Kontyû, Tokyo, **51** (2): 169–184. June 25, 1983

Ecological Studies of Floricolous *Drosophilella* in Burma with Descriptions of Three New Species from Burma and the Philippines (Diptera, Drosophilidae)

Masanori J. TODA

Institute of Low Temperature Science, Hokkaido University,
Sapporo, 060 Japan

and

Toyohi OKADA

Gotokuji 2–30–18, Setagaya-ku, Tokyo, 154 Japan

Synopsis Two new species of the genus *Drosophilella* DUDA (*D. monoconica* and *D. diconica*) breeding in the inflorescence of *Colocasia esculenta* (SCHOTT) in Burma are studied and their species-specific reproductive tactics are discussed in relation to the life histories. *D. monoconica* is considered more subject to abiotic density-independent mortality factors than *D. diconica* is, and consequently the former could be called '*r*-strategist' and the latter '*K*-strategist'. Another species of this genus, also associated with *Colocasia* flowers, is described from the Philippines (*D. toshiokai*). Taximetrical analyses over 7 species of *Drosophilella* including the three new species resulted in finding that the Burmese couple are nearest to the New Guinean couple (*D. stamenicola* and *D. pistilicola*) and *D. toshiokai* is remotest from any other species in consideration.

Six species have hitherto been recognized in the genus *Drosophilella*, one from Java (DUDA, 1924a, b; WHEELER, 1969), two from the Taiwan-Ryukyu district (OKADA, 1975, 1980), and three from New Guinea (DUDA, 1923; CARSON & OKADA, 1980). Most of them are known to be intimately associated with the flowers of *Colocasia* or *Alocasia* (Araceae). The present article adds three new species to this genus, two from Burma and one from the Philippines, collected from the flowers of *Colocasia esculenta* by the senior author and Dr. S. TOSHIOKA, respectively. Detailed ecological observations and discussions are given by the senior author, and brief taximetric analyses are made by the junior author.

Material and Methods

Some inflorescences of *Colocasia esculenta* were found by the senior author at the shore of Inya Lake in Rangoon. As it could not be determined from external appearance whether flies were present within or not, each inflorescence was imprisoned within a clear plastic bag. Following this, all flies that emerged from the inflorescence were caught with an aspirator. Later, such fly-bearing inflorescences were dissected and examined for preimaginal stages of drosophilids under a binocular microscope. All eggs and larvae found were collected and preserved in 70% alcohol separately for different parts of the spadix; namely, the pistillate, transitional and staminate regions (cf. CARSON & OKADA, 1980). In order to study later development, pupation and emergence, some young fruits found together with inflorescences were collected and each was kept on tissue paper within a plastic bag, and emerging flies were aspirated.

A part of the adult specimens obtained were preserved dried and others in alcohol. Descriptions of the two new species from Burma are based on the dried specimens for external structures, and on the alcohol-preserved material for internal structures of the digestive system and reproductive organs. Further, some females were examined for the following items: 1) thorax length (including scutellum), 2) ovarian conditions, 3) number of ovarioles, 4) number of mature eggs held, and 5) the size (length and width) of mature egg.

All larvae and a part of eggs were mounted in glycerin after heating in 10% KOH solution.

The other new species of this genus is based exclusively on dried material collected by Dr. S. TOSHIOKA from the flowers of *Colocasia esculenta* in Luzon, the Philippines.

Descriptions of New Species

Drosophilella monoconica TODA et OKADA, sp. n.

Figs. 1A–H, 2A–F_m

♂, ♀. Body about 1.8 mm in length. Eye brownish red, with short pile. Antenna with 2nd joint dark orange, black above, 3rd grayish yellow. Arista short, merely pubescent. Palpus yellowish gray, with a terminal seta. Ocellar triangle mat black; ocellars outside the triangle made by ocelli. Periorbit pruinose black. Frons dark brown, anteriorly paler, anteriorly as broad as median length, half as broad as head width. Face yellowish gray. Carina broad. Clypeus yellowish orange. Cheek gray, 2/5 as broad as the greatest diameter of eye. Anterior reclinate orbital 1/4 proclinate, nearer to proclinate than to posterior reclinate, which is as long as proclinate. Second oral thin, 1/4 vibrissa. Thorax entirely mat black. Humerals 2. Acrostichal hairs in 2 or 4 rows. Anterior dorsocentrals 4/7 posteriors, length distance of dorsocentrals slightly shorter than cross distance. Lateral scutellars convergent, 1/2 apicals, which are slightly nearer to each other than to laterals. Sterno-index 0.5. Legs yellowish gray, ultimate tarsal joints brownish black; 2nd tarsal joint of fore leg (Fig. 1-B) elongate apically below and with 3 stout black teeth. Fore metatarsus as long as 2 succeeding tarsal joints, mid and hind metatarsi as long as 3 succeedings. Wing (Fig. 1-A) hyaline, veins yellow, costa without heavy fringe, R_{2+3} gently curved to costa; R_{4+5} and M parallel. C-index

