Academic Press, London.
B. Geographical Survey of Drosophilidae.

6. Oriental Species, Including New Guinea

TOYOHI OKADA (1981)

Department of Biology
Tokyo Metropolitan University
Tokyo, Japan

I. The Oriental Region including New Guinea

A. Geographical Features

The Oriental Region occupies vast and complex areas of the Old World tropics and subtropics, ranging approximately from 30°N. to 10°S. latitude and from 60° to 130°E. longitude. Together with the Ethiopian Region and Madagascar, the Oriental Region belongs to the Paleotropical Realm (Müller, 1974), composed of the southeastern border of the Eurasian Continent and numerous larger and smaller islands surrounding the Equator. The main countries or provinces in this region are India, Pakistan, Nepal, Sri Lanka, South China, Formosa, the Ryukyu Islands of Japan up to Watase's or Miyake's Line, the Philippines, Burma, Laos, Thailand, Cambodia, Viet Nam, Malaysia, and Indonesia as far east as Wallace's or Weber's Line. Across this Line this region continues to the Australian Realm of the Mollucas

and the second largest island of the world, New Guinea (see Figs 2, 4, 6).

New Guinea is known to have flora and insect fauna resembling those of the Oriental Region rather than those of the Australian. Thus, the island is often included in the Papuan Subregion of the Oriental Region, mixed at it southern part with the Australian Region.

This region including New Guinea is rich in vegetation due to high temperatures and frequent rainfalls, as well as to complex topography, forming biomes of Tropical Rain forests (Malaya to New Guinea), Tropical Deciduous forests (northern India to South China) and Tropical Savannah Grassland (southern India) (Cox *et al.*, 1970). It contains high mountains in Nepal (8800 m), New Guinea (5000 m), Borneo (4100 m), Formosa (3900 m), Sumatra (3800 m), and Viet Nam (3200 m). At lower levels the mean annual temperature approximates 20–26°C., and the mean monthly rainfall is 40 cm in the summer in the northern continental areas and the same in the winter in the southern island areas.

B. Geological History

Like other families of higher Diptera, Drosophilidae is supposed to have originated in the Paleogene (Handlirsch, 1925). Consequently, a review of geology, especially paleogeography, of as early as the Mesozoic Era will be sufficient to facilitate an understanding of the composition and evolution of the drosophilid fauna of a given region.

The Oriental Region in the Triassic Period was composed of India, a part of Gondwanaland, and, interrupted from it by the Tethys Sea, the southern extension of Angaraland including South China, Formosa, the Philippines, Mollucas, and the northern part of Borneo. During the Jurassic Period, Angaraland extended southward to cover the Malay Peninsula, Sumatra, and a part of the Lesser Sunda Islands, while the Philippines (exclusive of Palawan), Formosa, and Mollucas were sunken in geosynclines. At the time of the Cretaceous Period, the Malay Peninsula, Sumatra, and the Lesser Sunda Islands were again sunken in the sea shelf. During Paleogene times the southern half of New Guinea was continuous with Australia, while Formosa, the Philippines, the northern half of Borneo, Sumatra, the Lesser Sunda Islands, and the northern half of New Guinea were below sea level. It was in the Early Neogene when the main uplifting movement of Himalayan Orogeny took the place of the Tethys Sea and the general topographical features attained a status near to that of the present (mainly after Minato *et al.*, 1965; Kummel, 1970).

In and after the Pleistocene Ice Ages, repeated eustatic movements of sea level changes occurred, and, especially, New Guinea was associated with Asia through fluctuating bridges or a series of stepping stones (Gressitt, 1961).

II. A Brief History of the Studies of Oriental and New Guinean Drosophilidae

The earlier studies of drosophilid fauna of the Oriental Region and New Guinea are those in the latter half of the 19th century by Walker (1857, 1859, 1860a, b, 1864, 1865a, b, 1868) on Sarawak, Celebes, Ceram, Salwatty and the eastern Archipelago, using the collections mostly of A. R. Wallace. These were supplemented by those of Van der Wulp (1886, 1892, 1896, 1897, 1898) on Java, Sumatra, and Ceylon, by Doleschall (1858) on Ambon, by Osten-Sacken (1882) on the Philippines, and by Kertész (1889, 1901) on New Guinea. In the early half of the 20th century, our knowledge of the fauna was much improved, especially by a number of extensive works by de Meijere (1906–1924) and Duda (1922–1936), which were focused on Viet Nam, Java, Sumatra, and Formosa. The famous Sauter collections were studied by Hendel (1913a, 1914), as well as by Duda (1924b). Frey (1917) and Senior-White (1921) treated the fauna of Ceylon; and Kahl (1917) and Sturtevant (1927) that of the Philippines, Formosa and India, Brunetti (1923), Malloch (1924a, 1929) and Chaudhuri and Muckerjee (1941) dealt with Indian species. Peng (1937) and Tan *et al.* (1949) focused on China including South China. Kikkawa and Peng (1938) dealt with the fauna of Japan including the Ryukyus and Formosa.

In his monograph on the North American species of *Drosophila*, Sturtevant (1921) enumerated 97 Oriental species of Drosophilidae belonging to 8 genera, of which three species were removed later from the family. Wheeler (1949b) published a complete list of world *Drosophila* species, in which he counted 108 Oriental species. Further revised lists were published by Wheeler (1959) and Wheeler and Hamilton (1972). Okada (1977b) listed 457 Oriental species, and Hennig (1941) listed 87 Formosan species of this family.

The main studies of local fauna since 1950 may be listed as follows:

New Guinea: Angus (1964, 1967), Ayala (1965a, b), Baimai (1970), Bock (1966), Bock and Baimai (1967), Mather (1961, 1968a, b), Mather and Dobzhansky (1962), Dobzhansky and Mather (1961), Carson and Okada (1980), Okada and Carson (1980).

India: Bächli (1973a), Dwivedi (1979), Dwivedi and Gupta (1979), Dwivedi *et al.* (1979), Gupta (1969, 1970, 1971, 1972, 1974a, b), Gupta and Ray-Chaudhuri (1970a, b), Gupta and Singh (1977, 1979), Parshad and Duggal (1966), Parshad and Paika (1964), Parshad *et al.* (1964), Parshad and Singh (1971), Prakash and Sreerama Reddy (1977, 1978), Sreerama Reddy and Krishnamurthy (1968, 1970, 1973), Sajjan and Krishnamurthy (1973), Singh (1974, 1976), Singh and Gupta (1974, 1977a, b), Vaidya and Godbole (1971, 1972, 1973, 1976).
Nepal: Okada (1955, 1966), Takada (1970).
Thailand: Okada (1964).
Malaysia: Mather (1968a), Okada (1976a, 1978), Takada and Momma (1975), Takada *et al.* (1973).
Indonesia: Burla (1954), Wheeler (1969), Carson and Wheeler (1973), Okada (1975, 1978).
Philippines: Delfinado and Hardy (1971), Takada (1976b).
Formosa: Lin and Ting (1971), Lin and Tseng (1971, 1972, 1973), Lin and Wheeler (1972), Okada (1971a, b, 1977a, 1978).
Ryukyus: Okada (1964, 1965, 1968a, b), Takada and Wakahama (1967).

Besides these studies of local fauna, or, more properly, based upon these faunal studies, detailed revision of a certain group of species, such as genus, subgenus, species group, and species-complex, has been one of the recent tendencies. Bächli (1971) treated the genus *Leucophenga* and *Paraleucophenga* of Africa, referring to some Oriental species. He (Bächli, 1973b) also revised the Southeast Asian species of the subgenus *Hirtodrosophila* described by Duda. Bock and Wheeler (1972) revised the *melanogaster* species group and divided it into 12 subgroups, of which 9 include Oriental species. Hackman (1959) subdivided the genus *Scaptomyza* into 9 subgenera, 2 of which include Oriental species. McAlpine (1968) revised the genera of Drosophilidae and allied families with pubescent arista. Okada (1967) investigated the subgenus *Hirtodrosophila* of the Old World and also (Okada, 1974) the genera *Sphaerogastrella* and *Liodrosophila* from the same area. Tsacas and Chassagnard (1976) studied in detail *Drosophila brunnea* and its allies. Tsacas and David (1977) analysed the *kikkawai*-complex species. Wilson *et al.* (1969) made a cytogenetic study of the *nasuta* subgroup of the *immigrans* species group and recognized 8 species and 3 subspecies.

Phylogenetic researches of Drosophilidae on a broad scale have been made by Throckmorton (1962a, b, 1968, 1975). Yang *et al.* (1972) calculated genetic distance among the species of the *bipectinata*-complex

to establish a phylogenetic tree, which was investigated further by Bock (1978) using a hybridization test. This work will be discussed later.

III. Faunal Composition and Biogeography

A. Taxonomic Overview

Twenty-eight genera, which are about half of those known in the world, and about 560 named species have hitherto been known from the Oriental Region including New Guinea. Seven genera and about 100 species belong to the subfamily Steganinae, and 21 genera and about 460 species to the subfamily Drosophilinae. Among the genera of Steganinae, *Leucophenga* has more than half of the total species, *Amiota* a quarter, and *Stegana* one sixth. The other genera, *Acletoxenus*, *Cacoxenus* (including *Gitonides*), *Eostegana*, and *Luzonimyia*, have only one or two described species each. Among the genera of the Drosophilinae, *Drosophila* has about 300 described species, *Liodrosophila* 36, *Microdrosophila* 20, *Mycodrosophila* 14, and *Scaptomyza* 12. The remaining genera—*Dettopsomyia*, *Chymomyza*, *Drosophilella*, *Hypselothyrea*, *Lissocephala*, *Nesiodrosophila*, *Phorticella*, *Colocasiomyia*, *Diathoneura*, *Neotanygastrella*, *Paramycodrosophila*, *Sphaerogastrella*, *Sphyrnoceps*, *Styloptera*, *Zaprionus* and *Zygothrica*—have less than ten species each.

With regard to the subgenera of *Drosophila*, of which eight are represented in the Oriental Region including New Guinea, nearly one third of the total known species belong to *Sophophora* and another one third to *Drosophila*, each involving nearly 100 described species. *Scaptodrosophila* has about 60 species and *Hirtodrosophila* about 35. The other subgenera, *Lordiphosa*, *Dorsilopha*, *Dudaica* and *Psilodorha*, have less than 5 species each. About 25 species of the genus *Drosophila* are not assorted to subgenus. Among the subgenera of the genus *Drosophila*, *Sophophora* is found in each of the 20 areas, *Drosophila* in 19, *Scaptodrosophila* in 15, *Hirtodrosophila* in 12, *Dorsilopha* in 7, *Dudaica* in 4, and *Lordiphosa* and *Psilodorha* in 2.

