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 SYSTEMATICS AND BIOGEOGRAPHY  
 OF THE *DROSOPHILA KIKKAWAI*-COMPLEX,  
 WITH DESCRIPTIONS OF NEW SPECIES  
 (DIPTERA, DROSOPHILIDAE)

BY

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## RÉSUMÉ

Un certain nombre d'espèces du sous-groupe *montium* (groupe *melanogaster*) présentent des affinités qui suggèrent leur appartenances à une branche phylétique distincte. Ces neuf espèces sont groupées sous le nom de complexe *kikkawai*. Les deux nouvelles espèces décrites : *leontia* de Singapour et *diplacantha* de l'Afrique occidentale et centrale sont celles qui ont les plus grandes affinités avec *kikkawai*. La distance entre elles est étudiée sur la base de 32 indices taxinomiques et caractères biométriques. Cette étude montre que *kikkawai* et *leontia* sont les plus proches et *leontia* et *diplacantha* les plus éloignés. *D. kikkawai* et *D. leontia* constituent un couple d'espèces jumelles offrant un cas rare dans le genre *Drosophila* : leurs genitalia sont pratiquement identiques.

La répartition géographique des neuf espèces du complexe montre que le groupe aussi bien que *D. kikkawai* elle même sont d'origine orientale. L'introduction de *kikkawai* en Afrique et en Amérique du Sud serait assez ancienne et indépendante de l'activité humaine. Seul *D. diplacantha* est une espèce endémique en Afrique.

MOTS-CLÉS : Evolution, Speciation, Colonizing species, Relationships, *melanogaster*-group, *montium*-subgroup.

*Drosophila montium* de Meijere, 1916, described from Java, was the first known *Drosophila* having a long comb on the first and second tarsal segments of the anterior legs. In fact this character is common to over 60 species and has been the source of many misidentifications. Thus Duda (1924, 1926, 1940) identified as *D. montium* flies from various regions in Southeast Asia and even Africa. Later geneticists and cyto-geneticists published papers on the chromatic and chromosomal polymorphism of a species named "*D. montium*". (bibl. in David, al., 1977). Finally Burla (1954) published a review on the identity of *D. montium* and described *D. kikkawai*. Hsu (1949) defined within the *melanogaster* group, the *montium*

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subgroup. Bock & Wheeler (1972) reviewed the group, established several new subgroups, and described new species close to *D. kikkawai*. After the discovery by one of us (J. D.), in the neighbourhood of Singapore, of a sibling species of *D. kikkawai* and the obtaining of a stock of *Drosophila* sp. aff. *kikkawai* (Tsacas, 1971) from Africa, we were able to study the systematics and biogeography of the species allied to *D. kikkawai*.

In the results presented below we will redescribe *D. kikkawai*, since a complete description of this species is lacking, and describe two new species. The relationships between these three species will be considered as a result of biometrical analysis of accepted taxonomic indices. Finally, the taxonomy and geographical distribution of the nine species at present known, which are close allied to *D. kikkawai* will be considered.

### REDESCRIPTION OF *D. KIKKAWAI* AND DESCRIPTION OF TWO NEW SPECIES

✓ *Drosophila kikkawai* BURLA, 1954 (Fig. 1, 4)

*Rev. Brasil. Biol.*, 14 : 47.

The species was described and figured by different authors : KIKKAWA & PENG (1938), as *montium*, PAVAN & DA CUNHA (1947) as *montium*, BURLA (1954) as *kikkawai* sp. n., OKADA (1956), WHEELER & TAKADA (1964), but none of these descriptions is complete. For this reason we give here a new description and figures of the male and female internal genital apparatus and the external genitalia.

*Male.* Head, width of the head : width of the frons — 1,9; width : height of frons = 1,3; frons reddish-brown bearing on the inferior part a yellow band, which is very variable, sometimes absent, sometimes extending up to ocellar triangle, and 6-8 hairs; orbits hardly distinguished, shining, and slightly velvety; orbital bristles normal, or 2 near to or 1 and displaced towards the outside; or 1 : or 3 = 1; or 1 : or 2 = 2,4. Ocellar triangle small, brown, shining, with three pairs of hairs in addition to the ocellar bristles. Postvertical bristles crossed. Antennae : second article yellow, third one brownish, arista with 4-5 upper branches and 3 lower ones in addition to the terminal fork. Face slightly whitish, not shining in its inferior part, red-brownish elsewhere; carina yellow, practically missing at the base of antennae, very narrow and little prominent beneath, it finishes in gentle slope before the epistoma. Peristome with two subequal oral bristles. Palpus yellow with one strong subapical bristle. Cheek narrow, yellow, length of the longer axis of eye : width of cheek = 16. Eye blood-red densely short pilose.

Thorax : reddish-brown; mesonotum paler in the anterior margin, 6 rows of ac, 2 pairs of dc, the anterior one equal to the 2/3 of the second; no prescutellar; two humeral bristles, the inferior one longer; scutellum lightly duller than the mesonotum, anterior scutellar bristles convergent,

orb ←

posterior ones crossed ( $a : p = 0,9$ ). Pleurae lighter than the mesonotum, not uniformly coloured, 2 sternopleural bristles (the intermediate reduced to an hair) and 3 - 4 hairs on the lower part of the sternopleuron, sterno-index = 0,56 (0,52-0,63). Legs yellow, a preapical dorsal bristle present on all tibiae, apical bristle present only on fore and middle tibiae; the tow proximal tarsal segments of forelegs with a longitudinal comb along entire length; metatarsal comb consisting of 22- 26 teeth, (mean 24,8, 15 specimens), the 2 lower slightly displaced from axis of remaining teeth, comb of second tarsal segment consisting of 17-24 teeth (mean 20,3, 15 specimens). Wings dark grey, transparent, veins brown-reddish; indices :  $c = 2,2$ ,  $4v = 0,42$ ;  $4c = 0,61$ ;  $5x = 2,12$ ;  $ac = 2,80$ ;  $c\beta$  fringe = 56 %; length : width = 2,5. Halteres yellowish.