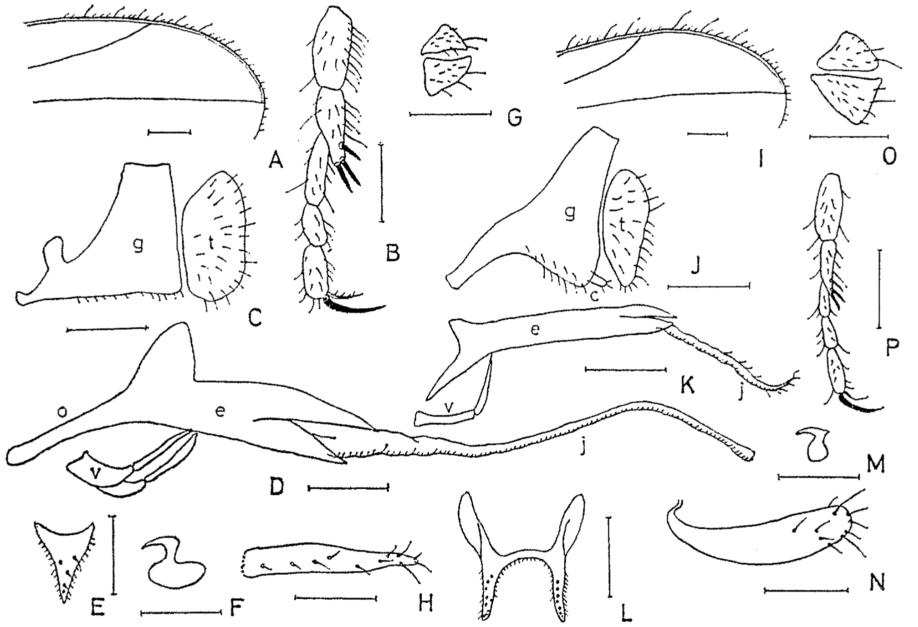


Fig. 1. A–H, *Drosophilella monoconica*; I–P, *D. diconica*. A, I, Wing; B, P, fore tarsus; C, J, periphallic organs; D, K, phallic organs; E, L, conical process of ♂ 6th abdominal sternite; F, M, ejaculatory apodeme; G, N, ♀ epiproct and hypoproct; H, N, ovipositor. c, Surstylus; e, aedeagus; g, epandrium; j, evaginated ejaculatory duct; o, apodeme of aedeagus; t, cercus; v, ventral fragma. Scales 0.1 mm.

1.9; 4V-index 2.7; 4C-index 1.4; 5x-index 1.5; Ac-index 3.0. Cl-bristle 1; C3-fringe undeveloped. Halteres yellow. Abdominal tergites grayish yellow. Male 6th sternite with a single conical process (Fig. 1-E), thus the specific name. Periphallic organs (Fig. 1-C) black, without surstylus. Phallic organs (Fig. 1-D) black, aedeagus with a large subbasal conical process. Ejaculatory apodeme (Fig. 1-F) broader than long. Female epiproct and hypoproct (Fig. 1-G) triangular. Ovipositor (Fig. 1-H) narrow.

Malpighian tubules with common stalks relatively long, posterior branches incompletely fused at apices (Fig. 2-A_m). Testis (te) pale orange, apically pointed; paragonia (pr) slender and once folded, slightly longer than testis (Fig. 2-B_m). Spermatheca (th) hyaline, elliptical; ventral receptacle absent (Fig. 2-C_m).

Larva and puparium (Fig. 2-D_m) with fine body spicules. Caudal abdominal segments elongate, without spicules, ending in paired short posterior spiracles (ps). Anterior spiracle (as) of puparium with about 12 long branches in a whorl; stalk about as long as branches. Mouth hook (mh) of the 1st instar larva (Fig. 2-$F1_m$) ventrally not dentate, relatively large, about 4/5 as long as dorsal wing (dw) of pharyngeal sclerite. In the 2nd (Fig. 2-$F2_m$) and 3rd (Fig. 2-$F3_m$) instar larvae: mouth hook ventrally dentate; latticed process (lp) of pharyngeal sclerite relatively broad and fused to dorsal wing; vertical bridge (vb) about 1/5 as long as dorsal wing.

Holotype ♂ (25002), 2 ♂, 9 ♀ paratypes, Inya Lake, Rangoon, Burma, 20.

XII. 1981, ex flowers of *Colocasia esculenta*, TODA leg. Holotype and 1 female paratype in National Science Museum, Tokyo.

This species resembles *D. stamenicola* CARSON et OKADA in having costal fringe undeveloped, and in the shape of ♂ and ♀ genitalia, but it differs from the latter in having grayish yellow abdominal tergites and in lacking surstylus.

Drosophilella diconica TODA et OKADA, sp. n.

Figs. 1I–P, 2A–F_d

♂, ♀. Body about 1.5 mm in length. Eye brownish black, with fine sparse pile. Antenna orange brown, 2nd joint black above, arista short and merely pubescent. Palpus gray, with a black seta apically. Ocellar triangle mat black, ocellars outside the triangle made by ocelli. Periorbit mat black. Frons mat black, with a pair of broad, anteriorly convergent, velvety black stripes, anteriorly as broad as median length, half as broad as head width. Face grayish white. Carina broad, flat above. Clypeus gray. Cheek gray, 1/3 as broad as the greatest diameter of eye. Anterior reclinate orbital 1/3 proclinate, nearer to proclinate than to posterior reclinate, which is as long as proclinate. Second oral thin, 1/3 vibrissa. Thorax entirely mat pruinose black. Humerals 2, long. Acrostichal hairs in 2 rows. Anterior dorsocentrals 4/7 posteriors, length distance of dorsocentrals slightly shorter than cross distance. Lateral scutellars parallel, 3/4 apicals, which are nearer to each other than to laterals. Sterno-index 0.5. Legs brown, femora and tibiae except for knee joints dark brown, ultimate tarsal joints black. Second tarsal joint of fore leg elongate distally below and with 3–4 stout black teeth (Fig. 1-P). Fore metatarsus as long as 2nd tarsal joint, mid as long as 2 succeeding tarsal joints, hind as long as the rest of tarsal joints. Wing (Fig. 1-I) hyaline, veins yellow, R_{2+3} nearly straight, R_{4+5} and M parallel, costa without heavy bristles. C-index 1.6; 4V-index 2.2; 4C-index 1.4; 5x-index 1.8; Ac-index 2.4. C1-bristle 1, C3-fringe undeveloped. Halteres yellow. Abdominal tergites pruinose black. Male 6th sternite (Fig. 1-L) with 2 parallel fingerlike processes, thus the specific name. Periphallic organs (Fig. 1-J) black, surstylus present. Ejaculatory apodeme (Fig. 1-M) longer than broad. Ovipositor (Fig. 1-N) broad, pale brown. Female epiproct and hypoproct (Fig. 1-O) triangular.

Malpighian tubules with common stalks short, posterior branches completely fused at apices (Fig. 2-A_d). Testis brownish orange, apically pointed; paragonia slender and folded twice or thrice, much longer than testis (Fig. 2-B_d). Spermatheca hyaline, oblong; ventral receptacle (re) conical (Fig. 2-C_d).