There remain, however, numerous undescribed species to be found in the future in the vast areas of this Region, especially New Guinea, and the figures given above will undoubtedly be multiplied.

B. Faunal Comparison Within the Oriental Region Including New Guinea

Out of the 28 genera of the family Drosophilidae which have hitherto been known from the Oriental Region including New Guinea, only

TABLE 1. The number of described species of Drosophilidae found in the major areas of the Oriental Region, including New Guinea

Genus and Subgenus	Nepal	India	Sri Lanka	Thailand	Viet Nam	Cambodia	Andaman, Nicobar	Sumatra
Acletoxenus		1						
Amiota				2				3
Cacoxenus		1						
Eostegana								
Leucophenga	15	7	5	1	2		1	8
Luzonimyia								
Stegana	1	1	1					3
Chymomyza		1	1					3
Colocasiomyia								
Dettopsomyia			1		2			2
Diathoneura	1							
Drosophila	30	68	15	31	5	7	7	69
Dorsilopha	1	1		1				1
Drosophila	12	22	6	8	1	2		16
Hirtodrosophila	2	1	2	1				15
Lordiphosa	3							1
Dudaica								1
Psilodorha								
Scaptodrosophila	4	9			1			18
Sophophora	8	35	7	21	3	5	7	9
Ungrouped								8
Drosophilella								
Hypselothyrea	1	3		2				1
Liodrosophila	4	4	4	2	4			7
Lissocephala		1	2					1
Microdrosophila	5	1						2
Mycodrosophila		1						5
Neotanygastrella								
Nesiodrosophila	2							
Paramycodrosophila	1			1				1
Phorticella		2						1
Scaptomyza	5	2						
Sphaerogastrella			1	2	1			1
Sphyrnoceps								1
Styloptera								
Zaprionus		1						
Zygothrica								
Total	**65**	**94**	**30**	**41**	**14**	**7**	**8**	**108**

Java	Borneo	Malaya	Singapore	Hong Kong	South China	Formosa	Ryukyus	Philippines	Celebes	Moluccas	New Guinea	Total
1												2
1	1	1				11	2	2			3	26
						1		1			1	1
								1			1	1
19	1	8	6	3		33	8	4			9	55
								1				1
6	2	2				7	2	1	1		1	17
2						1						5
1												1
3		2						2			2	8
												1
55	51	35	19	4	22	82	41	34	14	5	55	315
					1	1	1					1
11	18	9	4	2	13	36	12	12	4	1	14	96
5	1	2				12	7	2			5	34
												4
1								1			1	1
						1	1					2
15	1	3	4		1	11	5	2	2	2	20	59
15	31	20	11	2	7	19	15	15	8	2	14	93
8		1				2		2			1	25
1						2	2				3	6
1		3	1			2					6	10
11	6	13	4	4		8	4		1		2	36
5		6	2			2	2				1	9
4		2				7	6				1	20
3		2	3			2	5					14
	1											1
						1	1					4
1		1	1			1	1					1
2						4	1	1		1	1	5
2		2				4	2			1	1	12
1		1						1			1	2
												1
						1					2	3
												1
		2										2
119	62	80	36	11	22	169	77	48	16	7	76	560

three are endemic to the region; *Colocasiomyia* (Java), *Luzonimyia* (the Philippines) and *Sphyrnoceps* (Simeuluë Island near Sumatra). None of the 15 genera known from New Guinea are endemic to that area. The number of genera having been recorded is 18 from Java, 17 from Formosa, 16 from New Guinea, 15 from India and Sumatra, 14 from Malaya, 13 from the Ryukyus, 10 from the Philippines and Nepal, 9 from Sri Lanka, 7 from Singapore and Thailand, 6 from Borneo, and 5 from Viet Nam. From the other areas less than 3 genera are known, and from Burma and Laos seemingly none. The number of species in each of these 20 areas is shown in Table I.

The genus *Drosophila* is distributed in every area where the drosophilids are known: *Leucophenga* and *Liodrosophila* in 16; *Stegana* in 12; *Amiota* in 10; *Hypselothyrea* and *Lissocephala* in 9; *Microdrosophila, Paramycodrosophila, Phorticella, Scaptomyza* and *Sphaerogastrella* in 8; *Mycodrosophila* and *Dettopsomyia* in 7; *Chymomyza* in 5; *Cacoxenus* and *Drosophilella* in 4; *Nesiodrosophila* in 3; *Eostegana, Acletoxenus* and *Styloptera* in 2. *Luzonimyia, Colocasiomyia, Diathoneura, Zaprionus, Zygothrica, Neotanygastrella* and *Sphynoceps* are recorded from only a single area each.

Faunal comparison at the genus level within this region including New Guinea is attempted by means of the procedure of numerical taxonomy, taking areas as taxa ($t = 16$) and genera as characters ($n = 28$). The genus *Drosophila* is excluded because it is found in every area. The areas compared are those in which more than 10 species have been recorded: 1. Nepal; 2. India; 3. Sri Lanka; 4. Thailand; 5. Viet Nam; 6. Sumatra; 7. Java; 8. Borneo; 9. Philippines; 10. Malaya; 11. Singapore; 12. Hong Kong; 13. S. China; 14. Formosa; 15. Ryukyus; 16. New Guinea.

For proximity analysis (Carmichael and Sneath, 1969) a similarity coefficient S_o (Okada, 1970b) is used.

$$S_o = 1/n\ (2n_{JK} + n_{jk});\ thus\ S_o n = 2n_{JK} + n_{jk}$$

where n_{JK} is the number of genera present (coded 1) in both areas compared (J,K); N_{jk} is that absent (0) from both (j,k). The cluster analysis is made by means of UPGMA (Unweighted Pair Group Method Using Arithmetic Average).

The resulting phenogram is as shown in Fig. 1, from which a geographical map of faunal resemblance (Fig. 2) is provided. Cophenetic Correlation Coefficient (r_{cs}) between the original and derived $t \times t$ matrices is +0·78. The result shows in general reasonable biogeographical relationships, although somewhat distorted probably due to different degrees of completeness in the ~~the~~ various surveys. Two major clusters are recognized. One includes India, Nepal, Formosa, New

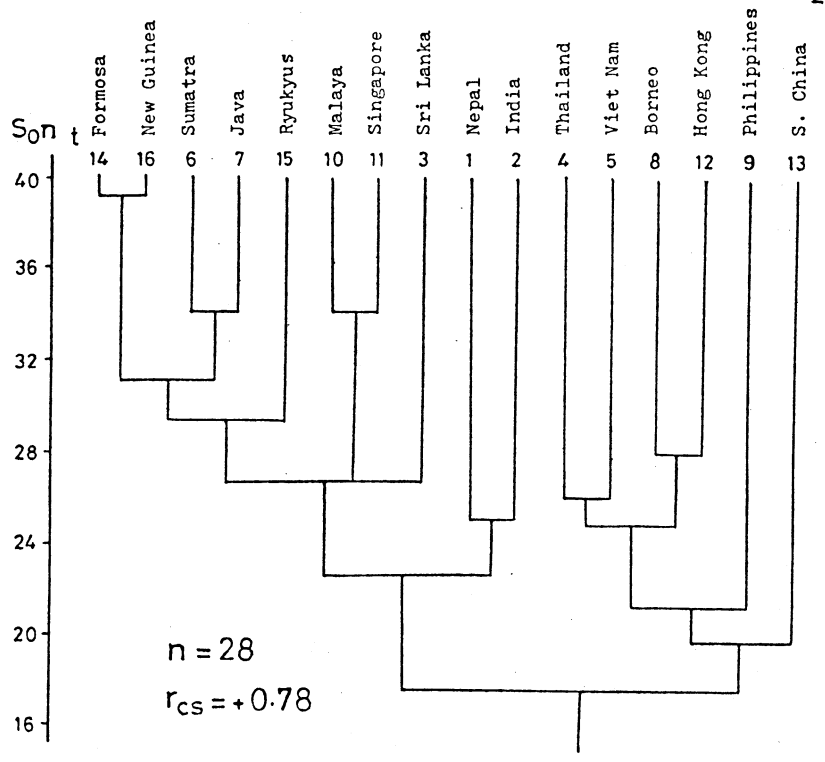

FIG. 1. A phenogram of faunal relationships of the family Drosophilidae at the genus level among 16 areas (t) within the Oriental Region including New Guinea. Proximity analysis by S_o; cluster analysis by UPGMA. R_{cs}: Cophenetic Correlation Coefficient between original and derived t × t matrices; n: number of genera.

Guinea, Sumatra, Java, the Ryukyus, Malaya, Singapore and Sri Lanka; and the other includes Thailand, Viet Nam, Borneo, Hong Kong, the Philippines and South China. The areas of the former cluster tend to be better surveyed than those of the latter. The former major cluster is divided into two subclusters, one including India and Nepal and the other the remaining areas. The latter major cluster shows no clear subdivision. Unexpectedly, the closest faunal resemblance is found between Formosa and New Guinea. The next closest relationship is found between Sumatra and Java and also between Malaya and Singapore, as expected. South China is remotest from other areas due certainly to poor survey in that area.

