

Thorax, ♂ and ♀: Brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Anterior scutellars strongly convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 14 teeth, uniform except lowermost which is curved and pointed.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.4; 4V index 2.4; 4C index 1.3; 5X index 2.4. Third costal section with heavy setation on basal 0.4. Wing lengths: ♂ 2.0 mm; ♀ 2.4 mm.

Abdomen, ♂ and ♀: Second to fifth tergites of both sexes yellowish with apical black bands; sixth tergite of both sexes black.

Periphallic organs (Fig. 137): Black. Genital arch broad dorsally and laterally; toe with about 10 bristles. Primary and secondary claspers present. Primary clasper with a lateral row of 4–5 irregularly spaced teeth and a ventromedial cluster of similar teeth, 1 elongated. Secondary clasper large, fused to anal plate, with 4 very large curved black medial teeth arising from long dark chitinous roots, a row of tiny teeth along the ventral and medial borders, and a few short thick teeth dorsally. Anal plate oval. Median lobe of decasternum strongly bicornute; decasternum with a pair of submedian strongly sclerotized circular patches each with a short thick bristle.

Phallic organs (Fig. 138): Black. Aedeagus long, slender, apically hirsute. Anterior parameres large, egg-shaped, with a few sensilla dorsolaterally in middle region. Posterior parameres long but not reaching tip of aedeagus, with very finely serrate margins. Caudal margin of hypandrium with deep strongly pigmented median convexity bearing a pair of small submedian spines.

Egg guide: Black, with about 15 teeth and a subterminal hair. Basal isthmus 0.2 length of lobe.

Internal structures, ♂ and ♀: Intestinal coiling index 2.0. Rectal index 1.7. Malpighian tubules large, yellow; 2 anterior, free, common trunk less than 0.1 total length; 2 posterior, free, common trunk less than 0.1 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes yellow, with 3 large outer coils ending in a blind arm, and a few small inner coils. Accessory glands very large. Ejaculatory bulb large, globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria small. Ventral receptacle very long, tightly coiled.

Egg filaments: 2 slender filaments, not flattened apically.