Larva and puparium (Fig. 2-D_d) with stout body spicules. Caudal abdominal segments much elongate, with fine spicules; posterior spiracles long and divergent. Anterior spiracle of puparium (Fig. 2-E_d) with about 5 short branches, and sessile. Mouth hook of the 1st instar larva (Fig. 2-$F1_d$) ventrally not dentate, small, and 3/10 as long as dorsal wing of pharyngeal sclerite. In the 2nd (Fig. 2-$F2_d$) and the

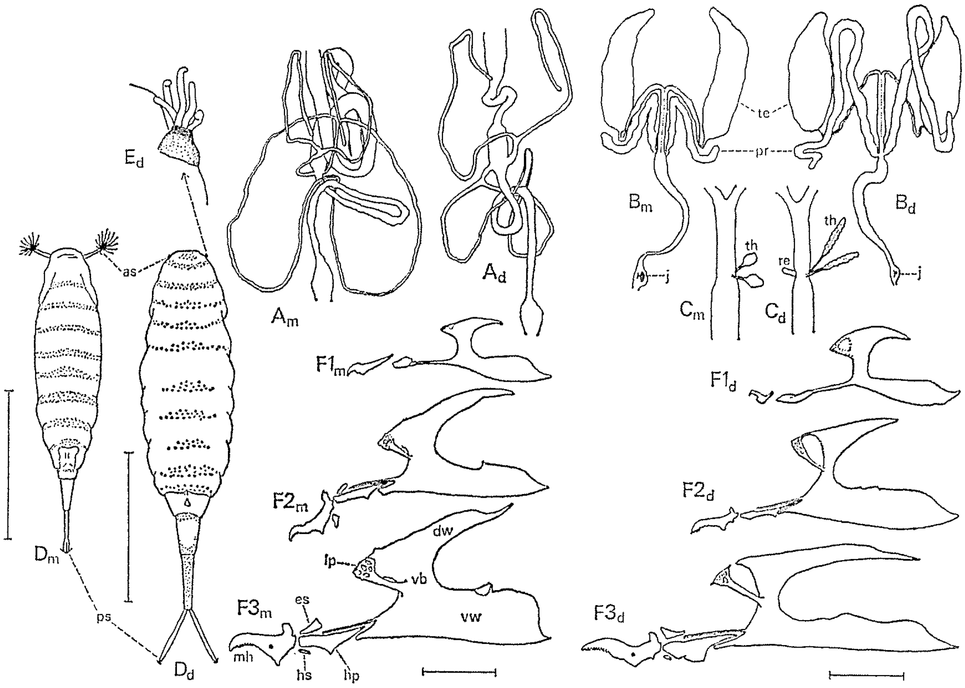


Fig. 2. Adult internal structures and preimaginal stages. m, *Drosophilella monoconica*; d, *D. diconica*. A, Digestive system; B, male internal reproductive organs; C, female internal reproductive organs; D, puparium (ventral aspect); E, anterior spiracle of puparium; F, cephalopharyngeal skeleton of 1st (1), 2nd (2) and 3rd (3) instar larva. te, Testis; pr, paragonia; th, spermatheca; re, ventral receptacle; as, anterior spiracle; ps, posterior spiracle; mh, mouth hook; es, epipharyngeal sclerite; hs, hypopharyngeal sclerite; hp, hypostomal sclerite; lp, latticed process of pharyngeal sclerite (phs); vb, vertical bridge of phs; dw, dorsal wing of phs; vw, ventral wing of phs. Scale 1 mm in D, 0.1 mm in F.

3rd (Fig. 2-F3$_d$) instar larvae: mouth hook ventrally dentate; latticed process of pharyngeal sclerite narrow, separated from dorsal wing incompletely in 2nd instar and completely in 3rd; vertical bridge about 1/10 as long as wing.

Holotype ♂ (25001), 9 ♂, 5 ♀ paratypes, Inya Lake, Rangoon, Burma, 20. XII. 1981, ex flowers of *Colocasia esculenta* together with the foregoing species, Toda leg. Types in National Science Museum, Tokyo.

This species resembles *D. pistilicola* Carson et Okada in having undeveloped costal fringe and in the shape of male and female genitalia, but it differs from the latter in having parallel fingerlike processes on male 6th abdominal sternite and in the tarsal joints of fore leg not compressed.

Drosophilella toshiokai Okada, sp. n.

Fig. 3A–H

♂, ♀. Body 1.5–1.7 mm in length. Head (Fig. 3-A) as broad as thorax. Eye dark purplish red, sparsely piled. Antenna with 2nd joint orange brown,

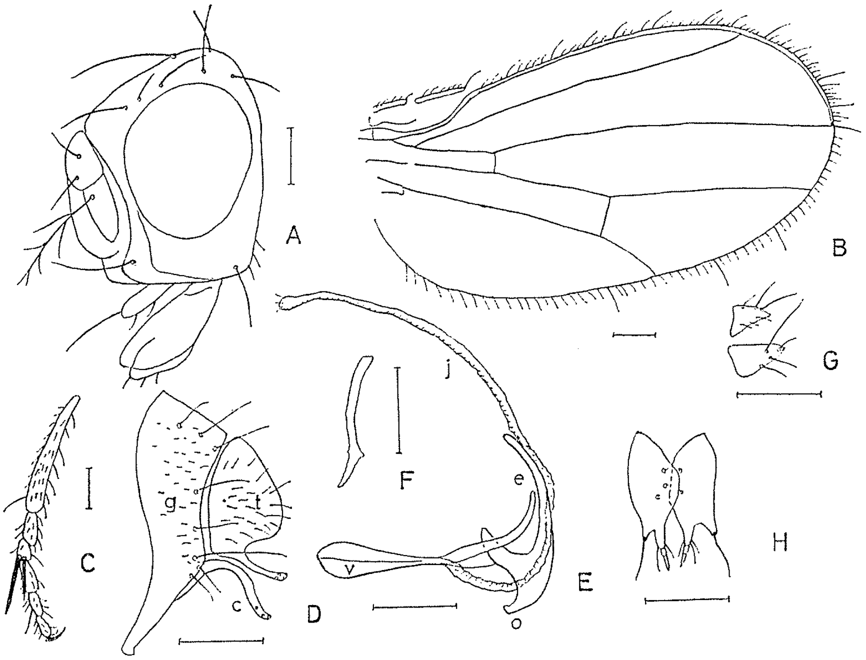


Fig. 3. *Drosophilella toshiokai*. A, Head; B, wing; C, tibia and tarsus of fore leg; D, periphallic organs; E, phallic organs; F, ejaculatory apodeme; G, ♀ epiproct and hypoproct; H, ovipositor. Signs as in Fig. 1. Scales 0.1 mm.