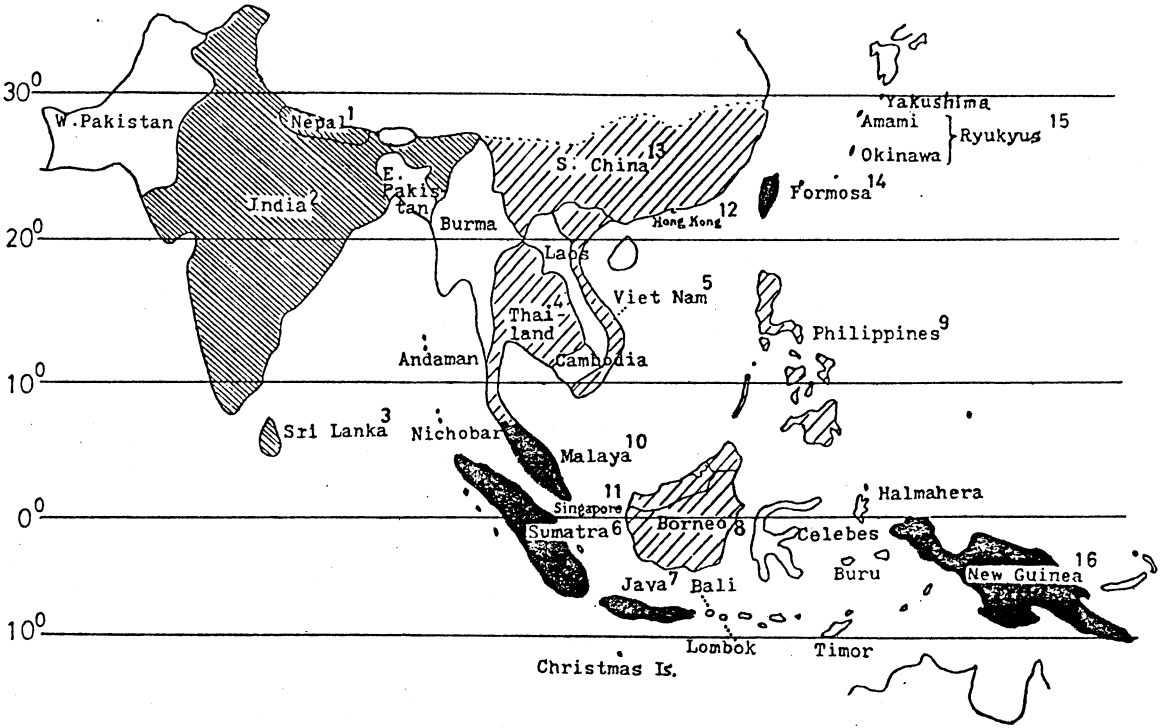

FIG. 2. Faunal relationships of the family Drosophilidae at the genus level among 16 areas (1–16) within the Oriental Region including New Guinea, derived from the phenogram (Fig. 1). The areas shaded black are clustered together, and areas densely striped and those sparsely striped are successively clustered to these.

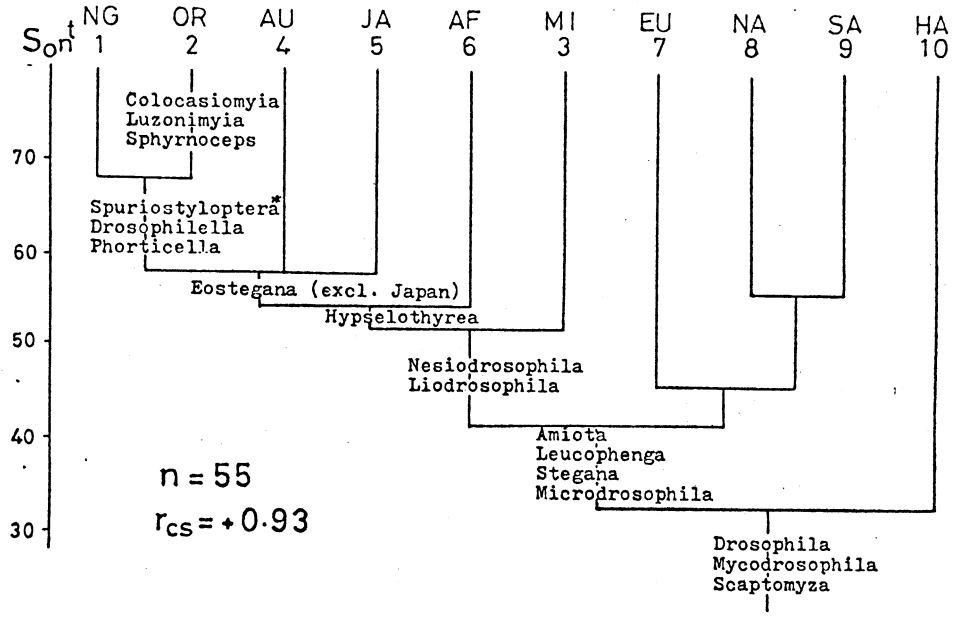

FIG. 3. A phenogram of faunal relationships of the family Drosophilidae at the genus level among 10 Regions (t) of the world: 1. New Guinea (NG), 2. Oriental Region (OR), 3. Micronesia (MI), 4. Australia (AU), 5. Japan (JA), 6. Africa (AF), 7. Europe (EU), 8. North America (NA), 9. South America (SA), 10. Hawaii (HA). The genera representing each cluster which involves the Oriental Region are shown on the stems of the phenogram. *Synonymous with the subgenus *Scaptodrosophila*. Other explanations as in Fig. 1.

C. FAUNAL COMPARISON WITH OTHER REGIONS

For the faunal comparison at the genus level among 10 geographical regions centering on the Oriental Region and New Guinea, the same methods of proximity and cluster analyses as used above are applied. The regions compared are: 1. New Guinea (NG), 2. the Oriental Region (OR), 3. Micronesia and Melanesia (MI), 4. Australia (AU), 5. Japan exclusive of the Ryukyus (JA), 6. Africa (AF), 7. Europe (EU), 8. North America (NA), 9. South America (SA), and 10. Hawaii and other Polynesian Islands (HA). In total 55 genera are incorporated, excluding, however, *Drosophila*, *Mycodrosophila*, and *Scaptomyza*, because these three genera are recorded from every one of the Regions under consideration.

The resulting phenogram and a geographical map of faunal relationships are shown in Figs. 3 and 4. The r_{cs} between the original and

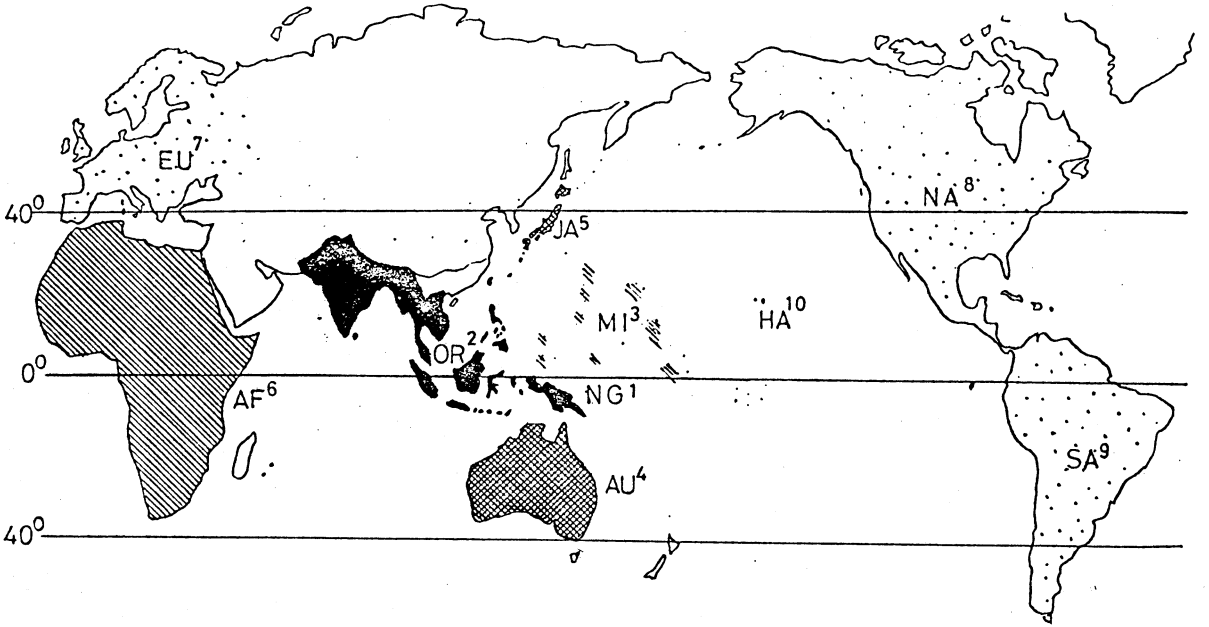

FIG. 4. Faunal relationships at the genus level of the family Drosophilidae among 10 Regions (1–10) of the world, derived from the phenogram (Fig. 3). The Regions shaded black make a cluster, to which the Regions cross-striped, densely striped, and dotted, are successively clustered.

derived $t \times t$ matrices is +0·93. The Oriental Region stands closest to New Guinea, and these two are clustered to Australia and Japan at the same level. To these four regions, Africa and Micronesia are successively associated. The representative genera of each cluster which involves the Oriental Region and New Guinea are shown on the stems of the phenogram (Fig. 3).

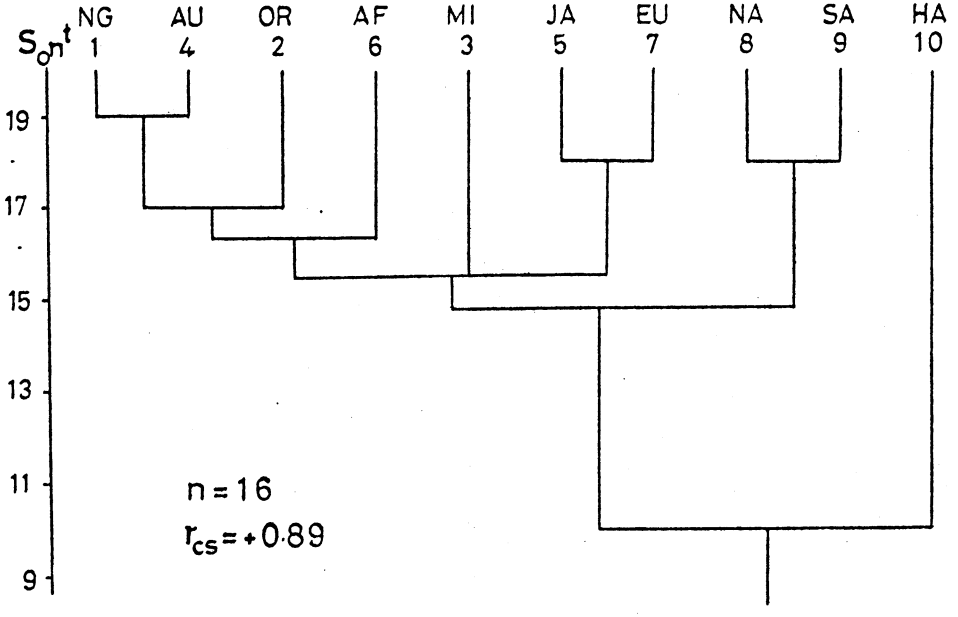

FIG. 5. A phenogram of faunal relationships of the genus *Drosophila* at the subgenus level among 10 Regions of the world. n: number of subgenera. Other explanations as in Fig. 3.

A similar method applied to the subgenus level of the genus *Drosophila* yielded the phenogram shown in Fig. 5. In this case, New Guinea stands closest to Australia, and these two are connected with the Oriental Region, Africa and Micronesia, successively, to make a cluster, to which are added Japan and Europe.

D. SPECIAL FEATURES OF THE FAUNA

1. Extensively diversified groups of species

Among the genus *Drosophila*, the *melanogaster* species group and the *immigrans* species group show an "interesting parallelism" (Bock and

Wheeler, 1972). Thus, each group shows extensive diversification in the Oriental Region including New Guinea. The groups comprise more than 90 and 50 described species, respectively.