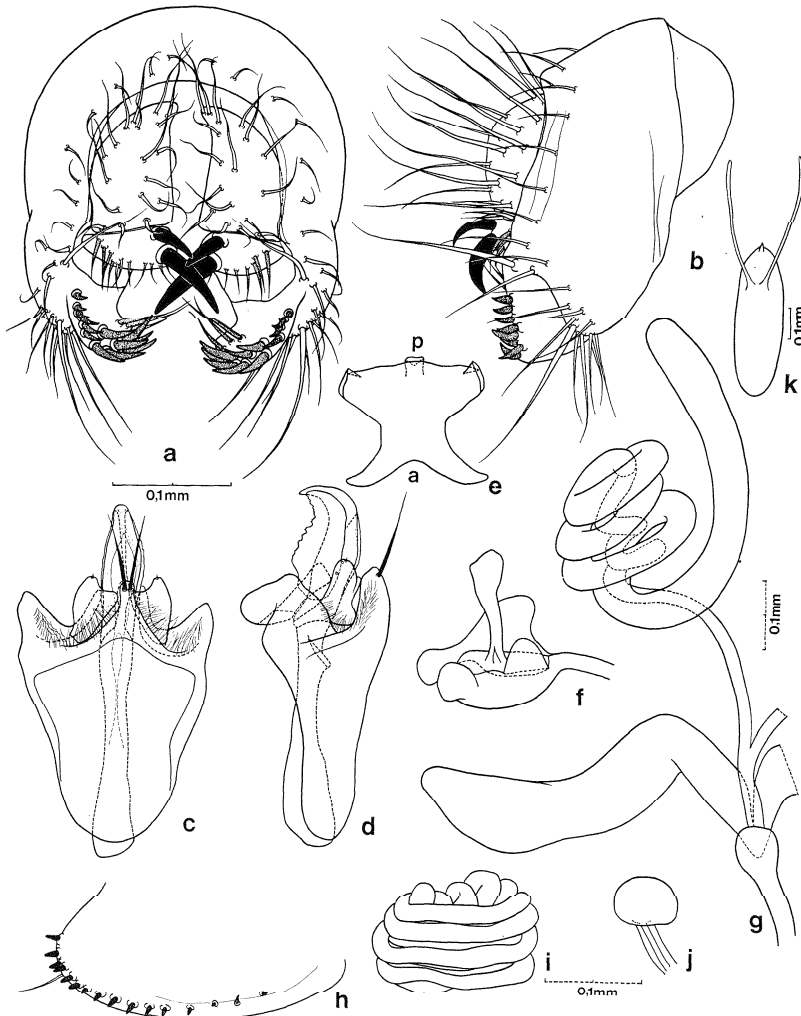


FIG. 1, *Drosophila kikkawai* Burla : a, epandrium and anal plates, caudal; b, the same, lateral; c, hypandrium, phallus and associated organs, ventral; d, the same, lateral; e, decasternum (bridge), ventral; f, ejaculatory bulb; g, testis and paragonium; h, ovipositor; i, ventral receptacle; j, spermatheca; k, egg. (a, anterior; p, posterior).

Abdomen yellow; tergites II - IV with brownish, ill-defined apical bands, the bands of the tergites III - IV occupy practically the entire length of the tergites in their median line; tergites V and VI often with a brown border along their apical margin; genitalia brownish coloured, anal plates almost black. Sternites light yellow.

*Female* : like the male except for the absence of sexual combs and the colour of the tergites which are sometimes clearer, sometimes darker than in the male; the marginal bristles of the tergites are much stronger than in the male, mainly the bristles of the tergites V and VI. Indices : head : frons = 1,9 ; width : height of frons = 1,5; eye : cheek = 16 - 17; orbitals : or 1 : or 3 = 0,88; or 1 : or 2 = 2,1; sterno- index = 0,56 (0,52 - 0,63); scutellar (a : p) = 0,89; wing indices : c = 2,03; 4v = 0,40; 4c = 0,58; 5x = 2,12; ac = 2,82; c3 fringe = 56 %; length : width = 2,4.

Body lengths : ♂, 2,3 mm, wings 2,2 mm

♀, 2,7 mm, wings 2,3 mm

Periphallial organs : yellow. Epandrium broad with one very long slightly brownish spot dorsally; toe pointed downwards, not covering clasper, with about 10 bristles on the inferior third of the posterior margin. Primary clasper with a row of 4 - 6 teeth dorsally followed by a cluster of about 7 strong ventro-posterior teeth, dorsally to this cluster 3 long and strong bristles. Secondary clasper fused to anal plate, with a very large curved black median tooth below and 1 (sometimes 2) smaller similar tooth above, and a row of tiny bristles along the ventral and lateral borders becoming larger laterally. Anal plate with long bristles 3 - 4 of them thickened below. Decasternum with the posterior lobes curved ventrally and on the posterior margin a tab curved dorsally. Anal plates not uniformly brownish.

Phallic organs : phallus slender, non-bifid, bare, apically tapered and curved dorsally, bearing very small spines around its opening, phallapodem not exceeding the anterior border of the ventral phragma. Anterior parameres large, broad, their tip rounded, with minute apical sensilla; posterior parameres long, reaching the tip of the phallus, laterally compressed, its dorsal margin serrate. Caudal margin of novasternum with long narrow median process and long hairs; submedian spines long, subapical and close on to the other.

Egg guide : yellowish, rounded, blunt, with about 15 close-set teeth and a large subterminal hair.

Internal genitalia, ♂ : testes light yellow, tightly coiled with 3 outer and 2 inner coils, their extremity long and free; paragonia large, swollen, bent twice; ejaculatory bulb with four lobes, two anterior and two smaller posterior.

Internal genitalia, ♀ : spermathecae bulky, not sclerotized, ventral receptacle long, tightly coiled, jointed to the vagina.

Egg : length about 0,5 mm, with 2 long filaments as long as the egg and slightly tapered apically.

Pupae : yellowish, anterior spiracles with 11 - 12, rarely 13, (mean 11, 4, 10 specimens) brown white apically branches; horn-index = 17,8.

DISTRIBUTION (Fig. 4) : East Palearctic, Oriental, Australian, Ethiopian and Neotropical zoogeographical regions. China, Korea, Japan, Nepal, India, Ceylan, Thailand, Viet-Nam, Malaya, Singapore, Sumatra, Java, Borneo, Philippines, Taiwan, Ryukyu Is, Caroline Is., Mariana Is., Samoa Is., Fiji Is., New Guinea, Reunion Is., Ivory-Coast (Mont Nimba), Brazil, Colombia.

MATERIAL EXAMINED

Living stocks from Réunion Is., July, 1975; Singapore, August, 1974 and Brazil, Sao Paulo, Mars 1973.

✓ *Drosophila leontia* (1) sp. n. (Fig. 2, 4)

This species is very close to *kikkawai* BURLA and is therefore described by comparison with it.