3rd grayish yellow. Arista longer than antenna, with 2 upper and 2 lower long branches and a small fork. Palpus orange yellow, apically with a long seta. Ocellar triangle and periorbit mat black, ocellars outside the triangle made by ocelli. Frons mat orange gray, with white pubescence, anteriorly orange, broader than median length, half as broad as head width. Face mat yellowish white, carina broad and long. Clypeus yellowish white. Cheek yellowish gray, 1/3 as broad as the greatest diameter of eye. Anterior reclinate orbital 1/4 proclinate, just between proclinate and posterior reclinate, which is as long as proclinate. Vibrissa very long and strong, 2nd oral fine. Mesoscutum and scutellum mat dark brown, thoracic pleura yellowish brown. Humerals 3, uppermost one small. Prescutellars weakly developed. Acrostichal hairs in 4 rows. Anterior dorsocentrals 2/3 posteriors, length distance of dorsocentrals slightly more than cross distance. Lateral scutellars somewhat divergent, 3/5 apicals, which are parallel and equally apart from each other and from laterals. Sterno-index 0.7. Legs yellowish gray, second tarsal joint of fore leg apically with 2 long stout unequal black bristles. Fore metatarsus as long as 2nd tarsal joint, mid and hind as long as 2 and 3 succeeding tarsal joints, respectively. Wing (Fig. 3-C) hyaline, broad, R_{2+3} nearly straight, R_{4+5} and M parallel. Costa without heavy bristles. C-index 2.1; 4V-index 1.6; 4C-index 1.1; 5x-index 2.6; Ac-index 3.7. C1-bristle 1, long; C3-fringe undeveloped. Halteres grayish black, stalks orange. Abdominal tergites mat black; sternites black, male

6th sternite without conical processes. Periphallic organs (Fig. 3-D) and phallic organs (Fig. 3-E) black; surstylus elongate and curved; male cercus caudoventrally narrowly prolonged; aedeagus slender, gently curved dorsally. Ejaculatory apodeme (Fig. 3-F) slender, black. Ovipositor (Fig. 3-H) pale brown, apically pointed and segmented.

Holotype ♂ (24812), 10 ♂, 15 ♀ paratypes, Sison, 40 km S of Surigao, Mindanao, Philippines, 17. VII. 1981, ex flowers of *Colocasia esculenta*, TOSHIOKA leg., thus the specific name. Holotype in National Science Museum, Tokyo.

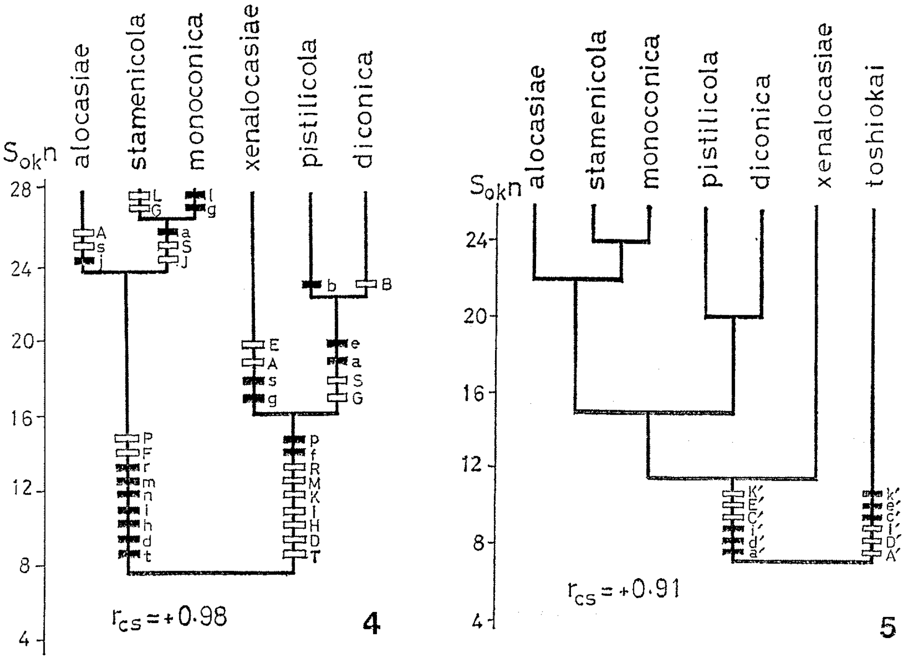
This species differs from ordinary members of *Drosophilella* in having plumose arista, exceedingly long apical bristles on 2nd tarsal joint of fore leg, no conical processes on male 6th abdominal sternite, slender ejaculatory apodeme, and segmented ovipositor. However, it agrees with other species of the genus in the general structures of male genitalia and the elongate evagination of ejaculatory duct (j in Figs. 1 & 3).

Taximetrical Analyses

The relationships of the 2 new species from Burma and 4 known species (*D. stamenicola* CARSON et OKADA and *D. pistilicola* CARSON et OKADA from New Guinea, *D. alocasiae* OKADA and *D. xenalocasiae* OKADA from Taiwan and the Ryukyus) of the genus *Drosophilella* were analysed taximetrically by means of S_{ok} proximity analysis and UPGMA cluster analysis over 29 diagnostic characters (A–T), which were as used in a previous paper (OKADA, 1980). The result is shown in Fig. 4. The Cophenetic Correlation Coefficient (r_{cs}) between original t × t matrix and that derived from the dendrogram is +0.98. Three stamenicolous species (*monoconica*, *stamenicola*, *alocasiae*) and three pistilicolous ones (*diconica*, *pistilicola*, *xenalocasiae*) are grouped in different major clusters. In each of the major clusters, Burmese and New Guinean species are more intimately associated with each other than they are with the species from Taiwan and the Ryukyus.