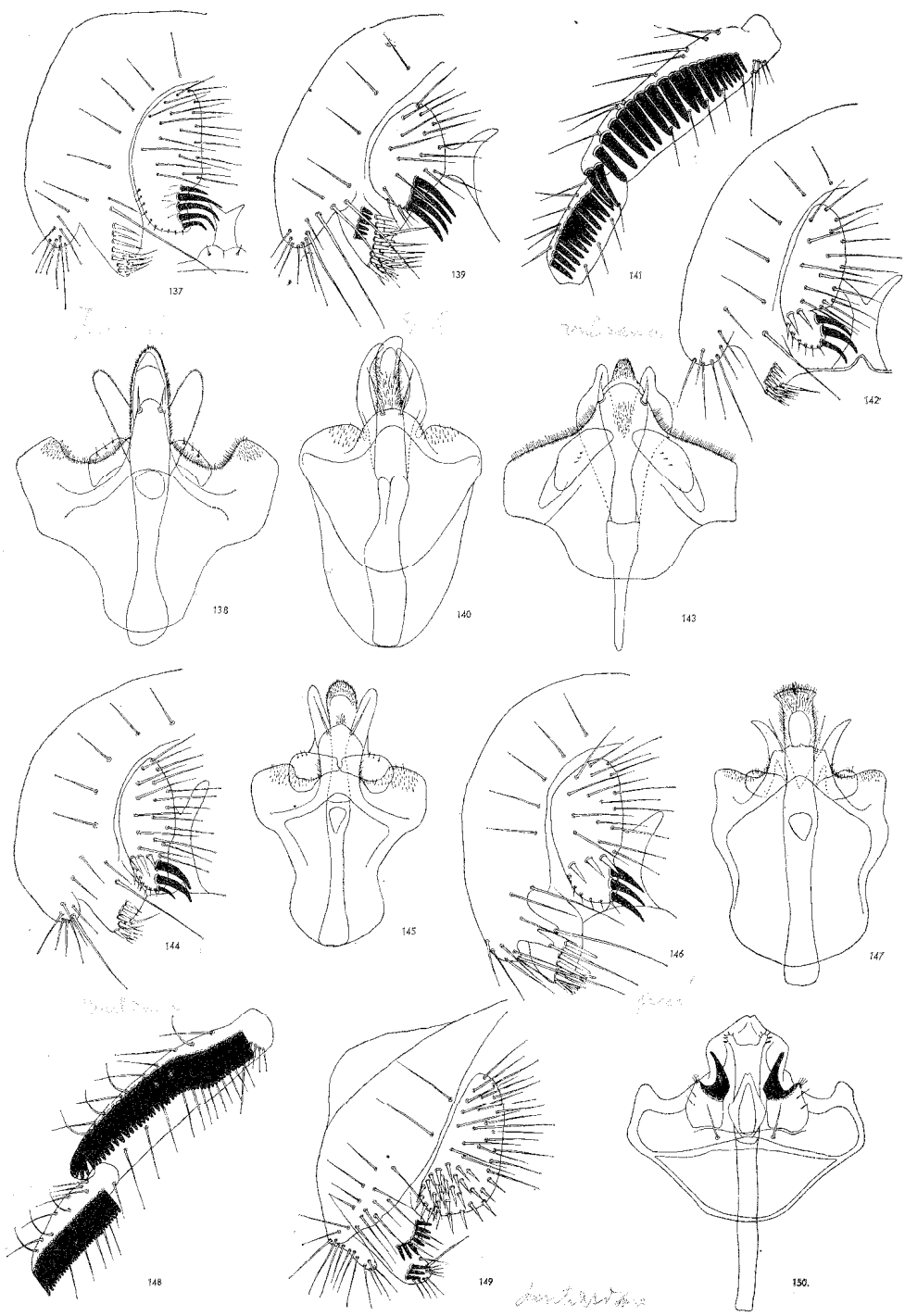


FIG. 137, 138: *D. tsacasi*, ♂ genitalia; 139, 140: "sp. A," ♂ genitalia; 141: *vulcana*, sex-comb; 142, 143: *vulcana*, ♂ genitalia; 144, 145: the same from another specimen—cf. differences in phallic organs; 146, 147: *greeni*, ♂ genitalia; 148, 149, 150: *dentissima*, sex-comb and ♂ genitalia.

Pupae: Anterior spiracles short, with about 10 black branches.
Distribution: IVORY COAST, AFRICA (Burla, 1954a).

38, 39. "sp. A" of Paterson and Tsacas (1967) and sibling species

The male genitalia of "sp. A" are depicted in Figs. 139 and 140. Paterson (personal communication) and Tsacas (personal communication) have detected another species extremely close to "sp. A" in the structure of the male genitalia but distinguishable by the setation of the primary clasper. The phallic organs of both these species lack anterior parameres.

40. Drosophila vulcana

D. vulcana Graber 1957. Zool. Jahrb. Abt. Syst. 85:309. *Type locality*: Mulungu, Kibati, and a wide area of Uganda, Africa; collected in flowers of *Adenopus abyssinicus* (Cucurbitaceae).

General features: External morphology described by Graber (1957). Complete description below (culture from Mt. Selinda, Rhodesia; collected by H. E. Paterson).

Body length: Male 2.2 m.m.; female 2.6 m.m.

Head, ♀ and ♂: Arista with 4 branches above, 3 below, plus the terminal fork. Front pale brown pollinose ,whitish in males. Orbital bristles in the ratio 3:1:3. Carina prominent, narrow. Ocelli orange; eyes red. Greatest width of cheek 0.14 greatest diameter of eye.

Thorax, ♂ and ♂: Mid- to dark brown. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 6 rows between dorsocentrals. Anterior scutellars convergent. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb of male (Fig. 141) longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 19 teeth, smaller above, lowermost 2 displaced from axis of remaining teeth; comb on second tarsal segment consisting of about 14 teeth, uniform except lowermost which is pointed and slightly curved.

Wings, ♂ and ♀: Transparent. Approximate indices: Costal index 2.2; 4V index 3.2; 4C index 1.5; 5X index 3.0. Third costal section with heavy setation on basal half or slightly less. Wing lengths: ♂ 2.0 m.m.; ♀ 2.3 m.m.

Abdomen, ♂ and ♀: Tergites of male shiny yellow-brown with broad dark apical bands. Tergites of female shiny dark brown with broad darker apical bands.

Periphallic organs (Figs. 142, 144): Black. Genital arch broad dorsally and laterally; toe with a few bristles. Primary and secondary claspers present. Primary clasper with a lateral row of about 5 teeth and a ventromedial cluster of teeth, 1 elongated. Secondary clasper oval, partially separated from anal plate, with 2–3 very large curved black medial teeth and smaller bristles along the ventral, lateral and dorsal borders, larger dorsally. Median lobe of decasternum bicornute, deeply concave laterally and apically.

Phallic organs (Figs. 143, 145): Variable. Aedeagus hirsute, subapically narrowed. Anterior parameres large, ovoid, with minute dorsolateral sensilla, hidden behind fragma or protruding dorsally. Posterior parameres almost level with tip

of aedeagus, with finely serrate margins. Caudal margin of novasternum with prominent median convexity of somewhat variable thickness bearing a pair of spines.