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*Male.* Head : frons similar to that of *kikkawai*; width of the head : width of the frons = 1,84; width : height of the frons = 1,33. Orbital bristles and antennae as in *kikkawai*; or 1 : or 3 = 1; or 1 : or 2 = 3,5; arista 5 rarely 4 upper branches. Face : white, shining in its lower part including the third inferior part of the carina, this character is the main difference between the two species; the white shining spot of the face of *leontia* looks more shining by contrast with the third antennal segment, the cheeks and the clypeus which are darker than in *kikkawai*; carina broader than in *kikkawai*. Cheek narrow, eye : cheek = 19 - 20. Eye colour lighter than in *kikkawai*.

Thorax : mesonotum as in *kikkawai* with 6 rows of ac, the anterior dc hardly reaching the posterior ones; index of scutellar bristles (a : p) = 0,78. Sterno-index = 0,53. The sexual combs of the anterior tarsi with a smaller number of teeth than in *kikkawai* : first segment, 16-23 teeth (mean 18,66, 10 specimens), second segment, 14-18 teeth (mean 15,94, 10 specimens). Indices of the wings : c = 1,70; 4v = 0,39; 4c = 0,63; 5x = 3,04; ac = 3,06; c3 fringe = 58 %; length : width = 2,4.

Abdomen : as in *kikkawai* except for the tergites V and VI which are darker and their marginal band always clean-cut.

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*Female.* Like the male, except for the sexual combs, the strong marginal bristles of the tergites IV and V and the wider marginal band of the tergites. Indices, head : frons = 1,88; width : height of frons = 1,33; orbitals or 1 : or 3 = 0,90; or 1 : or 2 = 3,1; eye : cheek = 19-20; sterno-index = 0,56; scutellars (a : p) = 0,85; wings : c = 1,90; 4v = 0,38; 4c = 0,60; 5x = 3,09; ac = 3,05; c3 fringe = 58 %; length : width = 2,30.

2, 6

Body lengths : ♂ 1,5 mm; wing : 1,5 mm  
♀ 1,7 mm; wing : 1,7 mm

Periphallalic organs : like those of *kikkawai* but with the following differences : dorsal epandrial dark spot conspicuous, larger epandrial phragma, longer primary forceps, larger secondary forceps, and with a great number of bristles, anal plates uniformly brown.

(1) Allusion to the origine of the species from Singapore, « city of lions » in local language, from greek λέων, λειοντ = lion

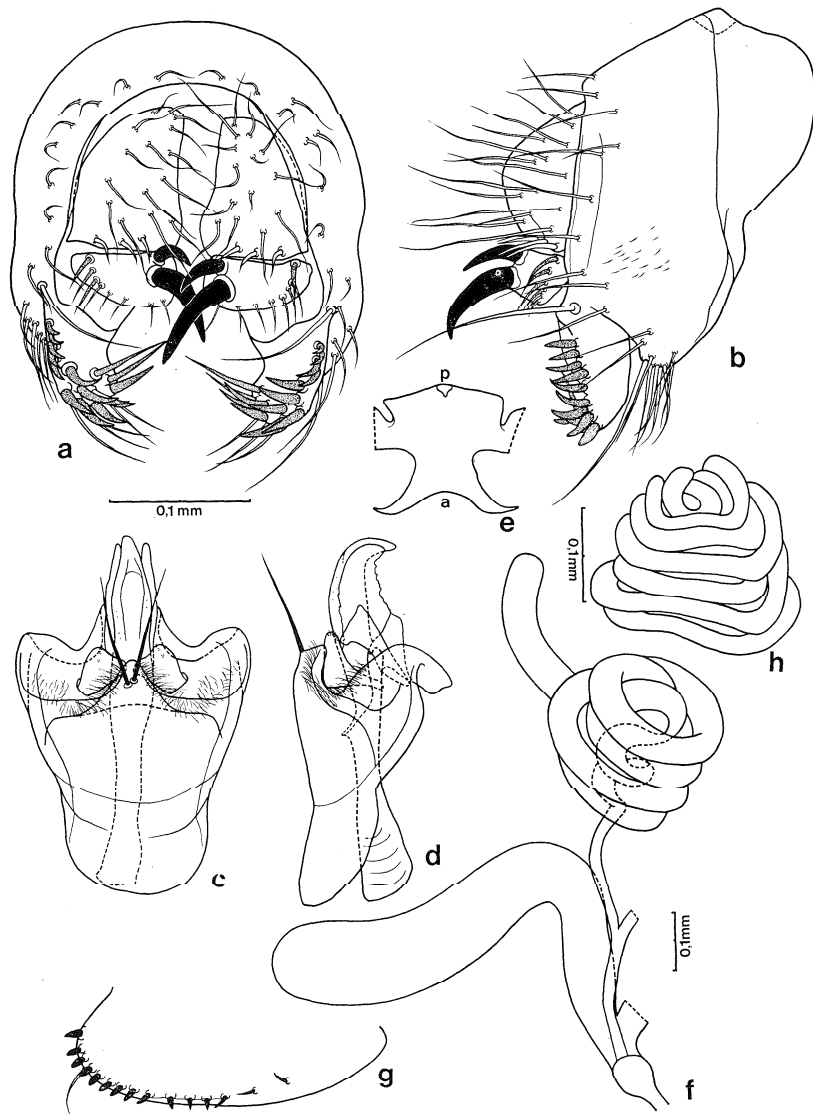


FIG. 2, *Drosophila leontia* sp. n. : a, epandrium and anal plates, caudal; b, the same, lateral; c, hypandrium, phallus and associated organs, ventral; d, the same, lateral; e, deca-sternum (bridge), ventral (a, anterior; p, posterior); f, testis and paragonium; g, ovipositor; h, ventral receptacle.

Phallic organs : like those of *kikkawai* but with the following differences : broader hypandrium; shorter median convexity of the caudal margin of novasternum, proportionality longer submedian spines, anterior parameres slightly different in shape.

Egg guide : practically as in *kikkawai*.

Internal genitalia ♂ : testes with 1 - 2 inner and 4 - 5 outer coils, apical free (not coiled) part longer than in *kikkawai*; unpaired ejaculatory canal longer than in *kikkawai*. Paragonia with single kneed.

Internal genitalia ♀ : spermathecae and parovaria as in *kikkawai*, ventral receptacle longer but less tightly coiled.

Egg : as in *D. kikkawai*.

Pupae : light yellow coloured, horn-index : 22,6; spiracles with 9 - 10, exceptionally 11, branches (mean 9,5, 10 specimens).

Chromosomes : see DAVID & al., 1977.