If *D. toshiokai* from the Philippines is combined with above 6 species, another dendrogram (Fig. 5) is obtained. In this case the analysis was made over 17 characters, 11 (A–K) of which are as used before and 6 are newly added. Each character is divided into two character states: presumed plesiomorph (large letter, coded 0) and presumed apomorph (small letter, coded 1).

"A′"	Arista plumose (A′=0), or pubescent (a′=1).
"C′"	Stout teeth of 2nd tarsal joint of fore leg short (C′=0), or very long (c′=1).
"D′"	Conical process of male 6th abdominal sternite absent (D′=0), or present (d′=1).
"E′"	Male cercus ventrally not prolonged (E′=0), or prolonged (e′=1).
"I′"	Ejaculatory apodeme slender (I′=0), or broad (i′=1).
"K′"	Ovipositor not segmented (K′=0), or segmented (k′=1).



Figs. 4–5. —— 4, A dendrogram to show relationships of 6 *Drosophilella* species established by means of S_{ok} proximity analysis and UPGMA cluster analysis; 5, a dendrogram to show relationships of 7 *Drosophilella* species including *D. toshiokai* established by means of S_{ok} proximity analysis and UPGMA cluster analysis. Large letters indicate presumed plesiomorphs and small letters presumed apomorphs.

The dendrogram gives a lower value for r_{cs} (+0.91), and shows that *toshiokai* is independently clustered from other species and that *xenalocasiae* is displaced from the pistilicolous group. *D. toshiokai* seems to have been separatedly derived from the ancestral stock of *Drosophilella*, retaining plumose arista, elongate ejaculatory apodeme, normal male 6th abdominal sternite, and probably eremoparasitism, not aquiring synhospitalism.

Ecological Notes on Breeding Habits

The breeding habits of *Drosophilella* species were studied in two remote regions, for *D. xenalocasiae* and *D. alocasiae* in the Ryukyus (YAFUSO, 1979, read at the Joint Ann. Meet. Ent. Soc. Jap. and Jap. Soc. appl. Ent. Zool., Fukuoka) and for *D. pistilicola* and *D. stamenicola* in New Guinea (CARSON & OKADA, 1980). The members of each couple share the same inflorescence of an araceous plant, *Alocasia odora* in Taiwan and the Ryukyus and *Colocasia esculenta* in New Guinea, as breeding site, but are microallotopic on the same spadix: *D. xenalocasiae* and *D. pistilicola* prefer pistillate region of spadix, while *D. alocasiae* and *D. stamenicola* staminate region. The breeding habits of the present new couple, *D. diconica* and *D. monoconica*, were examined and will be discussed in comparison with those of other couples.

Population constitution within inflorescence

Drosophilella populations including not only adults but also preimaginal stages were sampled from nine inflorescences (Table 1). But, two inflorescences, Nos. 1 and 2, were not examined for preimaginal stages. In the New Guinean species the age structure of *Drosophilella* populations harbored within an inflorescence proceeds successively with increasing age of inflorescence. Such a progressive development of population age structure was also detected in the present case, though the age classes of inflorescences were not recorded. The sampled inflorescences are tentatively classified into three stages according to the age structure of *Drosophilella* populations within them: 'adult–egg' (Nos. 3–4), 'egg–1st instar larva' (Nos. 5–7) and 'larva' (Nos. 8–9) stages corresponding to Stage 1, early Stage 2 and late Stage 2 by Carson and Okada (1980), respectively. The successive stages overlap one another to some extent. However, rather synchronous development of population members suggests more or less synchronous oviposition. In this connection, in the New Guinean species, the adults stay only for a single day within an inflorescence. If the total number of adult individuals collected reflects the natural population density in the surveyed area, the density of *D. diconica* is estimated to be about twice as high as that of *D. monoconica*.

Interspecific differentiation in oviposition, larval feeding and pupation sites

In order to examine whether any microtopic differentiation is present between *D. monoconica* and *D. diconica*, numbers of eggs and larvae were counted separately for different parts of spadix: pistillate, transitional and staminate regions. The data summed up for all examined inflorescences are shown in Table 2.

Because no clear difference such as recognized between the members of the New Guinean couple, except for size difference (cf. later), was found in egg morphology in the present couple, only a part of eggs, which contain developing 1st instar larva with sclerotized mouth hook (Fig. 2-F1), could be identified for species. Of the identified eggs, all deposited in staminate and transitional regions were of *D. monoconica*, while the eggs in pistillate region included both species in the proportion of 69.2% *D. diconica* to 30.8% *D. monoconica*. According to this result, all unidentified eggs in staminate and transitional regions should belong to *D. monoconica*, and those in pistillate region are assumed to include the two species in the proportion given above. Thus, a total of 177 eggs are referred to *D. monoconica* and 15 to *D. diconica*. The above result indicates a clear differentiation of oviposition sites between the two species: *D. diconica* exclusively oviposits on pistillate region, whereas *D. monoconica* mostly on staminate region and particularly on its lower part within about 1 cm from its base, though sometimes on transitional and, further, pistillate regions. This completely parallels the oviposition site differentiation observed for the New Guinean couple. The characteristic difference of ovipositor

Table 1. *Drosophilella* populations harbored within inflorescences of *Colocasia esculenta* at the shore of Inya Lake, Rangoon, Burma.

Inflorescence No. (Date)	Adult		Egg				Larva							
							monoconica				*diconica*			
	monoconica Total (♀/♂)	*diconica* Total (♀/♂)	*mono-conica*	*di-conica*	Unidentified	Total	1st	2nd	3rd	Total	1st	2nd	3rd	Total
1 (I-9)	46 (21/25)	67 (36/31)												
2 (I-9)	1 (0/ 1)	13 (10/ 3)												
3 (XII-19)	10 (7/ 3)	34 (21/13)	2	4	19	25	—	—	—	—	1	—	—	1
4 (I-13)	9 (6/ 3)	17 (6/11)	33	2	8	43	9	—	—	9	10	—	—	10
5 (XII-20)	—	13 (3/10)	34	—	63	97	5	—	—	5	3	—	—	3
6 (I-17)	—	1 (1/ 0)	2	1	11	14	33	—	—	33	8	—	—	8
7 (XII-20)	—	—	2	2	8	12	—	—	—	—	1	—	—	1
8 (XII-23)	—	—	—	—	1	1	4	3	—	7	—	7	—	7
9 (XII-19)	—	—	—	—	—	—	102	34	—	136	—	33	11	44
Total	66 (34/32)	145 (77/68)	73	9	110	192	153	37	—	190	23	40	11	74

Table 2. Distribution of preimaginal stages among different parts of spadix, summed up for seven inflorescences (Nos. 3 to 9 in Table 1).