Egg guide: Brown, with about 17 teeth and a subterminal hair. Basal isthmus 0.3 length of lobe.

Internal structures, ♂ *and* ♀: Intestinal coiling index 2.0. Rectal index 1.7. Malpighian tubules large, yellow; 2 anterior, free, common trunk 0.15 total length; 2 posterior, free, common trunk 0.15 total length; anterior and posterior of equal length.

Internal genitalia, ♂: Testes large, yellow, with 2 thick outer coils ending in an uncoiled arm and a swollen inner coil. Accessory glands very large. Ejaculatory bulb large, globular.

Internal genitalia, ♀: Spermathecae vestigial. Parovaria very small. Ventral receptacle relatively short, tightly coiled.

Egg filaments: 2 slender filaments, not flattened apically.

Pupae: Anterior spiracles short, with about 9 black branches.

Chromosomes: Male metaphase plate consists of 2 pairs of V's, a pair of dots, a rod-shaped X-chromosome, and a short J-shaped Y-chromosome.

Distribution: Widespread in southern AFRICA (Graber, 1957; Paterson, personal communication).

41. **Drosophila (Sophophora) greeni** SP. NOV. Bock and Wheeler

Type locality: Kanyemba, Rhodesia, Africa. Three preserved males collected by C. A. Green, January 1970.

This species is described on the basis of external male morphology only; the distinctive features of the genitalia should, however, permit ready and accurate comparison of any specimens subsequently obtained with the description.

Head: Arista with 5 branches above, 3 below, plus the terminal fork. Orbital bristles in the ratio 2:1:2. Carina small, convex. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.7. Sternoindex 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb longitudinal along entire lengths of metatarsus and second tarsal segment; metatarsal comb consisting of about 20 teeth, smaller above, lowermost 2 displaced from axis of remaining teeth; comb on second tarsal segment with about 14 uniform teeth.

Wings: Transparent. Approximate indices: Costal index 2.2; 4V index 3.1; 4C index 1.5; 5X index 3.0. Third costal section with heavy setation on basal half. Wing length: 2.1 m.m.

Abdomen: Tergites yellowish with apical black bands; sixth tergite completely black dorsally, yellowish laterally.

Periphallic organs (Fig. 146): Dusky. Genital arch broad dorsally and laterally; toe shallow, with a few long and a few short bristles; base of primary clasper covered by bilobed process arising from posterior margin of genital arch, each lobe apically with a long bristle. Primary and secondary claspers present.

Primary clasper with a row of long black teeth and a cluster of similar teeth ventromedially. Secondary clasper fused to anal plate, with 3 very large curved black medial teeth, the lowermost smaller than the upper two, and tiny ventral and lateral bristles. Anal plate oval, with long bristles above and a few short thick bristles below. Median lobe of decasternum bicornute.

Phallic organs (Fig. 147): Yellow. Aedeagus slender, apically curved and truncate, hirsute. Anterior parameres relatively small, broad, dorsally slightly concave, with fine lateral sensilla. Posterior parameres large, strongly sclerotized, smooth, curved laterally, apically pointed. Caudal margin of novasternum with convex median process, apically with crenulate margin and a pair of spines.

Distribution: Known only from Kanyemba, Rhodesia, AFRICA.

XI. THE DENTISSIMA SUBGROUP.—New subgroup

Preserved males of two sibling species from southern Africa provided by Dr. H. E. Paterson possess a combination of features requiring the establishment of a new subgroup. These flies are distinguished by very large sex-combs along the entire lengths of the first two tarsal segments composed of very many tightly packed teeth. The genitalia are strongly sclerotized. One clasper only is present. The anal plate possesses differentiated upper and lower bristles, long above, short below. Aedeagus long, slender, apically ornamented or hirsute. Anterior parameres large, apically black and pointed. Posterior parameres broad, sheathing aedeagus. Caudal margin of novasternum not convex medially. Ventral fragma shallow.

1. Drosophila (Sophophora) dentissima SP. NOV. Bock and Wheeler

Type locality: Magoeba's Kloof, Transvaal, Africa, collected by H. E. Paterson, January 1970.

Head: Arista with 4 branches above, 3 below, plus the terminal fork. Orbital bristles in the ratio 3:1:3. Carina relatively broad, convex. Greatest width of cheek 0.1 greatest diameter of eye.

Thorax: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 irregular rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.6. Sterno-index 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-comb (Fig. 148) longitudinal along entire lengths of metatarsus and second tarsal segment, each of these segments produced apically; metatarsal comb consisting of about 55 very fine teeth, tightly crammed together, slightly smaller above, lowermost 2–3 somewhat larger; comb on second tarsal segment consisting of about 34 teeth, uniform except for lowermost which is somewhat larger than the others.