*Holotype* ♂ and one hundred paratypes ♂ and ♀ from the type stock n° 178-11, Singapore, VIII. 1974 (leg. J. David) in Laboratoire de Biologie et Génétique Evolutives, Gif sur Yvette, preserved in Muséum National d'Histoire Naturelle de Paris. Paratypes also preserved in British Museum (N. H.), London and in *Drosophila* Type and Reference Collection, Genetics Foundation, the University of Texas, Austin.

TAXONOMY : sub-genus *Sophophora*, species-group *melanogaster*, subgroup *montium*.

DISTRIBUTION : (Fig. 4) Malay peninsula, neighbourhood of Singapore.

✓ *Drosophila diplacantha* (1) sp. n. (Fig. 3, 4)

*Drosophila* sp. aff. *kikkawai* BURLA, Tsacas 1971 : 35.

This species was briefly described as a species close to *kikkawai*. It is redescribed and figured here in detail. *D. diplacantha* sp. n. is easily differentiated from the two other species studied by the structure of its male genitalia, particularly the claspers.

*Male*. Head, width of the head : width of the frons = 2,28; width : height of frons = 1,17; frons yellow brownish. Orbits narrow, shining, slightly brownish and converging anteriorly; orbital bristles normal, or 1 : or 3 = 1,02; or 1 : or 2 = 2,68. Ocellar triangle small, brown with light-coloured ocelli and three or four pairs of hairs in addition to the ocellar bristles. Postvertical bristles crossed. Antennae : brownish particularly the third article, arista with five or six upper branches and three lower ones in addition to the terminal fork. Face white in its inferior part, carina short and narrow; peristome with two subequal oral bristles. Palpus yellow, narrow with one strong subapical bristle; cheek very narrow, eye = cheek = 17,50; eye, deep-red.

Thorax : reddish-brown, particularly in the posterior part of mesonotum; mesonotum with eight rows of ac; anterior scutellar bristles slightly convergent, posterior crossed (a : p = 0,89). Pleura a little lighter than the mesonotum; two sternopleural bristles (the intermediate reduced to a hair), sterno-index : 0,57 to 0,68 (mean 0,63, 10 specimens). Legs yellow, a preapical dorsal bristle present on all tibiae, apical one missing on third tibiae,

(1) From the greek διπλός = double and ἀκανθα = thorne.

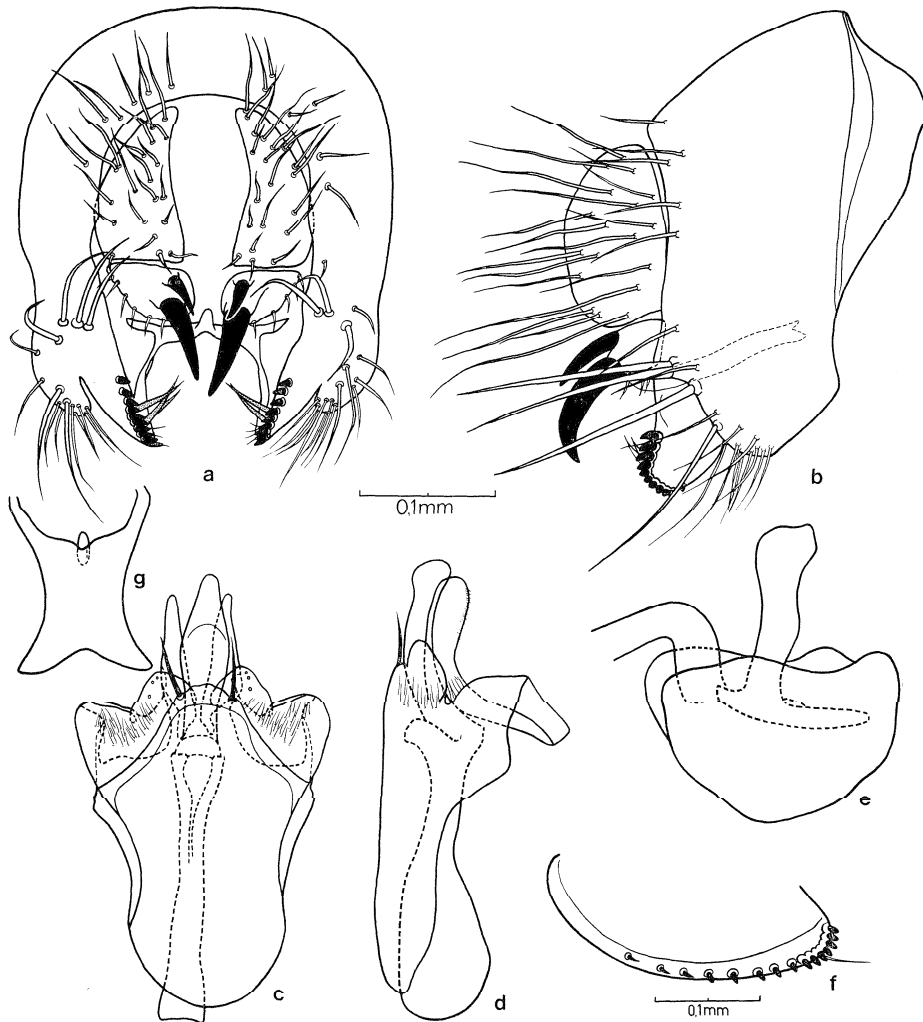


FIG. 3, *Drosophila diplacantha* sp.n. : a, epandrium and anal plates, caudal; b, the same, lateral; c, hypandrium, phallus and associated organs, ventral; d, the same, lateral; e, ejaculatory bulb; f, ovipositor; g, decasternum (bridge), ventral.

a long sexual comb on the two first tarsal segments of the forelegs; metatarsal comb consisting of 24-30 teeth (mean 27,12, 8 specimens), comb of second segment with 21-25 teeth (mean 22,62, 8 specimens). Wings and veins brownish; indices :  $c = 2,31$ ;  $4v = 0,40$ ;  $4c = 0,54$ ;  $5x = 2,31$ ;  $ac = 2,19$ ;  $c3$  fringe = 46 %-57 % (mean 51,75 %, 10 specimens); length : width = 2,41. Halteres brownish.

Abdomen rather shining; tergite I reddish-brown, tergites II - IV reddish - brown with a posterior brown band not reaching the lateral margins, the following ones and the genitalia are entirely brown. Sternites light yellow.