Spadix Region	Egg						Larva							
	Identified		Estimated		Total		*monoconica*				*diconica*			
	monoconica No. (%)	*diconica* No. (%)	*mono-conica*	*di-conica*	*mono-conica*	*di-conica*	1st	2nd	3rd	Total (%)	1st	2nd	3rd	Total (%)
Staminate	49 (100.0)	—	87	—	136	—	65	—	—	65 (100.0)	—	—	—	—
Transitional	20 (100.0)	—	14	—	34	—	27	—	—	27 (100.0)	—	—	—	—
Pistillate	4 (30.8)	9 (69.2)	3	6	7	15	61	37	—	98 (57.0)	23	40	11	74 (43.0)
Total	73	9	104	6	177	15	153	37	—	190	23	40	11	74

Table 3. Records of *D. diconica* adult emergence from young fruits.

Young Fruit (Collection Date)		No. of adults emerged Total (♀/♂)	
A	(XII-19)	21	(12/ 9)
B	(XII-20)	33	(13/20)
C	(ditto)	24	(13/11)
D	(ditto)	32	(16/16)
E	(I-9)	18	(7/11)
F	(ditto)	7	(5/ 2)
Total		135	(66/69)

morphology between the two Burmese species (Fig. 1-H, N) can be explained as adaptation to this differentiation. Distally narrowing ovipositor of *D. monoconica*, which is a common character shared with ecological equivalents in other regions, *D. stamenicola* and *D. alocasiae*, seems to be adapted for laying an egg into a very narrow space among male flowers packed compactly in staminate region. On the other hand, *D. diconica* with broad and blade-like ovipositor deposits its eggs on side wall of female flowers located relatively sparsely in pistillate region.

Larvae of the two species can be easily distinguished from each other on the basis of difference in posterior spiracles (Fig. 2-D). As expected from the species-specific egg distribution, larvae of the two species, at least of the 1st instar, were differently distributed on spadix. *D. diconica* larvae of every instar were exclusively restricted to pistillate region. On the other hand, all larvae found in staminate and transitional regions were referable to the 1st instar of *D. monoconica*, but 2nd instar larvae of this species were found exclusively from pistillate region together with a considerable number of 1st instar larvae of the same species. Consequently, *D. monoconica* occupied more than half (57.0%) of total *Drosophilella* larvae in pistillate region in spite of the fact that it occupied only 30.8% in egg population there. This percentage increase of *D. monoconica* population and the restriction of its 2nd instar larvae to pistillate region indicate the migration of its 1st instar larvae from upper regions. Thus, the two species entirely overlap in the larval feeding sites of the 2nd instar. No 3rd instar larvae of *D. monoconica* were found in the present study.

All adults emerged from young fruits were *D. diconica* (Table 3). In fact, upon opening a pistillate capsule by removing heavy outer green wall, many puparia of this species could be found on the surface of developing green berries. On the other hand, CARSON and OKADA (1980) observed that *D. stamenicola*, an ecological equivalent of *D. monoconica*, pupates in and emerges from drier portions of deliquescing spathe. Staminate and spathe remnants, together with pistillate capsule, were kept within a plastic bag to get adults emerge, but no adults of *D. monoconica* were obtained in the present study. The remnants of upper parts of inflorescence may have been too dry for drosophilid larvae, though not examined carefully for preimaginal stages there. It is supposed that before the young fruits were collected for the survey, 3rd instar larvae of *D. monoconica* had already emigrated from pistillate region to somewhere else outside the inflorescence, probably for pupation.

Female reproductive traits

Twenty-one *D. monoconica* and 35 (excluding one parasitized by nematodes) *D. diconica* females, obtained from inflorescence No. 1, were examined for some items with respect to reproductive tactics. The results are compared between the two species (Table 4).

First, inspection of ovarian conditions revealed that female adult populations of both species harbored within an inflorescence included a few young females with immature ovaries and pale body color. This suggests that the inflorescence provides not only ovipositing but also feeding sites for female adults. Further, judging from the fact that no *Drosophilella* flies caught by intensive sweeping either around the host plants or at various adjacent sites, adult flies of both species should spend their entire lifetime almost within the inflorescences except for brief periods during migration. On the other hand, in both species mature females each had only a single large mature egg in elongated vagina, whenever they had. Such females occupied approximately the same proportion in the two species: 57.1% in *D. monoconica* and 54.3% in *D. diconica.* This peculiar pattern of ovarian development was termed 'alternating ovarian development' by KAMBYSELLIS and HEED (1971). Further, in a few cases, a mature egg, still retained in vagina, contained a well grown 1st instar larva, suggesting the possibility of ovoviviparity. The same phenomenon was reported also for *D. xenalocasiae* (under the name *D. colocasiae*) by OKADA (1975).

The average number of ovarioles per female was relatively small in either species,

Table 4. Comparison of reproductive traits between *D. monoconica* and *D. diconica*.