The *melanogaster* species group is, as mentioned before, divided into 11 named species subgroups (Bock and Wheeler, 1972), of which 9 include Oriental and New Guinean species, *viz. melanogaster*, *takahashii*, *suzukii*, *elegans*, *denticulata*, *eugracilis*, *ficusphila*, *ananassae* and *montium* subgroups. Among them the *suzukii* subgroup alone does not enter New Guinea. The number of Oriental and New Guinean species of the *melanogaster* species group approximates 65% of the total species of this group in the world, and 98% of the total species of the subgenus *Sophophora* in this region including New Guinea.

It is remarkable, however, that in this region including New Guinea, *D. melanogaster* is rather rare and *D. simulans* has not been recorded except from Yakushima, Japan, just south of Miyake's Line (Fig. 6). The phenomenon of this rarity will be discussed in relation to the origin of the *melanogaster* subgroup later in this chapter.

The *immigrans* species group is divided into 5 named subgroups: *viz. immigrans*, *nasuta*, *quadrilineata*, *lineosa* and *hypocausta* (Wilson *et al.*, 1969). Each of these subgroups has been recorded from the Oriental Region and also from New Guinea. The number of the Oriental and New Guinean species in total exceeds 90% of the total species of the subgenus *Drosophila* in the Oriental Region including New Guinea.

2. *High Altitude species: Palearctic elements*

Tropical high mountains are often inhabited by animal species which are thought to be Palearctic or Holarctic elements and not necessarily autochthonous mountain species, that is, evolved on mountains *in situ* (Mani, 1968). Examples of Drosophilidae in this region are found in the *obscura*, *robusta* and *histrio* species groups of the genus *Drosophila*.

The *obscura* species group is a typical Holarctic element. *D. bifasciata* of this group has been found in Chandigarh and Manimajra, Punjab, India, (Parshad and Paika, 1964) and has also been found in Kashmir, India, together with two other species of this group, *D. epiobscura* and *D. helvetica*, (Parshad and Duggal, 1966). *D. bifasciata* has been found also in Ali Shan, Formosa, and in Yakushima, Japan. These localities are exclusively at high altitude.

The *robusta* species group, another Holarctic element, includes *D. cheda* and *D. pullata* from the mountain areas of South China. *D. lacertosa* of this group is widely distributed in the Japanese mainland and Korea, and is recorded also from Nepal, India (Uttar Pradesh) and Formosa

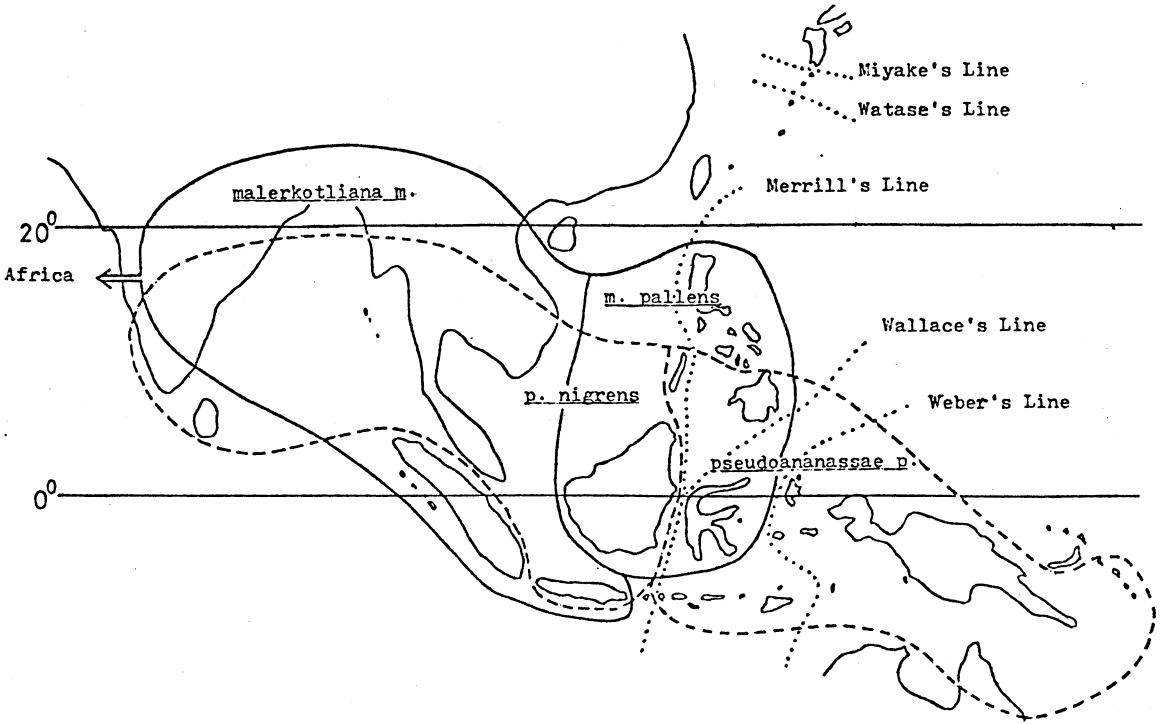

FIG. 6. Distribution of two subspecies (*malerkotliana*, *pallens*) of *Drosophila malerkotliana* and two subspecies (*nigrens*, *pseudoananassae*) of *D. pseudoananassae*, in relation to the Biogeographical Boundary Lines.

(several high mountains). In Ali Shan, Formosa, an undescribed species closely allied to *lacertosa* has also been found.

D. histrio is a typical Palearctic species, while a species closely similar to it has been collected also from Ali Shan.

Except for *D. cheda* and *D. pullata*, these examples probably are typical relict species whose distribution had certainly been confined to the Tropical high mountains during the Neogene Interglacial Ages.

E. Biogeographical Boundary Lines

Although the biogeographical line is not as distinct a boundary for insects as it is for higher vertebrata, particularly mammals (Gressitt, 1961), this concept helps to clarify biogeographical relationships and aids in understanding the fauna of complex interdigitating island archipelagos. Wallace's Line (Wallace, 1860) passing between Bali and Lombok through the south of the Philippines (Fig. 6) is a good example of this. It is also true for other boundary lines, especially for drosophilids which may be dispersed even by winds. A number of genera entering towards the east across Wallace's Line, e.g. *Eostegana*, *Drosophilella*, *Hypselothyrea*, *Liodrosophila*, *Sphaerogastrella* and *Styloptera*, seldom spread outside the Oriental Region including New Guinea.

D. pseudoananassae has two subspecies (Bock, 1971), *nigrens* distributed in India, Sri Lanka, Java, Borneo, and Malaya, and the nominate subspecies found in the Philippines, Lombok (Okada, unpublished observations) and New Guinea. The subspecific boundary in this case nearly, but not strictly, corresponds to Merrill's Line (Merrill, 1923), which passes between Bali and Lombok and between Borneo and the Philippines (Fig. 6). *D. malerkotliana* also has two subspecies (Bock, 1971). The nominate subspecies is distributed in India, Malaya, Indo-China, Java, Sumatra and Africa. The other subspecies, *pallens*, is found in the Philippines, Borneo and Celebes, crossing Wallace's Line eastward but not crossing Weber's Line (Weber, 1902), which passes between Celebes and Moluccas. Recently, Val and Sene (1980) found a form of this species from Brazil.

In both species the "dark" subspecies, with male distal abdominal tergites black, are more westward in distribution than the "pale" ones. Yang *et al.* (1972) analysed the genetic distance with biochemical characters between four species of the *bipectinata*-complex including subspecies, and found close phylogenetic relationships among *bipectinata*, *parabipectinata*, and *malerkotliana* (2 subspecies), with a greater divergence between them and *pseudoananassae* (2 subspecies). Bock (1978) reached a similar conclusion by detailed interspecific hybridization tests. Among

the *bipectinata*-complex, *D. bipectinata* is most widely distributed in the Oriental Region including New Guinea, Micronesia, Samoa and Fiji, with a northern limit of distribution on Watase's Line, which passes just north of Amami Islands, Japan (Fig. 6). *D. parabipectinata* occurs in the Philippines, Borneo, Christmas Island (Indian Ocean), Celebes, Indo-China and India, with the eastern limit of distribution similar to that of *D. malerkotliana*.

The genera *Drosophilella*, *Lissocephala* and *Phorticella* do not enter north of Watase's Line (Watase, 1912), while *Hypselothyrea*, *Liodrosophila*, *Nesiodrosophila* and *Styloptera* cross to the north of Miyake's Line (Miyake, 1919; Esaki, 1921).

IV. Patterns of Evolution in the Oriental and New Guinean Drosophilidae

Evolution of Drosophilidae is best discussed from a world-wide viewpoint as was done by Throckmorton (1962a, b, 1968, 1975). Treatment here is, consequently, limited to certain special lower taxa, *viz.*, the *obscura* species group, the *melanogaster* subgroup, the subgenus *Scaptodrosophila*, the *nasuta* species subgroup of the *immigrans* species group, and the genus *Drosophilella*.

The *obscura* species group is most closely related to the *melanogaster* species group, which is supposed to be derived from the former (Sturtevant, 1942) possibly through the *suzukii* subgroup. Sturtevant and Novitski (1941) mentioned that *D. suzukii* turns out in fact to be an intermediate between the *melanogaster* and *obscura* species groups; the anterior reclinate orbital is long as in the *obscura* group species, while the 2nd oral is long as in the *melanogaster* group species. In view of the structures of the phallic organs, Okada (1954) considered *D. suzukii* to be closest to the *obscura* group among the members of the *melanogaster* species group. The *suzukii* subgroup includes *suzukii*, *pulchrella*, *unipectinata*, *oshimai*, *tristipennis*, *immacularis*, *biarmipes*, *lucipennis* and *mimetica*. Their distribution ranges are somewhat restricted, no representatives being known from the major Southeast Asian islands (Borneo, the Philippines, etc.) east of the Malayan Peninsula (Bock and Wheeler, 1972), with an exception of *D. mimetica* which was recently found in Lombok (Okada, published observation). This species, as well as *D. unipectinata*, lacks hooked scaly bristles on the tibia and metatarsus of male mid legs. This is different from other members of the subgroup as well as the *takahashii*, the *ficusphila* and the *eugracilis* subgroups.

Bock and Wheeler (1972) considered that *D. melanogaster* may have either evolved in Africa or originated in India and then reached Africa,

subsequently undergoing further speciation. Throckmorton (1975) concluded that the *melanogaster* subgroup arose in Africa, while the *melanogaster* species group itself almost surely arose in South Asia. Tsacas and Lachaise (1974) are also rather in favor of the hypothesis of African origin of the *melanogaster* subgroup.