*Female* : like the male except for the absence of sexual combs and the colour of the last tergites which are sometimes clearer than in the male; the marginal bristles of the tergites are stronger than in the male; mainly on tergites V and VI. Indices : head : frons = 2,11; width : height of frons = 1,28; or 1 = or 3 = 1,01; or 1 : or 2 = 2,22; arista 5-6 superior and 3 inferior branches; e : c = 19,1; sc, a : p = 0,91; sterno-index = 0,61 (0,56 - 0,65); wings, c = 2,37; 4v = 0,38; 4c = 0,52; 5x = 2,23; ac = 2,29; c3 fringe = 52,22 % (47 %-57 %); L : w = 2,35.

Body lengths : ♂, 2,3 mm, wings, 2,2 - 2,4 mm.  
♀, 2,6 mm, wings, 2,3 - 2,5 mm.

Periphallalic organs : Epandrium broad, its inferior margin rounded with a tuft of bristles, and four long and strong bristles on the third inferior part of its posterior margin. Primary claspers pointed in caudal view but rounded in lateral view, with a comb of circa ten teeth on the posterior margin and three or four strong bristles on the inferior side. Secondary claspers well differentiated with two strong teeth, the inferior twice as long as the upper one. Anal plates rounded with numerous long bristles. Decasternum (bridge) laterally compressed, with a tubercle in the middle of the posterior margin.

Phallic organs : phallus pointed in ventral view, broadened at apex in lateral view; phallapodem projecting from the anterior border of the ventral phragma. Anterior parameres short and broad, the posterior one long slender and curved dorsally, bearing on their dorsal margin numerous, and minute hairs. Caudal margin of novasternum not prominent, just rounded, laterally with long hairs; submedian spines short and strong.

Egg guide : as in *kikkawai* but less rounded, the long bristle between the 4th and 6th teeth.

Internal genitalia, ♂ : testes very light yellow, coiled with two inner and three outer coils, their extremity as long as twice the diameter of the outer coils; paragonia bent twice, near the base and near the apex.

Internal genitalia, ♀ : spermathecae not sclerotized, ventral receptacle long, tightly coiled, joined to the vagina.

Egg : length about 0,6 mm with two long filaments as long as the egg and pointed apically.

Pupae : straw yellow; anterior spiracles with 13 - 17 (mean 15,04, 10 specimens) branches; horn-index : 18 - 24 (mean 20,91, 10 specimens).

*Holotype* ♂ and a hundred paratypes, ♂ and ♀, from the stock n° 188.7 (Laboratoire de Biologie et Génétique Évolutive - Gif-sur-Yvette) from Bafut Ngemba (Cameroon, Nord West Province) alt. 2000 m, x.1975 (Cameroon expedition, R.C.P. 318), preserved in the Museum national d'Histoire naturelle, Paris. Paratypes are also preserved in the British Museum (N. H.), London and in the *Drosophila* Type and Reference Collection, Genetics Foundation, The University of Texas, Austin.

ECOLOGY : This species has been collected on the fruits of a) *Pandanus candelabrum* (Lachaise & Tsacas, 1974), in a forest gallery and in its fringe

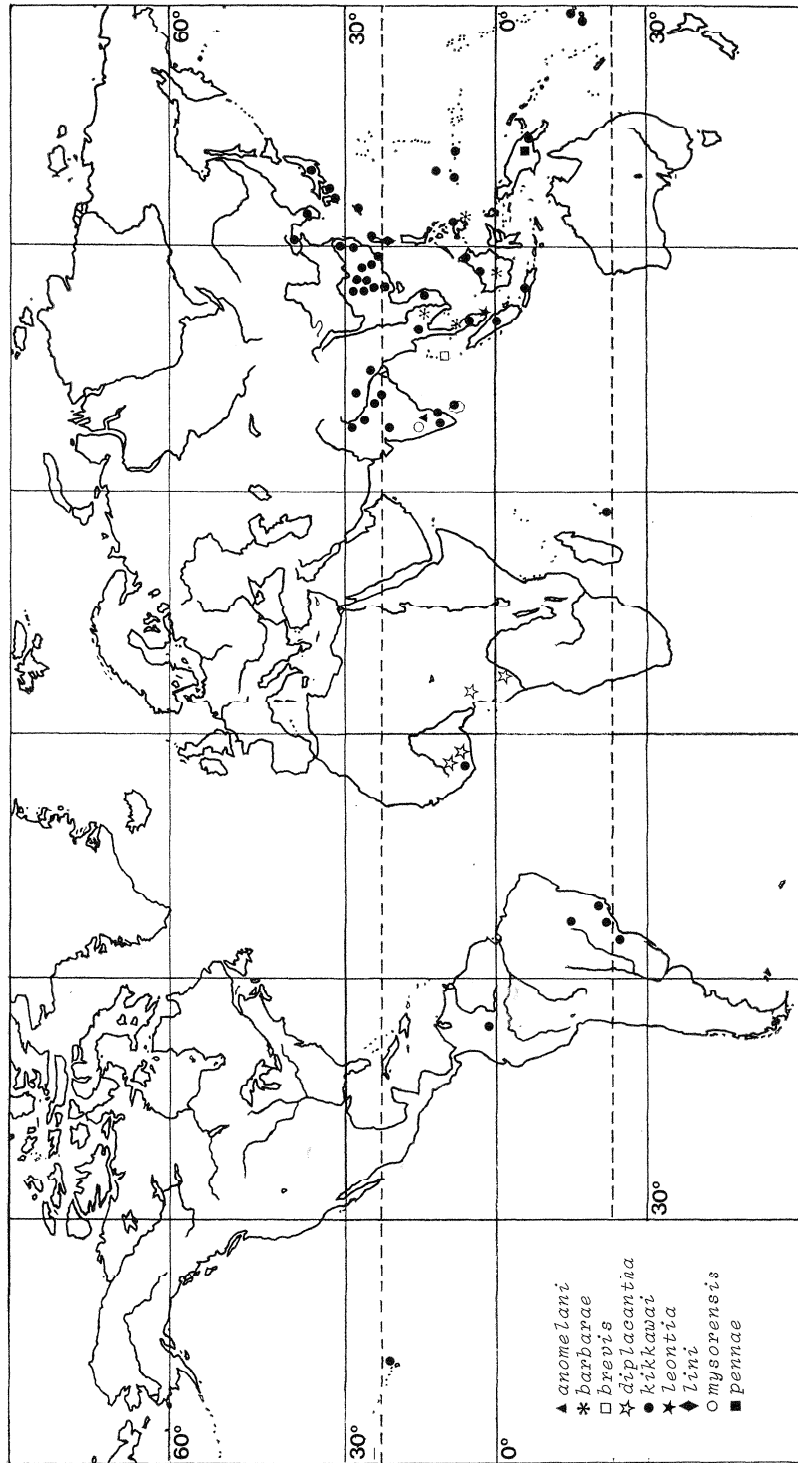


FIG. 4. Distribution of the species of the *D. kikukawai*-complex.