Items concerning reproductive traits	*D. monoconica*	*D. diconica*	t-test
No. of females examined	21	35	
Thorax length (L_T, mm)	0.772±0.059	0.654±0.068	$p<0.001$
Reproductive conditions			
% of immature young females	14.3	14.3	
% of females holding mature egg in vagina	57.1	54.3	
No. of ovarioles per female	9.05 ±1.91	3.86±0.65	$p<0.001$*
Mature egg size			
No. of eggs measured	12	19	
Length (L_E, mm)	0.683±0.042	0.727±0.061	$p<0.05$
Width (W_E, mm)	0.217±0.013	0.237±0.019	$p<0.005$
Index of volume ($\bar{L}_E \times \bar{W}_E^2$)	0.032	0.041	
Relative length to thorax length ($\bar{L}_E/\bar{L}_T$)	0.88	1.11	

* According to ASPIN-WELCH Method (cf. ISHII, 1975) in the case of unequal variance.

though the number for *D. monoconica* (9.05) was about 2.3 times as large as that for *D. diconica* (3.86). In general, a larger number of ovarioles indicates a higher potential fecundity. Details in the present case will be discussed later. The mature egg of *D. diconica* was significantly larger in both length and width than that of *D. monoconica*. The difference is more remarkable in volume. The eggs of both species are quite large in relation to the body size within Drosophilidae (Kambysellis & Heed, 1971; Enomoto *et al.* unpubl.); this is more pronounced in *D. diconica* with a significantly smaller body size.

Alternating ovarian development, possible ovoviviparity, relatively few ovarioles per female, relatively large eggs, and rather short stay of adult flies within a inflorescence, all common to both species, can be considered as adaptation for limited nutritional supply at particular breeding sites such as flowers. Similar adaptation in the reproductive traits was reported for Hawaiian flower-breeding drosophilids, the subgenus *Exalloscaptomyza* of the genus *Scaptomyza* specialized to morning-glory flowers (Kambysellis & Heed, 1971).

Life history and reproductive tactics

The life histories of the two species are summarized in Fig. 6. As mentioned above, the present synhospitalic couple of species, specialized to breed on *Colocasia*

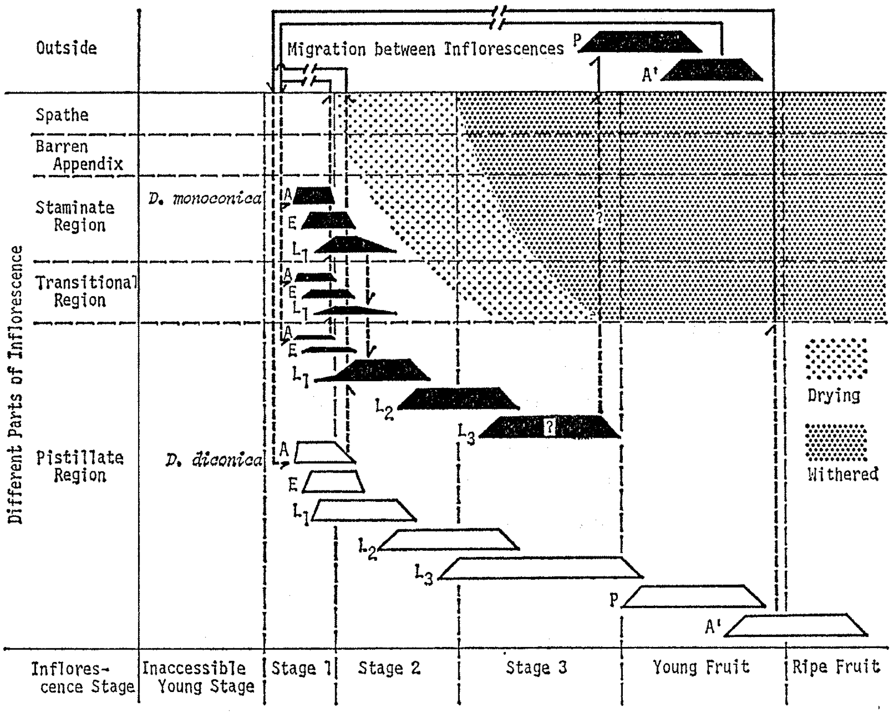


Fig. 6. Schematic representation of life histories of *D. monoconica* and *D. diconica* in dry season. Developmental stage——A, Adult; E, egg; L_1, 1st instar larva; L_2, 2nd instar; L_3, 3rd instar; p, pupa; A′, newly emerged adult. Solid arrow, migration outside inflorescence; broken arrow, migration within inflorescence.

inflorescences, exhibit a clear microallotopic niche differentiation. One of them, *D. diconica*, completes its preimaginal development within pistillate region and is well protected from the outside by heavy green wall of pistillate capsule throughout the development. On the other hand, *D. monoconica* first oviposits mostly near the base of staminate region. And then, as the inflorescence opens and the staminate region becomes exposed to open air (Stage 2), 1st instar larvae move to pistillate region. This results in complete co-habitation there with *D. diconica* larvae at least up to the 2nd instar. Although no 3rd instar larvae of *D. monoconica* were found in the present study, they are supposed to complete their development within pistillate region and to emigrate from there to the outside for pupation. This difference of the life histories is more or less comparable to that observed in other couples from New Guinea and the Ryukyus, *D. diconica* corresponding to *D. pistilicola* and *D. xenalocasiae*, and *D. monoconica* to *D. stamenicola* and *D. alocasiae*, though some variations can be detected, particularly in the latter combination. Young (probably 1st instar) larvae of *D. pistilicola* are distributed not only in pistillate region but also in transitional region and, further, near the base of staminate region, thus overlapping thoroughly with *D. stamenicola* larvae, in contrast to the case of *D. diconica* whose 1st instar larvae are exclusively restricted to pistillate region. At the 2nd instar stage, however, larvae of the two New Guinean species are supposed to move differently, *D. pistilicola* migrating downward and *D. stamenicola* upward, to accomplish larval niche segregation between them. Consequently, 3rd instar larvae of *D. stamenicola* are restricted to decaying staminate region and eventually pupate in deliquescing spathe*, while 3rd instars and puparia of *D. pistilicola* are found exclusively from pistillate region. Similar microallotopic separations of larval feeding site and pupation site within an inflorescence were observed, though only preliminarily, also in the couple occurring in the Ryukyus.

The inaccessibility of upper parts, staminate region, barren appendix and spathe, in aged inflorescences to the Burmese species is characteristic when compared with the other cases. These parts may be too dry at later inflorescence stages. As the inflorescence opens, the spathe and the upper part of spadix become dried more and more by the exposure to open air and eventually withered up instead of deliquesced or decayed in such a moderate moisture condition as to be accessible to drosophilids. However, the survey was made in the midst of dry season, which continues from November to April around Rangoon. The condition may be much different in other seasons. Therefore, it cannot be ruled out that avoiding upper inflorescence parts is no more than behavioral adjustment of the larvae to the dry season.