Wings: Transparent. Approximate indices: Costal index 2.6; 4V index 2.1; 4C index 1.0; 5X index 2.3. Third costal section with heavy setation on basal 0.4. Wing length: 2.7 m.m.

Abdomen: First 4 tergites brown with broad apical black bands; remainder of abdomen shiny black.

Periphallic organs (Fig. 149): Black. Genital arch broad laterally, constricted mid-dorsally. Toe long, broad above, very narrow below, with long bristles. Pri-

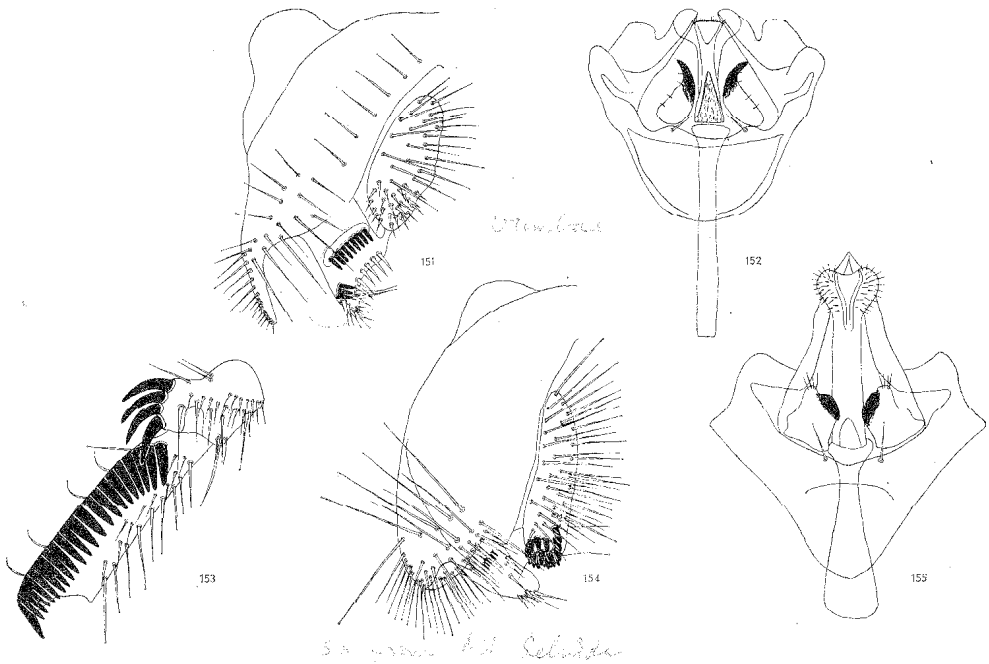


FIG. 151, 152: *D. vumbae*, ♂ genitalia; 153, 154, 155: sp. from Mt. Selinda, sex-comb and ♂ genitalia.

mary clasper only present, with a dorsolateral comb of about 9 strong rounded black teeth, 1 or a few similar teeth ventrolaterally, a ventromedial cluster of bristles, and a few dorsomedial bristles. Anal plate large, roughly pearshaped, broader below, with long bristles above and numerous shorter thicker bristles below.

Phallic organs (Fig. 150): Dark, strongly sclerotized. Aedeagus slender, apically with lateral projections bearing tiny elongate processes. Anterior parameres large, apically pointed and black, laterally expanded, with dorsolateral sensilla. Posterior parameres large, broad, sheathing aedeagus, ornamented with numerous tiny spherules. Caudal margin of novasternum almost straight, with a pair of small close submedian spines. Ventral fragma shallow; basal apodeme of aedeagus somewhat longer than fragma.

Distribution: Transvaal (Magoeba's Kloof, 7 specimens) and Natal (Giant's Castle, 1 specimen), AFRICA.

2. Drosophila (Sophophora) vumbae SP. NOV. Bock and Wheeler

Type locality: Vumba Mts., Rhodesia, Africa; collected by H. E. Paterson; January 1970.

Head: Arista with 4 branches above, 3 below, plus the terminal fork. Carina narrow, convex. Greatest width of cheek 0.12 greatest diameter of eye.

Thorax: Brown. Acrostichal hairs in 6 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.7. Sternoindex 0.5. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex-

comb longitudinal along entire lengths of metatarsus and second tarsal segment, both segments slightly produced apically; metatarsal comb consisting of about 38 fine contiguous teeth, slightly smaller above, lowermost few larger; comb on second tarsal segment consisting of about 22 contiguous teeth, uniform except for lowermost which is larger.