(Lachaise, 1974). b) Ronier Palm tree (Lachaise, 1975). It lives both in plains and mountains (Mont Nimba, Bafut Nguemba). It breeds easily in the laboratory on the usual maize-medium.

DISTRIBUTION : Cameroon, N'Kolbisson (nr. Yaoundé), Bafut Nguemba (nr. Bamenda); Ivory Coast, Lamto (nr. Toumodi), Mont Nimba; Guinea (Mont Nimba); Congo (Brazzaville). The species must be widely distributed in Central and West Africa.

### RELATIONSHIPS BETWEEN THE THREE SPECIES.

A biometrical comparison between *D. kikkawai* and *D. leontia* has been published elsewhere (DAVID *et al.*, 1977). Here we undertake a comparison between the three studied species on the basis of the usual taxonomic characters. The mean values of 15 indices and 4 biometrical traits are given in table I. These characters are distributed as follow : for both sexes, five on the head, two on the thorax, and seven on the wings; for males only, two on the legs; and two for the pupae. Thus the comparison has been made on a total of 32 characters concerning both sexes and the pupae.

In table II are given the characters which are highly significant (test t,  $p < 0,99\%$ ) between the three species taken in pairs. Because of the small number of measurements ( $n = 10$  to  $20$ ) and the indices used (15 indices in a total of 18 characters) the test t has only an indicative value. It is obvious that the species *kikkawai* and *leontia* are very close (fig. 5c) with only nine highly significant different characters. They concern the head (3), the legs (2), the wings (1) and the pupae (2).

The stocks used for this study were : n° 164.15 from the Reunion Island for *D. kikkawai*, n° 178.11 from Singapore for *D. leontia*, and n° 188.7 from Cameroon for *D. diplacantha*.

*D. kikkawai* is not as close to *diplacantha* as to *leontia* (15 highly significant different characters). *D. diplacantha* and *leontia* are the most distantly related of the three species (20 highly significant different characters). If both sexes are considered separately, the order of the distances between the three species does not change; but varies according to the sex considered (fig. 5 a, b). Thus, in females, there are only two highly significant different characters between *kikkawai* and *leontia*, but eight between the former and *diplacantha*. On the other hand, in males, there are five highly significant different characters between *kikkawai* and each of the other two species, *leontia* and *diplacantha*. It must be pointed out that the comparison between males is based on 16 characters and that of females on only 14, because of the absence of sex-combs on the tarsi of the forelegs of females.

The results of this analysis are corroborated by the hybridization experiments published elsewhere (David *et al.*, 1977).

TABLE 1

Comparison of taxonomic indices between *D. kikkawai* (Reunich Is. stock), *D. leontia* and *D. diplacantha*  
(or = orbital; L: length; H = high; a = anterior; p = posterior; p = weight)

	D. kikkawai		D. leontia		D. diplacantha	
	♂	♀	♂	♀	♂	♀
Head,						
or 1 : or 3	1.01±0.01 (20)	0.88±0.01 (20)	0.98±0.02 (10)	0.91±0.02 (10)	1.02±0.04 (10)	1.01±0.01 (10)
or 1 : or 2	2.43±0.06 (20)	1.97±0.05 (20)	3.65±0.23 (10)	3.21±0.21 (10)	2.68±0.15 (10)	2.22±0.10 (10)
Arista	4-5/3	4-5/3	5-4/3	5-4/3	6-5/3	6-5/3
Frons, L : H	1.34±0.02 (10)	1.44±0.03 (10)	1.34±0.03 (10)	1.33±0.02 (10)	1.17±0.03 (10)	1.29±0.02 (10)
Head : Frons	1.90±0.02 (10)	1.91±0.02 (10)	1.85±0.03 (10)	1.89±0.03 (10)	2.28±0.04 (10)	2.11±0.01 (10)
Eye : Cheek	15.88±4.01 (10)	16.57±0.60 (10)	21.23±1.02 (10)	20.23±1.20 (10)	17.50±0.19 (10)	19.10±0.13 (10)
Thorax,						
Sterno-index	0.56±0.01 (20)	0.55±0.01 (20)	0.53±0.02 (10)	0.53±0.02 (10)	0.63±0.00 (10)	0.61±0.00 (10)
Scutellar; a : p	0.89±0.01 (20)	0.89±0.01 (20)	0.87±0.01 (10)	0.85±0.02 (7)	0.89±0.02 (10)	0.91±0.01 (10)
Legs,						
Sex-combs	25.44±0.59 (9)	-	19.22±0.39 (18)	-	27.12±0.79 (8)	-
	20.55±0.71 (9)	-	16.09±0.34 (17)	-	22.62±0.53 (8)	-
Wings, L : W						
c - index	2.40±0.02 (11)	2.40±0.02 (11)	2.38±0.03 (15)	2.34±0.03 (10)	2.41±0.03 (10)	2.35±0.03 (10)
4 v - index	1.88±0.03 (11)	2.03±0.02 (11)	1.73±0.03 (15)	1.91±0.04 (10)	2.31±0.04 (10)	2.37±0.03 (10)
4 c - index	0.41±0.01 (11)	0.40±0.01 (11)	0.39±0.01 (15)	0.38±0.01 (10)	0.40±0.01 (10)	0.39±0.01 (10)
5 x - index	0.60±0.01 (11)	0.58±0.01 (11)	0.69±0.07 (15)	0.60±0.01 (10)	0.54±0.01 (10)	0.52±0.01 (10)
a c - index	2.55±0.05 (11)	2.20±0.06 (11)	3.04±0.07 (15)	3.16±0.17 (10)	2.31±0.05 (10)	2.37±0.05 (10)
Fringe c 3	2.81±0.08 (11)	2.84±0.03 (11)	3.12±0.12 (15)	3.07±0.09 (10)	2.19±0.04 (10)	2.29±0.02 (10)
Pupa, horn-index	55.73±1.76 (11)	55.93±0.66 (11)	58.52±0.94 (15)	58.20±1.49 (10)	51.75±1.04 (10)	52.23±1.04 (10)
Spiracular filaments	16.21±0.57 (10)	11.40±0.16 (20)	22.98±0.91 (10)	20.91±0.69 (10)	20.91±0.69 (10)	15.04±0.25 (10)