The species-specific reproductive tactics should be evaluated in connection with the life history. First, potential and realized fecundities should be estimated. If every ovariole of a female functions evenly, the potential fecundity can be expressed as a function of the number of ovarioles per female and the rate of egg maturation,

---

* According to CARSON (pers. comm.), the great proportion of *D. stamenicola* larvae also may leave the inflorescence entirely for pupation in adverse conditions of staminate and spathe remnants.

i. e., the number of eggs produced per ovariole in a unit time. Further, by assuming the latter factor to be inversely proportional to the egg volume, the index of potential fecundity was calculated at 282.8 in *D. monoconica*, which was about thrice as large as the value for *D. diconica* (94.1). On the other hand, the realized fecundity was evaluated from the data of Tables 1 and 2 as follows: [Total number of eggs and larvae]/[Adult population density]. The adult population density was estimated to be about twice higher in *D. diconica* than in *D. monoconica*. The resulting index value was 367=(177+190)/1 in *D. monoconica*, about 8 times as large as that for *D. diconica*, 44.5=(15+74)/2. The difference much greater in the realized fecundity may suggest the suppressed realization of potentiality in *D. diconica*, which may have been caused by the density-dependent effects of intraspecific competition within a limited space of pistillate region. Further in general, it could be said that the population of *D. diconica*, well protected within pistillate region, is controlled more density-dependently by biotic factors such as inter- and intra-specific competition, predation and parasitism. On the contrary, *D. monoconica* is more subject to abiotic environmental factors causing density-independent mortality at particular stages of its life cycle, e. g., at hatching and pupation. Especially in dry season the low humidity of air must increase such an abiotic environmental stress. When hatching out of eggs in staminate region is delayed, the danger for eggs or 1st instar larvae to be dried up would increase. The interspecific difference of adult population densities estimated in the present study may reflect such an environmental stress affecting differently between the two species and more adversely to *D. monoconica*. Further, it would be expected that the population of *D. monoconica*, being more subject to abiotic density-independent mortality factors, fluctuates seasonally more greatly than the population of *D. diconica* does.

It should be noted that the above discussion is not conclusive but only tentative or hypothetical because the field surveys are much limited in both time and intensity. However, the general reproductive traits, common to the two flower-feeding species, should indicate the characteristic reproductive tactics adaptive to the particular breeding site with limited nutritional supply. This interpretation may be supported by other flower-feeding drosophilids such as the Hawaiian *Exalloscaptomyza*. Further, the specific reproductive traits can be explained in connection with the life history in terms of *r*- and *K*- selection (PIANKA, 1970, 1972). Although these concepts have been subjected to criticism (e. g., STEARNS, 1976, 1977; SOUTHWOOD, 1977; HORN, 1978; PARRY, 1981), they may be still valid at least to some extent. In conclusion, *D. monoconica* could be called '*r*-strategist', and *D. diconica* '*K*-strategist' in a comparative sense.

Acknowledgments Part of this work was carried out in the 3rd Expedition of the "Family Drosophilidae for the Pan-Indian Ocean, South East Asia and the Pacific Ocean Areas" conducted by Prof. O. KITAGAWA, Tokyo Metropolitan Univ., and supported by Grant-in-Aid for Overseas Scientific Survey from the Ministry of Education, Japan (No. 56041049, No. 57043044). We are thankful to Prof. H. L. CARSON, Department of Genetics, University of Hawaii, for his reading of the manuscript and giving us valuable suggestions, and also to Drs. Nyi Nyi and Mya Maung, Department of Zoology, Rangoon Arts and Science University, for their help in the field survey in Rangoon. Our hearty thanks are also due to Dr. S. TOSHIOKA who kindly provided us with material from the Philippines.

Literature Cited

CARSON, H. L., & T. OKADA, 1980. Drosophilidae associated with flowers in Papua New Guinea. I. *Colocasia esculenta*. *Kontyû, Tokyo*, **48**: 15–29.

DUDA, O., 1923. Die orientalischen und australischen Drosophiliden Arten (Dipteren) des Ungarischen National-Museums zu Budapest. *Ann. hist.-nat. Mus. natn. Hung.*, **20**: 24–59.

——— 1924 a. Beitrag zur Systematik der Drosophiliden unter besonderer Berücksichtingung der paläarktischen und orientalischen Arten (Dipteren). *Arch. Naturg.*, **90**A(3): 172–234.

——— 1924 b. Die Drosophiliden (Dipteren) des Deutschen Entomologischen Institutes d. Kaiser Wilhelm Gesellschaft (früheres Deutsches Entomologisches Museum) aus H. SAUTER's Formosa Ausbeute. *Ibid.*, **90**A(3): 235–259.

HORN, H. S., 1978. Optimal tactics of reproduction and life-history. *In* KREBS and DAVIES, *Behavioural Ecology*: 411–429. Blackwell Scientific Publications, Oxford.

ISHII, S., 1975. Seibutsu-Tôkeigaku-Nyûmon. (Introduction to Statistics in Biology.) 288 pp. Baifukan, Tokyo. (In Japanese.)

KAMBYSELLIS, M. P., & W. B. HEED, 1971. Studies of oogenesis in natural populations of Drosophilidae. I. Relation of ovarian development and ecological habitats of the Hawaiian species. *Am. Nat.*, **105**: 31–49.

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

——— 1980. Synhospitalic evolution of the genus *Drosophilella* DUDA (Diptera, Drosophilidae) with description of a new species from Okinawa and Taiwan. *Ibid.*, **48**: 218–225.

PARRY, G. D., 1981. The meanings of r- and K-selection. *Oecologia*, **48**: 260–264.

PIANKA, E. R., 1970. On r- and K-selection. *Am. Nat.*, **104**: 592–597.

——— 1972. r and K selection or b and d selection? *Ibid.*, **106**: 581–588.

SOUTHWOOD, T. R. E., 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.*, **46**: 337–365.

STEARNS, S. C., 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.*, **51**: 3–47.

——— 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.*, **8**: 145–171.

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