Wings: Transparent. Approximate indices: Costal index 2.9; 4V index 2.1; 4C index 1.0; 5X index 2.5. Third costal section with heavy setation on basal 0.3. Wing length: 2.7 m.m.

Abdomen: First 4 tergites yellowish with thin faint apical bands; last 2 tergites shiny black.

Periphallic organs (Fig. 151): Black. Genital arch very broad laterally, constricted dorsally. Toe elongate, very narrow, with long bristles. Primary clasper only present, broad, with a comb of about 9 strong rounded black teeth dorsolaterally, a similar comb of about 4 teeth ventrolaterally, a row of stout medial bristles, and a ventromedial cluster of bristles. Anal plate large, oval, with long bristles above and shorter bristles below; margin of anal plate with ventromedial concavity.

Phallic organs (Fig. 152): Dark. Aedeagus slender, apically truncate with a row of fine bristles. Anterior parameres large, crescentic, apically black and pointed, with fine sensilla scattered along lateral margin. Posterior parameres large, broad, not ornamented, sheathing aedeagus. Caudal margin of novasternum slightly concave, with a pair of submedian spines. Ventral fragma shallow; basal apodeme of aedeagus considerably longer than fragma.

Distribution: Rhodesia, AFRICA (Vumba Mts.).

The exact affinities of the *dentissima* subgroup are uncertain. The periphallic organs are strongly reminiscent of those of the *suzukii* subgroup species, but the mid-tibiae of the *dentissima* subgroup flies lack the short hooked bristles characteristic of most of the *suzukii* subgroup species. The sex-combs of the *dentissima* subgroup flies are closest to the typical *montium* subgroup type, but the substantial differences between the male genitalia in these latter two subgroups suggest that the superficial resemblance is deceptive.

XII. Subgroup for an undescribed species from Rhodesia, Africa

One male supplied by Dr. H. E. Paterson from Mt. Selinda, Rhodesia possesses distinctive genitalia (Figs. 154, 155) and a very distinctive sex-comb (Fig. 153), the metatarsus being very small while the second tarsal segment is elongate. This fly is probably best placed in a new species group and is illustrated here for future comparative purposes.

XIII. The "Questionable" Species.

The following five species are unknown apart from their original (brief) descriptions of external morphology only (except *miki*, see below). All were described before the *melanogaster* group as such was recognized, but in general morphology apparently show some resemblance to the established *melanogaster* group species, or have been provisionally included in the *melanogaster* group by

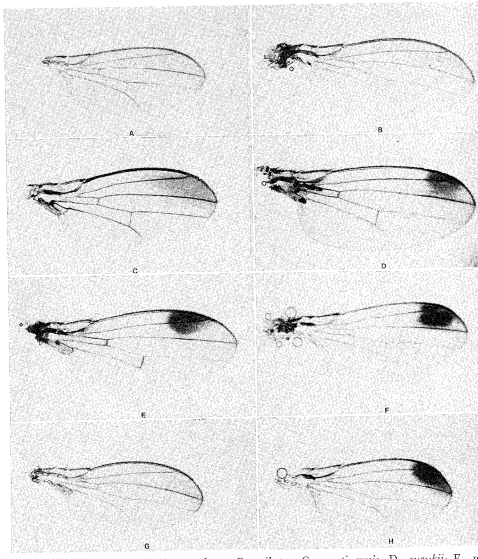


FIG. 156: Male wings of: A—*paralutea*; B—*trilutea*; C—*prostipennis*; D—*suzukii*; E—*pulchrella*; F—*rajasekari*; G—*lucipennis*; H—*elegans*.

previous workers. Unless further fresh material or the original types are, however, examined and described more fully (with particular emphasis on the structure of the male genitalia), the precise status of these species (except *miki*) must remain uncertain.

1. Drosophila apectinata

D. apectinata Duda 1932. Arch. Hydrobiol. 9(suppl.):194. *Type locality*: Eastern Java.

Duda (1932) provided a brief description of the external morphology of this species (2 males only were available for study), noting that it closely resembled *unipectinata* and to some extent *ananassae*, differing from the former species in

its lack of a sex-comb and from the latter also in possession of longer second and third tarsal joints, more hirsute external genitalia, and different disposition of wing veins. The mesonotum of *apectinata* was also noted to be darker in the region of the middle 4 rows of acrostichal hairs, although Duda emphasized that since the specimens he examined were preserved in spirit, his descriptions of coloration may not correspond with that found in living flies. It is conceivable that Duda's *apectinata* may be a member of the *melanogaster* species group, if so probably the *suzukii* subgroup, but unless specimens can be examined in more detail it will not be possible to decide one way or the other. Duda gave no indication of the fate of the type specimens.