Table 2

Comparison of taxonomic indices (test t) between the three species taken two by two (+ character highly significant, 99 %)

	kikkawai leontia			kikkawai diplacantha			leontia diplacantha					
	♂	♀	p	♂	♀	p	♂	♀	p			
1	or 1 : or 3						+					
2	or 1 : or 2			+ +			+ +					
3	Frons, L : H						+ +			Head ♂, ♀		
4	Head : Frons						+ +					
5	Eye : Cheek			+			+					
-----												
6	Sterno-index						+ +			Thorax ♂, ♀		
7	Scutellar ; a : p											
-----												
8	Segment I			+			+			Legs ♂		
9	Sex-combs, Segment II			+			+					
-----												
10	Wings, L : W									Wings ♂, ♀		
11	c - index						+ +					
12	4 v - index											
13	4 c - index						+					
14	5 x - index			+ +			+ +					
15	a c - index						+ +					
16	Fringe c 3						+ +					
-----												
17	Pupa, Horn-index			+			+			Pupa		
18	Spiracular digitations			+			+					
-----												
Total, ♂, ♀, pupa				5	2	2	5	8	2	10	9	1
Total for the species				9			15			20		

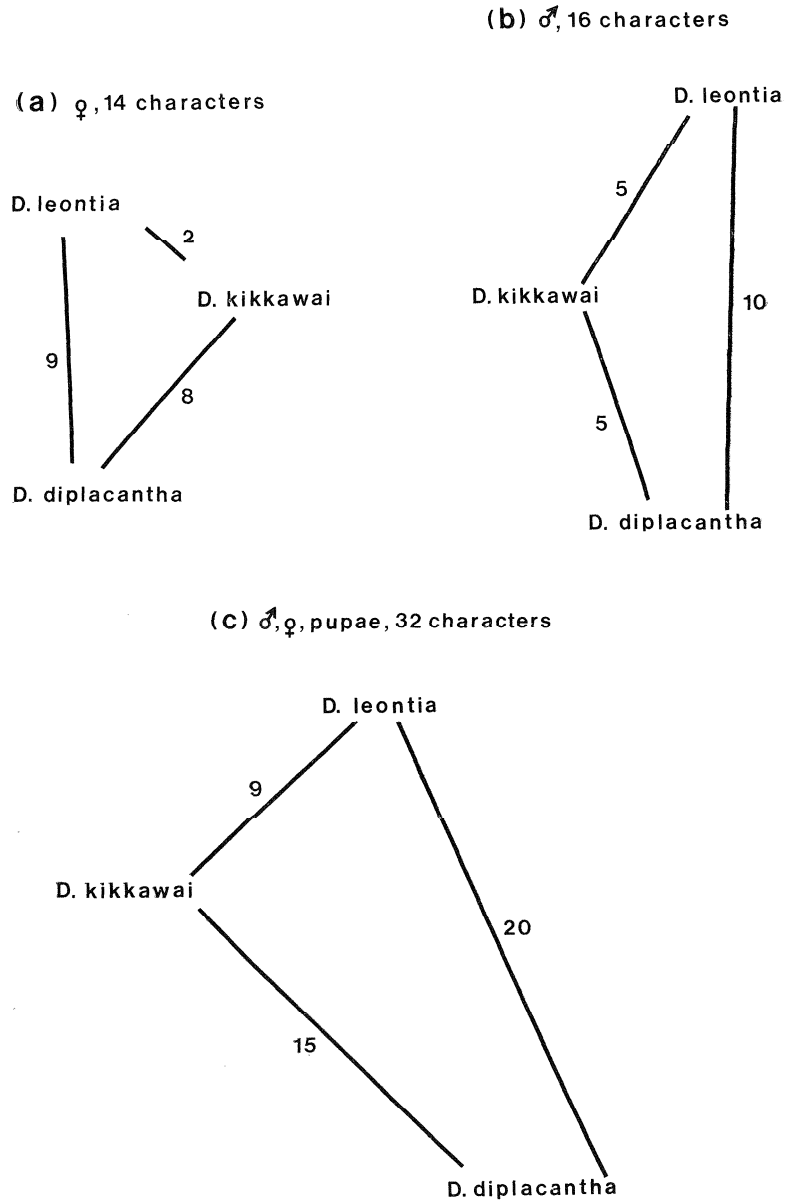


FIG. 5. Relationships between *D. kikkawai*, *D. leontia* and *D. diplacantha* (the numbers indicate the significantly different characters between the species).

#### TAXONOMY OF THE NINE SPECIES OF THE *KIKKAWAI*-COMPLEX

The three species can be distinguished by several taxonomic characters which are described below. *D. kikkawai* and *D. leontia* have almost identical ♂ genitalia and it is impossible to identify them by an examination of these

structures. This phenomenon is very rare in the genus *Drosophila* (Futch, 1973, Tsacas, 1976) and the present case must be pointed out. In spite of the similarity of the male genitalia, *kikkawai* and *leontia* can be easily identified by the brilliant, velvety, white spot on the inferior part of the face in *leontia*. In *D. diplacantha*, the male genitalia differ greatly in all their structures from those of the other two species. Thus the identification of *diplacantha* is easy and non-ambiguous.

Within the *montium* subgroup it is possible to distinguish a cluster of species which contains the species closely allied to *D. kikkawai* and may be named the *kikkawai*-complex. BOCK & WHEELER (1972) noticed this fact, and concluded that «these species together with *kikkawai* appear to constitute one phylogenetic branch within the *montium* subgroup». But they neither defined nor mark the limits of these species; they only pointed out the similarity in the structure of the male genitalia between *D. kikkawai* and *D. lini*. The *kikkawai*-complex cannot be defined by only one character. Three characters are essential for the definition of the complex: two long sex-combs on the tarsi of forelegs, two teeth on the secondary claspers and, especially, the slender posterior parameres. Some other species possess, for example, two teeth on the secondary claspers (*nigriallata* TAKADA, MOMMA & SHIMA, *penicillipennis* TAKADA, MOMMA & SHIMA, *serrata* MALLOCH etc.) but their posterior parameres and phallus are very different. A more complete definition of this complex is as follows: sex-comb on the first two segments of the foreleg tarsi very long, occupying the entire length of the segment; secondary clasper fused or attached to anal plate via membranous connection; secondary clasper with 2 very large subequal, or one large and one smaller above, black median teeth; no strong teeth on the anal plate; phallus slender, bare, or rarely hirsute, apically recurved dorsally; caudal margin of novasternum with strong, generally slender, median convexity and a pair of close submedian spines which are usually long; posterior parameres long, slender often reaching the tip of phallus. The following species belong to this complex: *kikkawai* BURLA, *barbarae* BOCK & WHEELER, *lini* BOCK & WHEELER, *pennae* BOCK & WHEELER, *brevis* PARSHAD & SINGH, *leontia* n. sp., *D. diplacantha* n. sp., *mysorensis* REDDY & KRISHNAMURTHY, *anomelani* REDDY & KRISHNAMURTHY. The last two species do not fit well with all the characters of the definition, and are tentatively included in the *kikkawai*-complex. *D. montium* with which *D. kikkawai* was confused for a long time, probably does not belong to this complex. We were not able to examine the type-specimens and the figures done by BURLA (1954) are not conclusive.