I am inclined to suppose that the ancestral species of the *obscura* species group originated in the Oriental Region. During the Neogene Glacial Ages it is supposed that it underwent splitting in species and spread geographically. In the succeeding Interglacial Ages some of these yielded various species of the *melanogaster* species group. A warmer climate could then have driven the *obscura* group species northwards into the Holarctic Realm. Likewise, the replacement through competition of the *melanogaster* subgroup species by other subgroup species might have resulted in the present status of rarity of that subgroup in the Oriental Region.

The subgenus *Scaptodrosophila* of the genus *Drosophila* is abundant in species in the Oriental Region, New Guinea, and especially in Australia, and is supposed to have originated in tropical Asia (Throckmorton, 1975; Bock and Parsons, 1978). This subgenus belongs to the early drosophiline radiation prior to the Sophophoran one (Throckmorton, 1975). Kurokawa and Hihara (1976) discovered the important fact that the more primitive forms of the genus *Drosophila* tend to show a larger number of multiplication division of spermatogonia: *Scaptodrosophila* 6, the *obscura* group 5, and the *melanogaster* group 4, showing a clear evolutionary trend of *Scaptodrosophila*—the *obscura* group—the *melanogaster* group, as discussed above.

In their extensive studies of taxonomy, cytogenetics and crossing tests, Wilson *et al.* (1969) recognized seven biological species in the *nasuta* subgroup of the *immigrans* species group. Among them, *D. pallidifrons* is the only highly distinct species, while the other six from the Oriental Region including New Guinea are hardly distinguishable from each other even by the features of the male genital organs. An exception is *D. pulaua* from Sarawak. It should certainly be an exception from a definition of "sibling species" in *Drosophila*, referred to by Bock and Wheeler (1972), that "the species the females of which are virtually identical and the males of which are only separable by detailed examination of sex-combs and/or genitalia."

According to Kitagawa (1979), *D. nasuta* is distributed in the Seychelles, Madagascar, Africa, Sri Lanka and India. Thus, it is highly plausible that this species originated in the Oriental Region and invaded the Ethiopian Region through the Neogene land bridge between India and Africa.

A score of species of the genus *Zaprionus* are found in Africa, while only one, *Z. indiana*, is found in the Oriental Region. The genus *Phorticella*, which is closely allied to, and often treated as a subgenus of, the genus *Zaprionus*, is found in the Oriental region and could have replaced most of the members of *Zaprionus*. Thus, even the genus *Zaprionus* could have originated in the oriental Region and later invaded Africa. Along the same line of reasoning, the few Oriental or New Guinean species sometimes assigned to *Zaprionus*, e.g. *obscuricornis* and *silvistriatus*, should perhaps be better placed in the genus *Phorticella*.

Finally, a special feature of evolution presented by the genus *Drosophilella* will be discussed. Six species have been discovered to the present in the genus, 3 in the Oriental Region and 3 in New Guinea. All except *D. seminigra* from New Guinea are found associated with the flowers of two genera of Araceae, *Colocasia* or *Alocasia*. The flies and larvae of ~~of~~ the two species in Formosa and the Ryukyus are found microallopatrically in one and the same flower of *Alocasia odora* (Honda, in Okada, 1975). Those of the other two species in Papua New Guinea are also microallopatric in one and the same flower of *Colocasia esculenta*. One species of Formosa and the Ryukyus is morphologically and ethologically most closely related to one species of Papua New Guinea, and another species of the former areas is closely related to another species of the latter area (Carson and Okada, 1980).

Through the courtesy of Drs. Th. van Leeuwen and B. Brugge of the Zoological Museum, University of Amsterdam, I have recently examined the Lectotype female of *D. colocasiae* from Java and found it to be distinct from any of the species from Formosa–Ryukyus and New Guinea. The Lectotype of *D. colocasiae* was collected from the flower of *Colocasia antiquarum* (= *C. esculenta*, according to Yen and Wheeler, 1968).

V. Conclusion

The faunal surveys in this Region including New Guinea are still insufficient to make available any further comparison especially at the species level of the fauna. Numerous species remain unnamed or undiscovered. Carson's personal communication estimates more than 90 species of the subgenus *Scaptodrosophila* to occur in Papua New Guinea, although at present only eight described species are known. Indeed, he discovered that about 15 *Scaptodrosophila* species were associated with flowers in the Morobe District, Papua New Guinea in 1977.

The recent tendency to multiply the species number comes about

not only by exploration in poorly surveyed areas, but also by recovering synonyms of certain species to valid names of distinct species, such as in the *nasuta* subgroup (Wilson *et al.*, 1969), the *brunnea*-complex of the subgenus *Scaptodrosophila* (Tsacas and Chassagnard, 1976), and the subgenus *Hirtodrosophila* (Bächli, 1973b). On the other hand, the concept of subspecies, which had been rarely applied to *Drosophila* taxonomy, has increasingly been developed recently. For example, three subspecies of *D. sulfurigaster* have been recognized (Wheeler, in Wilson *et al.*, 1969). An east Asiatic and an Indian subspecies of *D. suzukii* are described by Parshad and Paika (1964). As cited before two each for *D. pseudoananassae* and *D. malerkotliana* have also been recognized. There is a case, on the contrary, where a subspecies was raised to a good species, *viz. D. unicolorata exilis* from Yakushima, Japan (Bächli, 1973b).

Like most other insect groups, the greatest percentage of genera, subgenera, and species groups of the family Drosophilidae are supposed to have originated in the Oriental Region. This would be true even for certain groups or species which are at present very rare or absent from the Oriental Region. Such rarity or absence may partially be caused by the replacement of less adapted forms by other more successful members through competition.

Indeed, the center of dispersal of a group of animals is likely also to be the area in which the group is represented by the greatest number of species, but often a group may gain access to another area than its place of origin and undergo rapid speciation and multiplication of individuals there (Cox *et al.*, 1976; Dobzhansky, personal communication).

References

Angus, D. (1964). *D. tetrachaeta*: a new species of *Drosophila* from New Guinea. *Univ. Queensl. Pap.* **2**, 155–159.

Angus, D. (1967). Additions to the *Drosophila* fauna of New Guinea. *Univ. Queensl. Pap.* **3**, 31–42.

Ayala, F. J. (1965a). Sibling species of the *Drosophila serrata* group. *Evolution* **19**, 538–545.

Ayala, F. J. (1965b). *Drosophila dominicana*, a new sibling species of the *serrata* group. *Pacif. Ins.* **7**, 620–622.

Bächli, G. (1971). *Leucophenga* und *Paraleucophenga* (Diptera Brachycera) Fam. Drosophilidae. Exploration du Parc National de l'Upemba. 192 pp. Mission G. G. Witte Fondation pour favoriser les recherches Scientifiques en Afrique. Bruxelles.

Bächli, G. (1973a). Beitrag zur Kenntnis der Drosophiliden-Fauna (Diptera) des Kanha-Nationalparkes. *Viertenjahrsschrift naturforsch. Gess. Zürich* **118**, 23–30.

Bächli, G. (1973b). Revision der von Duda beschriebenen Südostasiatischen Arten

des *Drosophila*—Subgenus *Hirtodrosophila* (Diptera: Drosophilidae). *Mitt. zool. Mus. Berl.* **49**, 267–315.

BAIMAI, V. (1970). *Drosophila pseudomayri*, a new species from New Guinea (Diptera: Drosophilidae). *Pacif. Ins.* **12**, 21–23.

BOCK, I. R. (1966). *D. argentostriata*: a new species of *Drosophila* from New Guinea. *Univ. Queensl. Pap.* **2**, 271–276.

BOCK, I. R. (1971). Taxonomy of the *Drosophila bipectinata* species complex. *Univ. Texas Publ.* **7103**, 273–280.

BOCK, I. R.(1978). The *bipectinata* complex: A study in interspecific hybridization in the genus *Drosophila* (Insecta: Diptera). *Austral. J. biol. Sci.* **31**, 197–208.

BOCK, I. R. and BAIMAI, V. (1967). *D. silvistriata*: a new species of *Drosophila* from New Guinea. *Univ. Queensl. Pap.* **3**, 19–25.

BOCK, I. R. and PARSONS, P. A. (1978). The subgenus *Scaptodrosophila* (Diptera: Drosophilidae). *Syst. Ent.* **3**, 91–102.

BOCK, I. R. and WHEELER, M. R. (1972). The *Drosophila melanogaster* species group. *Univ. Texas Publ.* **7213**, 1–102.

BRUNETTI, E. (1923). A new Indian drosophilid fly. *Rec. Ind. Mus.* **25**, 303–304.

BURLA, H. (1954). Distinction between four species of *melanogaster* group "*Drosophila seguyi*", "*D. montium*", "*D. kikkawai*", and "*D. auraria*" (Drosophilidae, Diptera). *Rev. Brasil. Biol.* **14**, 41–54.

CARMICHAEL, J. M. and SNEATH, F. H. A. (1969). Taxometic maps. *Syst. Zool.* **18**, 402–415.

CARSON, H. L. and OKADA, T. (1980). Drosophilidae associated with flowers in Papua New Guinea I. *Colocasia esculenta*. *Kontyû* **48**, 15–21.

CARSON, H. L. and WHEELER, M. R. (1973). A new crab fly from Christmas Island, Indian Ocean. *Pacif. Ins.* **15**, 199–208.

CHAUDHURI, R. and MUCKERJEE, D. P. (1941). Genetic and systematic studies on Indian *Drosophila*. *Ind. J. Ent.* **3**, 215–224.

COX, C. B., HEALEY, I. N. and MOORE, P. D. (1976). "Biogeography, an Ecological and Evolutionary Approach." 194 pp. Blackwell Sci. Publ. London.

DELFINADO, M. D. and HARDY, D. E. (1971). Type specimens of Philippine Diptera. *Notul. ent.* **51**, 15–32.

DOBZHANSKY, T. and MATHER, W. B. (1961). The evolutionary status of *Drosophila serrata*. *Evolution*, **15**, 461–467.

DOLESCHALL, C. L. (1858). Derde bijdrage tot de kennis der dipteren fauna van Nederlandsch Indië. *Natuurk. Tijdschr. v. Ned. Indië*, **17**, 73–128.

DUDA, O. (1922). *Liodrosophila* und *Sphaerogastrella*, zwei neue, zu den Drosophiliden und nicht zu den Camilliden gehörige Dipteren-Gattungen aus Südostasien. *Arch. Naturgesch.* **88A(4)**, 150–160.