2. Drosophila biarmipes

D. biarmipes Malloch 1924. Mem. Dept. Agric. India (Entomol. Ser.) 8:64. *Type Locality*: Coimbatore, India.

This species as described by Malloch possesses the general facies of a *melanogaster* group fly, including in the male a sex-comb in 2 rows on the metatarsus, and was provisionally included in the *melanogaster* group by Wheeler (1949a). The arrangement of the sex-comb is strongly reminiscent of that in *rajasekari* Reddy and Krishnamurthy; however Malloch mentioned no apical black patch in the male *biarmipes* wing, as is possessed by *rajasekari*, although the *biarmipes* male wing was observed to possess "a faint darker tinge at apices of second vein". The two species are therefore apparently distinct. Malloch did not indicate where the types were deposited.

3. Drosophila hypopygialis

Tanygastrella hypopygialis Duda 1924. Arch. Naturgesch. 90:254. *Type locality*: Sumatra.

It has already been pointed out above that Duda relegated *Tanygastrella* as a subgenus of *Drosophila* when the species *eugracilis* was further examined, and we are synonymizing *Tanygastrella* with *Sophophora*. Since the 2 species *eugracilis* ("*gracilis*") and *hypopygialis* were included in *Tanygastrella*, the species *hypopygialis* should be considered for possible inclusion in the *melanogaster* group. The description of *hypopygialis* was based on 3 males in the collection of the Amsterdam Museum. We have not examined the types; we are of the opinion, however, that this species is probably not a member of the *melanogaster* group. It possesses no sex-comb—a fact which of itself would not exclude the species from the *melanogaster* group (cf. *lucipennis* and *tristipennis*)—but the thorax and scutellum of *hypopygialis* were also observed by Duda to be black, a characteristic certainly found in no other species of the *melanogaster* group. The characters on which Duda based the genus *Tanygastrella* were of a somewhat trivial nature, as he himself later acknowledged; *hypopygialis* may prove, on thorough examination of the type specimens, to be not at all closely related to *eugracilis*.

4. Drosophila illata

D. illata Walker 1860, Proc. Linn. Soc. London 4:168. *Type locality*: Macassar, Celebes.

This species was provisionally included in the *melanogaster* group by Wheeler (1949a). Sturtevant (unpublished) examined the type of this species and recorded it in his notes as "headless and hopeless." It is, therefore, impossible to make a precise determination of the systematic position of this fly.

5. Drosophila miki

D. miki Duda 1924. Ent. Medd. 14:274. *Type locality*: Vienna, Austria.

This species, described by Duda (1924c) as possessing a longitudinal sex-comb on the distal portion of the metatarsus and the entire length of the second tarsal segment, was also provisionally included in the *melanogaster* group by Wheeler (1949a). Mr. E. B. Basden of Edinburgh has examined the type of *miki* and very kindly made his unpublished drawing of the male genitalia and notes available to us; it is now clear that the male genitalia of this species places it in the *obscura* group.

Discussion

The number of species now known in the *melanogaster* group ranks it as one of the major species groups in *Drosophila*, with over 5% of the total species described in the genus. We have enumerated or described, in the preceding pages, some 76 named species and mentioned several more partially described, known only from single or a few preserved specimens.

There can be little doubt that additional species remain to be discovered. Whole regions within the general limits of the range of the *melanogaster* group are unexplored for their *Drosophila* faunas. The large island of Celebes is untouched (apart from the single old collection from which *illata* was described), there are hundreds of additional unexplored small islands, and no recent collections have been made on the large islands of Java and Sumatra. Some of the better-known parts of Southeast Asia have still only been partially collected. The untouched far northern part of eastern Australia, in particular, might well yield some very interesting material, and there is evidently considerable scope for further work on the African fauna. It would obviously be highly speculative to suggest the number of remaining *melanogaster* group species which the most intensive collection possible in all regions could yield. One may, however, be reasonably confident, since most collections to date in new areas have revealed new species, that quite a few *melanogaster* group species remain to be described.

Apart from the widespread *melanogaster*, *simulans*, *ananassae* and *kikkawai*, most of the known species of the *melanogaster* group are restricted in distribution to parts of the Oriental, Australian, and eastern Palaearctic biogeographic zones, covering an area from India in the west to Korea and Japan in the northeast and to Micronesia, New Guinea and far northern Australia in the southeast. A few species occur more extensively in Australia, and several are also known from Fiji and Samoa and other Pacific islands. An independent burst of speciation has evidently occurred in the Aethiopian biogeographic zone. Three species of the *melanogaster* subgroup are endemic to the African continent, and several species of the *montium* subgroup and the two known species of the *dentissima* subgroup are also endemic to this region. Tsacas (1971) reported, in addition, a species

of the *ananassae* subgroup from Africa ("*malerkotliana*?") apart from the widespread *ananassae* itself. The substantial number of species of the *melanogaster* group in Southeast Asia, however, suggests that the species group originally arose in this general region and subsequently underwent prolific speciation along the major phylogenetic lines represented by the various subgroups. A few species presumably extended their ranges to Africa and speciated there.