#### GEOGRAPHICAL DISTRIBUTION OF THE SPECIES OF THE *KIKKAWAI*-COMPLEX

Up to now several species close to *kikkawai* have been described which can be distinguished only by a careful examination of their genitalia (Bock & Wheeler, 1972, T<sup>ô</sup>KADA, MOMMA & SHIMA, 1975). It is therefore difficult

to regard as correct all previous determinations. This taxonomic problem coupled with the lack of information from large geographic areas must be taken into account when discussing the geographical distribution of these species.

Figure 4 shows the distribution of *D. kikkawai* as it is presently known. The species is widespread throughout the entire intertropical zone around the world. Southward the distribution reaches the tropic of Capricorn on the American continent, and Northward it goes beyond the tropic of Cancer, reaching the 40th parallel on the Asian continent.

Thus the species occupies the entire oriental zoogeographical region, part of the East-Palaearctic and Neotropical regions and part of the Australian (New Guinea). If large continental areas (Burma) or important islands (Celebes) appear unoccupied, this is certainly due to a lack of information. On the other hand, it is probably absent from the Australian continent.

On the African mainland *D. kikkawai* has been collected only in Mount Nimba, (Ivory Coast). Intensive collections in other parts of Ivory Coast, Cameroun and to a lesser degree in Gabon and Congo were unsuccessful.

It is therefore reasonable to consider that this species is rare in Western and Central Africa where it probably occupies a specialized niche. In the Ivory Coast and also Réunion Island (DAVID & Tsacas, 1975) it was found only in altitude, suggesting that in the Ethiopian region it could be confined to the mountains. However, recent attempts to collect *D. kikkawai* made by us (October-November 1975), in the mountains of West Cameroun, were negative.

In South America *D. kikkawai* seems to be more widespread (Brazil, Colombia); *D. diplacantha* is an endemic African species and *D. leontia* known only from Singapore. The six other species of the *kikkawai*-complex are all oriental (fig. 4): two from India (*mysorensis* and *anomelani*), three from islands (*lini*, Taiwan; *brevis*, South Andamans; *pennae*, New Guinea) and one both from the Asian continent and islands (*barbarae*, Malay Peninsula, Thailand, Borneo and Philippine).

## DISCUSSION

Considering the distribution of the *kikkawai*-complex as a whole, we may deduce that *D. kikkawai* probably originated in the Oriental region. Starting from there *D. kikkawai* colonized many islands and spread on the continent up to the 40th N. parallel. The colonization of Africa and South America is more difficult to explain. Its presence in Reunion Island is probably due to human activities for this island is situated on the ancient road to the East Indies (David & Tsacas, 1975). However, it is very difficult to explain the presence of *D. kikkawai* in South America and on Mount Nimba (Ivory Coast) by such an hypothesis. An ancient introduction, independent of human activities seems more plausible to explain these facts.

In Africa there exists one endemic species, *D. diplacantha* which seems widespread (Ivory-Coast, Cameroun, Congo). This species has certainly differentiated from an ancestor which was introduced into Africa. It probably



occupies a niche very similar to that of *kikkawai*, and its presence perhaps, prevented the latter, when it was introduced to this continent, from becoming widespread in Africa. Its presence in Mount Nimba and Reunion Island, from where *D. diplacantha* is absent suggests this interpretation. The absence of the competitor in South America has allowed *D. kikkawai* to become widely dispersed on this continent.

These facts suggest that :

— the *kikkawai*-complex originated in the Oriental zoogeographical region.

— the introduction of this complex to Africa is sufficiently ancient to allow the development of an endemic species.

— *D. kikkawai* was the only species of the complex which reached such a cosmopolitan state and colonized the American continent.

— this distribution confirms the antiquity of the relationship between the Drosophilid faunae of the Ethiopian and the Oriental zoogeographical regions (DAVID & TSACAS, 1975; TSACAS, 1974).

*D. kikkawai* was considered as a domestic species (PAVAN & DA CUNHA, 1947). In Africa it was found only in wild localities, i.e. Mount Nimba, far from any human habitation. *D. diplacantha* was found in both wild and domestic localities eg. Mount Nimba, far from any human habitation, and Brazzaville, in the University campus. It is, therefore, more reasonable to consider this species as ubiquitous. *D. leontia* is probably a domestic species as it is found near human habitations in Singapore.

It is generally admitted that cosmopolitan or subcosmopolitan colonizing species were dispersed recently by human transportation (DOBZHANSKY, 1965; CARSON, 1965). Such an hypothesis is probably not entirely true for *D. melanogaster* (David & al., 1976). The present results also suggest that *Drosophila* species could travel and colonize continents without human intervention.

The hypothesis that sympatric allied species possess discriminant genital structures has been verified by several examples in the Drosophilids (TSACAS, 1972, 1976). The case of the three species studied here constitutes an exception, the sympatric species *leontia* and *kikkawai* having identical genitalia.

It is interesting to note that the two indices of the pupae are very significant. These results contrast with the general opinion that the pupal as well as the larval characters are not useful in systematics of *Drosophila*. Another fact, important in the case of the two species *kikkawai* and *leontia*, is that their genital characters are less discriminating than some other taxonomic indices. This fact is probably very rare in the Drosophilids (FUTCH, 1973, Tsacas, 1976) but no data from similar studies has been published concerning the known sibling-species. PASTEUR (1970) in his careful study of the semispecies of the *D. paulistorum* found differences using the average value of biometrical traits but not the usual taxonomic indices. Thus it is interesting to compare these indices when the genitalia do not give good taxonomic characters.

The *montium*-subgroup with its large number of species (over 60) from different biogeographical regions is obviously a polyphyletic group. In another paper, presently in preparation, this problem is studied in relation to those of the whole *melanogaster*-group. Within the *montium*-subgroup it is possible to distinguish some clusters of species which constitute different phylogenetic branches, the *kikkawai*-complex constitutes one of these. A study of the whole *montium*-group should allow a better comprehension of the phylogenetic relationships between the clusters of species from which it is composed, as well as the relationships between the allied subgroups within the *melanogaster*-group.

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