DUDA, O. (1923). Die Orientalischen und Australischen Drosophiliden-Arten (Dipteren) des Ungarischen National-Museums zu Budapest. *Annls hist.-nat. Mus. natn. hung.* **20**, 24–59.

DUDA, O. (1924a). Beitrag zur Systematik der Drosophiliden unter besonderer Berücksichtigung der paläarktischen u.orientalischen Arten (Dipteren). *Arch. Naturgesch.* **90A(3)**, 172–234.

DUDA, O. (1924b). Die Drosophiliden (Dipteren) des Deutschen Entomologischen Institutes der Kaiser Wilhelm-Gesellschaft (Früh. Deutsches Entomolog. Museum) aus H. Sauter's Ausbeute. *Arch. Naturgesch.* **90A(3)**, 235–259.

DUDA, O. (1926a). Fauna sumatrensis, Beitrag N. 26, Drosophilidae (Dipt.) *Supplta ent.* **14**, 42–116.

DUDA, O. (1926b). Die orientalischen und australischen Drosophiliden-Arten (Dipteren) des Ungarischen National Museums zu Budapest. Nachtrag. *Annls hist.-nat. Mus. natn. hung.* **23**, 241–250.

DUDA, O. (1928). Beitrag zur Kenntnis der südostasiatischen Drosophilidengattung *Hypselothyrea* de Meijere (Dipt.). *Annls hist.-nat. Mus. natn. hung.* **25**, 79–90.

DUDA, O. (1929). Fauna Buruana, Diptera, Acalyptrata. *Treubia* **7**, 415–422.

DUDA, O. (1931). Chloropidae, Drosophilidae, Dipterologischer Beitrag zu der von H. J. Feuerborn, F. Ruttner und A. Thienemann im Jahre 1928 nach Java, Sumatra und Bali unternommenen limnologischen Forschungereise. *Arch. Hydrobiol. Suppl.* **9**, 192–198.

DUDA, O. (1936). Weitere neue africanische und orientalische akalyptrate Musciden des British Museums. *Ann. Mag. nat. Hist.* **18(10)**, 337–351.

DWIVEDI, Y. N. (1979). Description of two new species of subgenus *Drosophila* (Drosophilidae: Diptera) from Darjeeling, India. *Proc. Ind. Acad. Sci.* **B88**, 299–304.

DWIVEDI, Y. N. and GUPTA, J. P. (1979). Three new drosophilids (Diptera: Drosophilidae) from North East India. *Entomon* **4**, 183–187.

DWIVEDI, Y. N., SINGH, B. K. and GUPTA, J. P. (1979). Further addition to the Indian fauna of Drosophilidae. *Orient. Ins.* **13**, 61–74.

ENDERLEIN, G. (1922). Einige neue Drosophiliden. *Deut. ent. Z.* **22**, 295–296.

ESAKI, T. (1921). On the geographical distribution of insects in Japan, with some notes on its boundary lines, (in Japanese, with English summary). *Zool. Mag.* **33**, 444–466.

FREY, R. (1917). Ein Beitrag zur Kenntnis der Dipteren-fauna Ceylons. *Finska Vetensk. Forhandl.* **59A(20)**, 1–36.

GRESSITT, J. L. (1958). Zoogeography of insects. *Ann. Rev. Ent.* **3**, 207–230.

GRESSITT, J. L. (1961). Problems in the zoogeography of Pacific and Antarctic Insects. *Pacif. Ins. Monogr.* **2**, 1–94.

GRESSITT, J. L. (1970). Biogeography of Laos. *Pacif. Ins. Monogr.* **24**, 573–626.

GUPTA, J. P. (1969). A new species of *Drosophila* Fallén (Insecta: Diptera, Drosophilidae) from India. *Proc. Zool. Soc. Calcutta* **22**, 53–61.

GUPTA, J. P. (1970). Description of a new species of *Phorticella Zaprionus* (Drosophilidae) from Indian. *Proc. Ind. natn. Sci. Acad.* **36**, 62–70.

GUPTA, J. P. (1971). A new species of *Drosophila* (*Scaptodrosophila*) from Varanasi, India. *Am. Midl. Nat.* **86**, 493–496.

GUPTA, J. P. (1972). *D. orissaensis*, a new species of *Drosophila* from Orissa, India. *Orient. Ins.* **6**, 561–563.

GUPTA, J. P. (1974a). Indian species of Drosophilidae, exclusive of the genus *Drosophila*. *J. Ent.* (B) **43(2)**, 209–215.

GUPTA, J. P. (1974b). The family Drosophilidae in India. *Ind. Biologist* **5**, 7–30.

GUPTA, J. P. and RAY-CHAUDHURI, S. P. (1970a). The genus *Drosophila* (Diptera: Drosophilidae) in Andaman and Nicobar Islands, India. *Orient. Ins.* **4**, 169–175.

GUPTA, J. P. and RAY-CHAUDHURI, S. P. (1970b). Some new and unrecorded Species of *Drosophila* (Diptera: Drosophilidae) from India. *Proc. Roy. ent. Soc. Lond.* **B39**, 57–72.

GUPTA, J. P. and SINGH, B. K. (1977). Two new and two unrecorded Indian species of *Drosophila* (Dipt.) from Kurseong, Darjeeling. *Ent. Month. Mag.* **113**, 71–78.

GUPTA, J. P. and SINGH, B. K. (1979). Two new species of *Drosophila* (Diptera: Drosophilidae) from Shillong, Meghalaya. *Entomon* **4**, 167–172.

HACKMAN, W. (1959). On the genus *Scaptomyza* Hardy (Dipt., Drosophilidae) with descriptions of new species from various parts of the world. *Acta Zool. fenn.* **97**, 1–73.

HARDY, D. E. (1965). Family Drosophilidae. *In:* "Insects of Hawaii", Vol. 2. Diptera: Cyclorrhapha II, Series Schizophora, Section Acalypterae I. Family Drosophilidae. 814 pp. Univ. Hawaii Press.

HARDY, D. E. and WHEELER, M. R. (1960). *Paracacoxenus*, new genus, with notes on *Cacoxenus indagator* Loew (Diptera: Drosophilidae). *Ann. ent. Soc. Am.* **53**, 356–359.

HANDLIRSCH, A. (1925). "Handbuch der Entomologie", band III. Geschichte, Literatur, Technik, Paläontologie, Phylogenie, Systematik. 1202 pp. Gustav Fischer, Jena.

HENDEL, F. (1913a). Acalyptrate Musciden (Dipt.) II. Sauter's Formosa Ausbeute. *Supplta ent.* **2**, 77–112.

HENDEL, F. (1913b). Neue Drosophiliden aus Südamerika und Neuguinea. *Ent. Mitt.* **2**, 386–390.

HENDEL, F. (1914). Acalyptrate Musciden (Dipt.) III. *Supplta ent.* **3**, 90–117.

HENNIG, W. (1941). Verzeichnis der Dipteren von Formosa. *Ent. Beihef.* (*Berlin-Dahlem*) **8**, i–iv, 1–239.

KABURAKI, T. (1932). Zoogeography (in Jap.). Iwanami Seibutsugaku Koza, 60 pp.

KHAL, H. (1917). Notes upon the genus *Leucophenga* Mik (Diptera) with descriptions of some new species from South America, West Africa, and the Philippine Islands. *Ann. Carneg. Mus.* **11**, 364–393.

KERTÉSZ, K. (1899). Verzeichniss einiger von L. Biró in New Guinea und an Malayischen Archipel gesammelten Dipteren. *Természetr. Füz.* **22**, 173–195.

KERTÉSZ, K. (1901). Neue und bekannte Dipteren in der Sammlung des Ungarischen National-Museums. *Természetr. Füz.* **24**, 403–432.

KIKKAWA, H. and PENG, F. T. (1938). *Drosophila* species of Japan and adjacent localities. *Jap. J. Zool.* **7**, 507–552.

KITAGAWA, O. (1979). Microevolution and speciation in *Drosophila* (in Jap.). *Iden* (*Genetics*) **32(10)**, 29–34.

KNAB, F. (1914). Drosophilidae with parasitic larvae. *Insec. Insci. Menst.* **2**, 165–169.

KUMMEL, B. (1970). "History of the Earth". 707 pp. Freeman.

KUROKAWA, H. and HIHARA, F. (1976). Number of first spermatocytes in relation to phylogeny of *Drosophila* (Diptera: Drosophilidae). *Int. J. Ins. Morphol. Embryol.* **5**, 51–63.

LIN, F. J. and TING, J. I. (1971). Several additions to the fauna of Taiwan Drosophilidae (Diptera). *Bull. Inst. Zool. Acad. sinica* **10**, 17–35.

LIN, F. J. and TSENG, H. C. (1971). A new species of *polychaeta* species group of subgenus *Drosophila* from Taiwan (*Drosophila*, Drosophilidae, Diptera). *Bull. Inst. Zool. Acad. sinica* **10**, 69–72.

LIN, F. J. and TSENG, H. C. (1972). A new species of subgenus *Psilodorha* Okada, 1968 from Taiwan (*Drosophila*, Drosophilidae, Diptera). *Bull. Inst. Zool. Acad. sinica* **11**, 9–11.

LIN, F. J. and TSENG, H. C. (1973). The *Drosophila immigrans* species group in Taiwan with descriptions of five new species. *Bull. Inst. Zool. Acad. sinica* **12**, 13–26.

LIN, F. J. and WHEELER, M. R. (1972). The Drosophilidae of Taiwan. *Univ. Texas Publ.* **7213**, 237–256.

MALLOCH, J. R. (1924a). Two Drosophilidae from Coimbatore. *Mem. Dept. Agric. Ind. Ent. Ser.* **8(6)**, 63–65.

MALLOCH, J. R. (1924b). Notes on Australian Diptera. No. IV. *Proc. Linn. Soc. N.S.W.* **49**, 348–359.

MALLOCH, J. R. (1926). Notes on Oriental Diptera, with descriptions of new species. *Phil. J. Sci.* **31**, 491–513.

MALLOCH, J. R. (1929). Exotic Muscariae (Diptera).—XXV. *Ann. Mag. Nat. Hist. Ser.* **10**, 545–564.

MANI, M. S. (1968). "Ecology and Biogeography of High Altitude Insects. xi + 527 pp. Junk, Hague.

MATHER, W. B. (1961). *D. pararubida*, a new species of *Drosophila* from New Guinea. *Univ. Queensl. Pap.* **1**, 251–256.

MATHER, W. B. (1968a). The genus *Drosophila* in New Guinea and Sabah. *Univ. Queensl. Pap.* **3**, 47–50.