The status of two of the widespread species—*melanogaster* and *simulans*, the best-known members of the group—is interesting. The four species *melanogaster*, *simulans*, *ananassae* and *kikkawai* occur over substantial areas of the world. The latter two species are also abundant in Southeast Asia and likely originated in this general region. It is widely assumed that the extensive distributions of *melanogaster* and *simulans* are to be explained by movements in association with human activities, habitations and migrations; indeed wherever these two species are found, it is generally about cities, towns or villages, there being in most areas no evidence that either *melanogaster* or *simulans* has become established in natural habitats. These two species are, however, largely or entirely absent from Southeast Asia. It appears that *melanogaster* does occur in the region, although it is very rare (cf. distributional records given above); as far as may be determined from published collection analyses and our own collections, *simulans* is absent altogether from India, Southeast Asia and New Guinea. It is, therefore, difficult to envisage either *melanogaster* or *simulans* as having originated in the Southeast Asian area. These species are widespread in Africa, Australia, north and south America, and Europe. Amongst these areas Africa and Australia possess endemic *melanogaster* group species. Africa possesses endemic species in the *melanogaster* subgroup; it is thus conceivable that both *melanogaster* and *simulans* could have evolved in the Aethiopian biogeographic zone and have only become widespread relatively recently in human history in association with human movements (e.g. the slave expeditions from the American continents), although *melanogaster* itself is well-established in India and has been shown to possess some intraspecific differentiation of several morphological characters (Parshad, Narda and Paika, 1964). Perhaps the most likely mode of evolution of the *melanogaster* subgroup is as follows. *D. melanogaster* may have originated in India. It is most likely that the populations ancestral to the present African endemics in the *melanogaster* species group reached that continent from India, the closest region in the presumed general area of origin of the group. *D. melanogaster* then reached Africa and underwent further speciation. A study of reproductive isolations between the various populations of *melanogaster* from the major regions of the world should help clarify the evolutionary status of this species.

One further feature of the distribution of the *melanogaster* species group deserves some comment. A *Drosophila* collection made in any part of the Southeast Asian or New Guinea area reveals that, although many species may be collected at any particular locality, only two species groups comprise all or practically all of the catch, i.e., the *melanogaster* species group of the subgenus *Sophophora* and the *immigrans* species group of the subgenus *Drosophila* (see Wilson *et al.*, 1969: 211–212, for a tentative summary of the taxonomic composition of the *immigrans* group). There are some interesting parallels between these two groups. Both groups have evidently originated in the Southeast Asian area and

speciated widely within this region. In each group a few species have, however, become considerably more widespread (*immigrans* itself occurs in north and south America, as well as parts of Southeast Asia and Australia). Each group possesses common and rare species, and species showing little or much polytene chromosome polymorphism, although these phenomena are not of course confined to the *melanogaster* and *immigrans* groups. Amongst Drosophilid faunas, the almost total dominance of only two species groups belonging to different subgenera of *Drosophila* in a substantial area of the world is a unique phenomenon.

The taxonomic composition of the *melanogaster* species group and the geographic distributions of its component species provide some insight into the pattern of speciation which has occurred. There are several major lines of descent in the group represented by the various subgroups; the populations ancestral to each of these subgroups presumably arose somewhere in the general Southeast Asian area from the ultimate ancestral population of the group. Several of the eleven subgroups possess three or more known species. The members of each subgroup presumably represent variations about a basic adaptive theme, of the original burst of speciation which occurred in the "primaeval" *melanogaster* species group, those species the gene pools of which were best suited to particular sets of environmental conditions presumably underwent subsequent bursts of speciation as they extended their ranges to produce the subgroups and species as they are now known. Unfortunately practically nothing is known of the ecology of the *melanogaster* group flies, including whether or not microecological isolation is important in keeping separate otherwise sympatric species; this would doubtless be a fruitful field for future investigation. The major subgroups of the *melanogaster* group are sympatric in most parts of the Oriental-New Guinea region in the sense that one or more representatives of each subgroup may be collected together. Within each subgroup, however, many of the species are generally allopatric. The most likely picture that therefore emerges regarding the evolution of the *melanogaster* species group is one of origin and initial speciation in the general Southeast Asian region; the most successful species expanded their ranges to overlap with those of other species and underwent further bursts of speciation. Representatives of at least three subgroups (*melanogaster*, *ananassae* and *montium*) reached the African continent and speciated further there within at least the *melanogaster* and *montium* subgroups (the affinities of the *dentissima* subgroup are unclear). A few species have become adapted to the special conditions about human activities and habitations and have apparently become very widespread in association with them.