MATHER, W. B. (1968b). A third race of *Drosophila rubida*. *Univ. Queensl. Pap.* **3**, 75–77.

MATHER, W. B. and DOBZHANSKY, T. (1962). Two new species of *Drosophila* from New Guinea. *Pacif. Ins.* **4**, 245–249.

MCALPINE, J. F. (1968). An annotated key to drosophilid genera with bare or micropubescent aristae and a revision of *Paracacoxenus* (Diptera: Drosophilidae). *Can. Ent.* **100**, 514–532.

MEIJERE, J. C. H. DE. (1906). Über einige Indo-australische Dipteren des Ungarischen National-Museums, bez. des Natur-Historischen Museums zu Genua. *Annls hist.-nat. Mus. natn. hung.* **4**, 165–196.

MEIJERE, J. C. H. DE. (1908a). Studien über südostasiatische Dipteren, II. *Tijdschr. Ent.* **51**, 105–180.

MEIJERE, J. C. H. DE. (1908b). Studien über südostasiatische Dipteren, III. *Tijdschr. Ent.* **51**, 191–332.

MEIJERE, J. C. H. DE. (1911). Studien über südostasiatische Dipteren, VI. *Tijdschr. Ent.* **54**, 258–432.

MEIJERE, J. C. H. DE. (1914). Studien über südostasiatische Dipteren, IX. *Tijdschr. Ent.* **57**, 137–276.

MEIJERE, J. C. H. DE. (1915a). Fauna simalurensis. *Tijdschr. Ent.* **58**, suppl., 1–63 (appeared in 1916).

MEIJERE, J. C. H. DE. (1915b). Studien über südostasiatische Dipteren, X. *Tijdschr. Ent.* 58, suppl., 64–67.

MEIJERE, J. C. H. DE. (1916). Studien über südostasiatische Dipteren, XI. *Tijdschr. Ent.* **59**, 184–213.

MEIJERE, J. C. H. DE. (1918). Studien über südostasiatische Dipteren, XIV. *Tijdschr. Ent.* **60**, 275–369.

MEIJERE, J. C. H. DE. (1924). Studien über südostasiatische Dipteren, XV. *Tijdschr. Ent.* **67**, suppl., 1–64.

MERRILL, E. D. (1923). An enumeration of Philippine flowering plants, **1**, 1–240; **2**, 1–530; **3**, 1–620.

MINATO, M., GORAI, M. and HUNAHASHI, M. ed. (1965). The geologic development of the Japanese islands. 442 pp. Tsukiji Shokan, Tokyo.

MIYAKE, T. (1919). General Treatise on Entomology ("Konchûgaku Hanron"). Vol. 2. p. 513.

MÜLLER, P. (1974). Aspects of Zoogeography. 208 pp. Junk, Hague.

OKADA, T. (1954). Comparative morphology of the drosophilid flies I, Phallic organs of the *melanogaster* species group. *Kontyû* **22**, 36–46.

OKADA, T. (1955). Fauna and flora of Nepal Himalaya, *Drosophila. Scientific results of the Japanese expeditions to Nepal Hymalaya*, 1952–1953 **1**, 387–390.

OKADA, T. (1964). Drosophilidae (Diptera) of Southeast Asia, collected by the Thai-Japanese Biological Expedition 1961–1962. *Nature and Life in Southeast Asia* **3**, 439–466.

OKADA, T. (1965). Drosophilidae of the Okinawa Islands. *Kontyû* **33**, 327–350.

OKADA, T. (1966). Diptera from Nepal, Cryptochaetidae, Diastatidae & Drosophilidae. *Bull Brit. Mus. (Nat. Hist.) suppl.* 6 : 1–129.

OKADA, T. (1967). A revision of the subgenus *Hirtodrosophila* of the old world, with descriptions of some new species and subspecies (Diptera, Drosophilidae, *Drosophila*). *Mushi*, **41**, 1–36.

OKADA, T. (1968a). Addition to the fauna of the family Drosophilidae of Japan and adjacent countries (Diptera). I. Genera *Stegana, Amiota, Leucophenga*, and *Microdrosophila*, with discussion on the homology of phallic organs. *Kontyû* **36**, 303–323.

OKADA, T. (1968b). Addition to the fauna of the family Drosophilidae of Japan and adjacent countries (Diptera). II. Genera *Paramycodrosophila, Mycodrosophila, Liodrosophila*, and *Drosophila* including a new subgenus *Psilodorha*. *Kontyû* **36**, 324–340.

OKADA, T. (1970a). Preliminary classification of the *nigriventris*-complex of the genus *Leucophenga* Mik, having sexually dimorphic palpi (Diptera, Drosophilidae). *Proc. Jap. Syst. Zool.* **(6)**, 16–22.

OKADA, (1970b). A faunal analysis of the drosophilids at genus level centering around New Guinea. *Kontyû* **38**, 187–194.

OKADA, T. (1971a). Systematic and biogeographical analyses of the *denticeps* group, with description of two new species (Diptera, Drosophilidae). *Bull. Biogeogr. Soc. Jap.* **26**, 29–38.

OKADA, T. (1971b). A revision and taxometric analysis of the genus *Amiota* Loew of Japan and adjacent countries (Diptera, Drosophilidae). *Kontyû* **39**, 82–98.

OKADA, T. (1971c). A revision and taxometric analysis of the genus *Stegana* Meigen of Japan and adjacent countries (Diptera, Drosophilidae). *Mushi* **45**, 81–99.

OKADA, T. (1974). A revision and taxometric analysis of the genus *Sphaerogastrella* Duda and *Liodrosophila* Duda of the world (Diptera, Drosophilidae). *Mushi* **48**, 29–63.

OKADA, T. (1975). The Oriental drosophilids breeding in flowers. *Kontyû* **43**, 356–363.

OKADA, T. (1976a). Drosophilidae (Diptera) of Sabah, Borneo, of Dr. Imadate's collection in 1968. *Nature and Life in Southeast Asia* **3**, 343–346.

OKADA, T, (1976b). New distribution records of the drosophilids in the Oriental Region (in Jap.). *Makunagi* **(8)**, 1–8.

OKADA, T. (1976c). Subdivision of the genus *Chymomyza* Czerny (Diptera, Drosophilidae), with description of three new species. *Kontyû* **44**, 496–511.

OKADA, T. (1977a). The subgenus *Phortica* Schiner of the genus *Amiota* Loew of Japan and Oriental region, with reference to anti-Burla's rules. *Bull. biogeogr. Soc. Jap.* **32**, 17–31.

OKADA, T. (1977b). Family Drosophilidae. p. 342–387. *In:* A Catalog of the Diptera of the Oriental Region, ed. by N. D. Delfinado, and D. E. Hardy, 854 pp. Univ. Press Hawaii, Hononlulu.

OKADA, T. (1978). *Pseudostegana*, a new subgenus of the genus *Stegana* Meigen (Diptera, Drosophilidae). *Kontyû* **46**, 392–399.

OKADA, T. and CARSON, H. L. (1980). Drosophilidae associated with flowers in Papua New Guinea II. *Alocasia* (Araceae). *Pacif. Ins.* **22**, 217–236.

OSTEN-SACKEN, C. R. (1882). Diptera from the Philippine Islands brought home by Carl Semper. *Berl. ent. Z.* **26**, 187–254.

PARSHAD, R. and DUGGAL, K. K. (1966). Drosophilid survey of India III. The Drosophilidae of Kashmir Valley. *Res. Bull. (N. S.) Panjab Univ.* **17**, 277–299.

PARSHAD, R. and PAIKA, I. J. (1964). Drosophilid survey of India II. Taxonomy

and cytology of the subgenus *Sophophora* (*Drosophila*) *Res. Bull.* (*N. S.*) *Panjab Univ.* **15**, 225–252.

PARSHAD, R. and SINGH, A. (1971). Drosophilid survey of India IV. The Drosophilidae of South Andamans. *Res. Bull.* (*N. S.*) *Panjab Univ.* **22**, 385–399.

PARSHAD, R., NARDA, R. D. and PAIKA, I. J. (1964). Drosophilid survey of India I. Variation in the five strains of *Drosophila melanogaster* Meigen and their relationship with *Drosophila emulata* Ray-Chaudhuri and Muckerjee. *Res. Bull.* (*N. S.*) *Panjab Univ.* **15**, 7–17.

PENG, F. T. (1937). On some species of *Drosophila* from China. *Annotnes zool. jap.* **16**, 20–27.

PATTERSON, J. T. and STONE, W. S. (1952). "Evolution in the Genus *Drosophila*." 610 pp. MacMillan, New York.

PRAKASH, H. S. and SREERAMA REDDY, G. (1977). Two new species of *Drosophila* (*melanogaster* species group) (Diptera: Drosophilidae). *Orient. Ins.* **11**, 597–604.

PRAKASH, H. S. and SREERAMA REDDY, G. (1978). *Drosophila agumbensis*, sp. nov. from Karnataka, South India (Diptera: Drosophilidae). *Orient. Ins.* **12**, 259–263.

SAJJAN, S. N. and KRISHNAMURTHY, N. B. (1973). *Drosophila neonasuta*, a new species of *Drosophila* from Mysore (Diptera: Drosophilidae). *Orient. Ins.* **7**, 267–270.

SENIOR-WHITE, R. A. (1921). New Ceylon Diptera. *Spolia Zeylan.* **11**, 381–395.

SINGH, A. (1974). Description of a new species of the subgenus *Hirtodrosophila* (*Drosophila*: Drosophilidae: Diptera: Insecta), from Chandigarh, India. *Zool. J. Linn. Soc.* **54**, 161–166.

SINGH, A. (1976). Descriptions of new species of the genera *Sinophthalmus* and *Scaptomyza* (Insecta: Diptera: Drosophilidae) from Chandigarh, India. Rec. zool. Surv. India. **69**, 187–202.

SINGH, B. K. and GUPTA, J. P. (1974). The genus *Leucophenga* (Diptera: Drosophilidae) in India. *Ind. J. Zootom.* **15**, 23–26.

SINGH, B. K. and GUPTA, J. P. (1977a). The subgenus *Drosophila* (*Scaptodrosophila*) in India (Diptera: Drosophilidae). *Orient. Ins.* **11**, 237–241.

SINGH, B. K. and GUPTA, J. P. (1977b). Two new and two unrecorded species of the genus *Drosophila* Fallén (Diptera: Drosophilidae) from Shillong, Meghalaya, India. *Proc. zool. Soc.* (*Calcutta*) **30**, 31–38.

SREERAMA REDDY, G. and KRISHNAMURTHY, N. B. (1968). *Drosophila rajasekari*—A new species from Mysore (India). *Proc. Ind. Acad. Sci.* **68**, 202–205.

SREERAMA REDDY, G. and KRISHNAMURTHY, N. B. (1970). *Drosophila mysorensis*—A new species of *Drosophila* (Diptera: Drosophilidae) from Mysore, South India. *J. biol. Sci.* **13(2)**, 24–29.

SREERAMA REDDY, G. and KRISHNAMURTHY, N. B. (1973). Two new species of the *montium* subgroup of genus *Drosophila* (Diptera: Drosophilidae). *Orient. Ins.* **7**, 259–265.

STURTEVANT, A. H. (1921). The North American Species of *Drosophila*. *Carneg. Inst. Wash. Publ.* **301**, 1–141.

STURTEVANT, A. H. (1927). Philippine and other Oriental Drosophilidae. *Philip. J. Sci.* **32**, 361–374.

STURTEVANT, A. H. (1939). On the subdivision of the genus *Drosophila*. *Proc. U. S. natn. Acad. Sci.* **25**, 137–141.

STURTEVANT, A. H. (1942). The classification of the genus *Drosophila*, with descriptions of nine new species. *Univ. Texas Publ.* **4213**, 5–51.

STURTEVANT, A. H. and NOVITSKI, E. (1941). The homologies of the chromosomal elements in the genus *Drosophila*. *Genetics* **26**, 517–541.

TAKADA, H. (1970). *Scaptomyza* (*Parascaptomyza*) *pallida* (Zetterstedt) and two related new species, *S.* (*P.*) *elmoi* n. sp. and *S.* (*P.*) *himalayana* n. sp. (Diptera: Drosophilidae). *Annotnes zool. jap.* **43**, 142–147.

TAKADA, H. (1976a). Distribution and population constitution of *Drosophila* in Southeast Asia and Oceania III. The genus *Zygothrica* with description of three new species. *Kontyû* **44**, 65–72.

TAKADA, H. (1976b). A new species of *Dettopsomyia* (Diptera, Drosophilidae) from the Philippines. *Kontyû* **44**, 169–171.

TAKADA, H. and MOMMA, E. (1975). Distribution and population constitution of *Drosophila* in South East Asia and Oceania. II. Drosophilidae in the suburbs of Kuala Lumpur, West Malaysia, *J. Fac. sci. Hokkaido Univ.* VI **20**, 9–48.

TAKADA, H. and WAKAHAMA, K. (1967). A *Drosophila* survey in Okinawa Main Island. *Annotnes zool. jap.* **40**, 56–60.

TAKADA, H., MOMMA, E. and SHIMA, T. (1973). Distribution and population constitution of *Drosophila* in South East Asia and Oceania. I. Drosophilidae at Mt. Kinabalu, East Malaysia. *J. Fac. Sci. Hokkaido Univ.* VI **19**, 73–94.

TAN, C. C., HSU, T. C. and SHENG, T. C. (1949). Known *Drosophila* species in China with descriptions of twelve new species. *Univ. Texas Publ.* **4920**, 196–206.

THROCKMORTON, L. H. (1962a). The problems of phylogeny in the genus *Drosophila*. *Univ. Texas Publ.* **6205**, 207–343.

THROCKMORTON, L. H. (1962b). The use of biochemical characters for the study of problems of taxonomy and evolution in the genus *Drosophila*. *Univ. Texas Publ.* **7205**, 415–487.

THROCKMORTON, L. H. (1968). Concordance and discordance of taxonomic characters in *Drosophila* classification. *Syst. Zool.* **17**, 355–387.

THROCKMORTON, L. H. (1975). The phylogeny, ecology and geography of *Drosophila* *In:* "Handbook of Genetics", (R. C. King ed.) **3**, 421–469.

TSACAS, L. (1967). *Drosophila nigriventris* Macquart, 1843, nouveau synonyme de *D. melanogaster* Meigen, 1830 (Dipt. Drosophilidae). *Bull. Mus. natn. hist. nat.* 2e Ser. **39**, 158–159.

TSACAS, L. and CHASSAGNARD, M. T. (1976). Identité *Drosophila brunnea* de Meijere et description de nouvelles espéces orientales et africaines à pointe du scutelium blanche (Diptera, Drosophilidae). *Zool. Mus. Univ. Amsterdam* **5**, 89–109.

TSACAS, L. DAVID, J. (1977). Systematics and biogeography of *Drosophila kikkawai*-complex, with descriptions of new species (Diptera, Drosophilidae). *Annls Soc. ent. Fr.* (*N. S.*) **13**, 675–693.

TSACAS, L. and LACHAISE, D. (1974). Quatre nouvelles espèces de la Cote d'Ivoire du genre *Drosophila*, groupe *melanogaster* et discussion de l'origine de sous-groupe *melanogaster* (Diptera: Drosophilidae). *Ann. Univ. Abidjan, Ser. E* (*Ecol.*) **7**, 193–211.

VAIDYA, V. G. and GODBOLE, N. N. (1971). Systematic study of Drosophilidae in Poona and neighbouring areas—I. *J. Univ. Poona, Sci. Tech. Sect.* (**40**), 49–61.

VAIDYA, V. G. and GODBOLE, N. N. (1972). Systematic study of Drosophilidae in Poona and neighbouring areas—II. *J. Univ. Poona, Sci. Tech. Sect.* (**42**), 93–94.

VAIDYA, V. G. and GODBOLE, N. N. (1973). Systematic study of Drosophilidae in Poona and neighbouring area—III. *J. Univ. Poona, Sci. Tech. Sect.* (**44**), 41–43.

VAIDYA, V. G. and GODBOLE, N. N. (1976). Systematic study of Drosophilidae in Poona and neighbouring areas—IV. *J. Univ. Poona, Sci. Tech. Sect.* (**48**), 85–92.

VAL, F. C. and SENE, F. M. (1980). A newly introduced *Drosophila* species in Brazil (Diptera, Drosophilidae). *Papeis Avulsos Zool., S. Paulo* **33(19)**, 293–298.

WALKER, F. (1857). Catalogue of the Dipterous insects collected at Sarawak, Borneo, by Mr. A. R. Wallace, with descriptions of new species. *J. Proc. Linn. Soc. Lond. (Zool.)* **1**, 105–136.

WALKER, F. (1859). Catalogue of the dipterous insects collected in the Aru Islands by Mr. A. R. Wallace, with descriptions of new species. *J. Proc. Linn. Soc. Lond. (Zool.)* **3**, 77–131.

WALKER, F. (1860a). Catalogue of the dipterous insects collected at Makessar in Celebes, by Mr. A. R. Wallace, with descriptions of new species. *J. Proc. Linn. Soc. Lond. (Zool.)* **4**, 90–172.

WALKER, F. (1860b). Catalogue of the dipterous insects collected in Amboyna by Mr. A. R. Wallace, with descriptions of new species. *J. Proc. Linn. Soc. Lond. (Zool.)* **5**, 144–168.

WALKER, F. (1864). Catalogue of the dipterous insects collected in Waigiou, Mysol, and North Ceram by Mr. A. R. Wallace, with description of new species. *J. Proc. Linn. Soc. Lond. (Zool.)* **7**, 202–238.

WALKER, F. (1865a). Descriptions of new species of the dipterous insects of New Guinea. *J. Proc. Linn. Soc. Lond. (Zool.)* **8**, 102–130.

WALKER, F. (1865b). Descriptions of some new species of dipterous insects from the Island of Salwatty, new New Guinea. *J. Proc. Linn. Soc. Lond. (Zool.)* **8**, 130–136.

WALKER, F. (1868). Synopsis of the Diptera of the eastern Archipelago discovered by Mr. Wallace, and noticed in the "Journal of the Linnean Society". *J. Proc. Linn. Soc. Lond. (Zool.)* **9**, 1–30.

WALLACE, A. R. (1860). On the zoological geography of the Malay Archipelago *J. Proc. Linn. Soc. Lond. (Zool.)* **4**, 173–184.

WATASE, S. (1912). Footnote, p. 109. *In:* Holmgren, N. Die Termiten Japans. *Annotns zool. jap.* **2**, 108–111.

WEBER, M. (1902). "Der Indo-australische Archipel und die Geschichte seiner Tierwelt." Verl. G. Fischer, Jena.

WHEELER, M. R. (1949a). The two "varieties" of *Drosophila montium*. *Evolution* **3**, 286.

WHEELER, M. R. (1949b). Taxonomic studies on the Drosophilidae. *Univ. Texas Publ.* **4920**, 157–195.

WHEELER, M. R. (1959). A nomenclatural study of the genus *Drosophila*. *Univ. Texas Publ.* **5914**, 181–205.

WHEELER, M. R. (1960). A new subgenus and species of *Stegana* Meigen (Diptera: Drosophilidae). *Proc. Ent. Soc. Wash.* **62**, 109–111.

WHEELER, M. R. (1969). A note on the genus *Drosophilella* Duda (Diptera: Drosophilidae). *Pacif. Sci.* **23**, 544–545.

WHEELER, M. R. and HAMILTON, N. (1972). Catalog of *Drosophila* species names. *Univ. Texas Publ.* **7213**, 275–268.

WILSON, F. D., WHEELER, M. R., HARGET, M. and KAMBYSELLIS, M. (1969). Cytogenetic relations in the *Drosophila nasuta* subgroup of the *immigrans* group of species. *Univ. Texas Publ.* **6918**, 207–253.

WULP, F. M. VAN DER. (1886). Diptera. *In:* Midden-Sumatra, Reizen en Onder: zoekingen der Sumatra-Expeditie, etc. *Nat. Hist.* **4**, 1–60.

WULP, F. M. VAN DER (1892). Eenige Uitlandsche Diptera. *Tijdschr. Ent.* **34**, 193–217.

WULP, F. M. VAN DER (1896). Catalogue of the described Diptera from South Asia, iii + 219 pp. (The Hague, Martinus Nijhoff.). Published by Dutch Entomological Society.

WULP, F. M. VAN DER. (1897). Zur Dipteren-fauna von Ceylon. *Termeszetr. Füz.* **20**, 136–144.

WULP, F. M. VAN DER (1898). Diptera aus New Guinea in der Sammlung des ungarischen national Museums. *Termeszetr. Füz.* **21**, 409–426.

YANG, S. Y., WHEELER, L. L. and BOCK, I. R. (1972). Isozyme variations and phylogenetic relationships in the *Drosophila bipectinata* species complex. *Univ. Texas Publ.* **7213**, 213–227.

YEN, D. E. and WHEELER, J. M. (1968). Introduction of Taro into the Pacific: The indications of the chromosome numbers. *Ethnology* **7**, 259–267.