The genus *Drosophila* is well known for the large number of pairs or groups of sibling species it contains, i.e., species which are morphologically very difficult to distinguish but which are nevertheless reproductively isolated. The *melanogaster* group possesses numbers of such sibling species. In the genus *Drosophila* it is a characteristic of sibling species that they may generally be separated only by reference to the structure of the male genitalia and/or sex-combs, the females being indistinguishable; in fact the females of many species, the males of which are quite different (possibly belonging to different subgroups) are frequently barely distinguishable. "Sibling species" as understood in the present context (and in general when reference is made to *Drosophila* species), refer, then, to

species the females of which are virtually identical and the males of which are only separable by detailed examination of the sex-combs and/or genitalia, frequently involving dissection of the latter. (It is recognized that the designation does involve a certain subjective element since an experienced taxonomist may have little difficulty in separating males which at first glance appear identical to the untrained observer). The best-known sibling species in the *melanogaster* group are of course *melanogaster* and *simulans* (cf. discussion in the *melanogaster* subgroup). The species of the *takahashii* subgroup are also very similar. Males of *nepalensis* are unique in this subgroup in possession of black patches in the wings, and males of *prostipennis* are also unique in possession of apically diffusely darkened wings; older males of *trilutea* also possess slightly darkened wings. However *takahashii* and *pseudotakahashii* may be regarded as a pair of siblings, as may *lutea* and *paralutea*; pigmentation of the last abdominal segment in females distinguishes *takahashii* from *lutea*. Within the *ananassae* subgroup, several pairs of siblings are found including the pale subspecies of *malerkotliana* and *pseudoananassae*, the dark subspecies of the same, *ananassae* (light) and *nesoetes*, and *ananassae* (dark) and *phaeopleura*; as already noted, *ananassae* (dark) and *pallidosa* are distinguishable in both sexes by coloration differences even though male genitalia are virtually identical. Finally the *montium* and *dentissima* subgroups provide a number of examples of sibling species including *serrata* and *birchii*, the members of the *auraria* complex, *mayri* and *pseudomayri*, *kikkawai* and those species like it of the same coloration, the members of the African *seguyi* complex, and the two known species of the *dentissima* subgroup.

It may, in the absence of more comprehensive chromosomal and biochemical studies, be somewhat premature to attempt a discussion of inter-subgroup relationships within the *melanogaster* group, but a few points can be made on the basis of the morphological evidence. The subgroups constitute major phylogenetic lines; several, however, possess features in common suggesting particularly close relationships. The members of the *ananassae* and *montium* subgroups alone possess both primary and secondary claspers, the latter lacking in the remaining species. It is tempting to envisage an initial phylogenetic dichotomy destined to produce, on the one hand, the *ananassae* and *montium* subgroups, on the other, the remaining subgroups. Within the latter lineage, the *takahashii*, *suzukii*, *ficusphila* and *eugracilis* subgroups may be descendants of a further single branch. Okada (1964a) has drawn attention to the presence of small hooked bristles on the mid-tibiae of males in these subgroups, and certain similarities are also evident in their genitalia. It seems best to defer further consideration of evolution within the *melanogaster* species group until considerably more chromosomal and biochemical evidence has been accumulated.

A few words may finally be said about the suitability of *melanogaster* group material for future research. Apart from the obvious and basic need for more collections to be made in unexplored areas and the taxonomy associated with these to be added to present knowledge, the group offers considerable scope for a variety of genetic and evolutionary studies. Very few of the *melanogaster* group species have been studied for chromosomal polymorphism in natural populations; many may be interesting subjects for such studies (cf. discussion of *birchii* in the taxonomic section above). The large number of sibling species in the group

probably offers scope for many investigations of reproductive isolation and hybrid sterility between as well as within species, and where interspecific hybrids may be obtained, analysis of the larval polytene chromosome rearrangements could provide further insight into the importance of inversions in evolution. The expanding field of biochemical analysis of species differences by the method of starch gel electrophoresis of enzymes, when applied to the *melanogaster* group (cf. Yang, Wheeler and Bock, this *Bulletin*) will hopefully permit clarification of the relationships between the various subgroups and the establishment of a somewhat more complete and reliable phylogeny.

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