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Synhospitalic Evolution of the Genus *Drosophilella* DUDA (Diptera, Drosophilidae), with Description of a New Species from Okinawa and Taiwan

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Synopsis The process of synhospitalic evolution of *Drosophilella* species in the Oriental Region including New Guinea is presumed on the basis of a taximetrical analysis of morphological and ethological characters of these species as well as of geological evidence. The "center of origin" principle is found preferable to the "vicariance" principle in understanding the process. *D. xenalocasiae* sp. n. is described from Okinawa and Taiwan for the species formerly misidentified as *D. colocasiae* DUDA.

1. Description of a New Species

Through the courtesy of Drs. Th. van LEEUWEN and B. BRUGGE of the Zoological Museum, University of Amsterdam, I have been able to borrow for study a lectotype female (designated by WHEELER 1969) of *Drosophilella colocasiae* DUDA from Java. The species from Okinawa and Taiwan formerly assorted to this species by me (OKADA, 1975) was consequently found to be a different species, which is to be described here as a new species.

Drosophilella xenalocasiae sp. n.

(Fig. 1)

Drosophilella colocasiae: OKADA, 1975. Kontyû, Tokyo, **43**: 356 (nec DUDA, 1924. Arch. Naturg., **90A** (3): 178, 226)

♂ and ♀. Body about 1.5 mm in length. Eye black, with thick pile. Ocellars inserted outside ocellar triangle. Antenna yellowish brown, 3rd joint black, 2nd broader than 3rd. Arista merely pubescent, slightly longer than antenna. Mouthparts yellow. Palpus yellow. Periorbit brownish black, broad and long. Ocellar triangle brownish black, 1/3 as long as frons. Frons mat black, anteriorly broader than median length. Face yellow. Carina strong, not reaching buccal margin. Cheek very broad, pale yellowish grey. Orbitals at anterior half of frons; proclinate slightly shorter than posterior reclinate; anterior reclinate fine but distinct, outside and somewhat behind proclinate. Second oral fine.

Mesoscutum brownish black; scutellum short, glossy brownish black. Thoracic pleura brownish black, glossy above. Humerals 2. Acrostichal hairs in 4 rows. Apical scutellars convergent, slightly nearer to each other than to laterals.

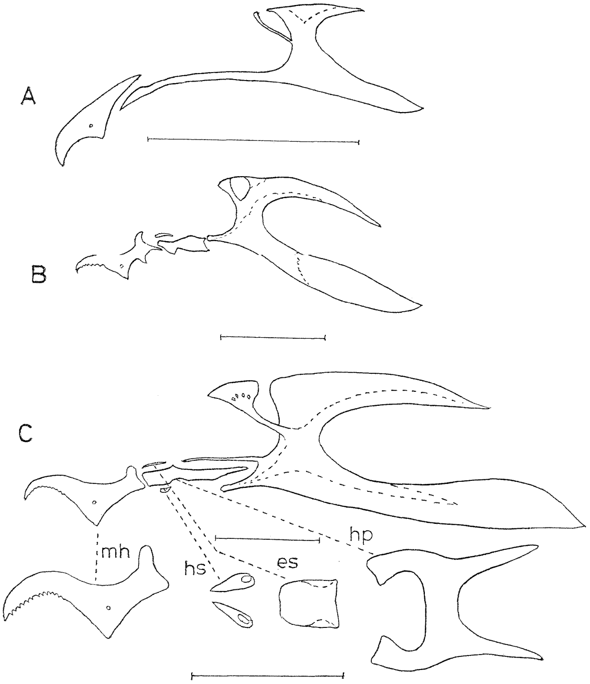

Fig. 1. Cephalopharyngeal skeletons of 1st (A), 2nd (B) and 3rd (C) instar larvae of *Drosophilella xenalocasiae*. es, epistomal sclerite; hs, hypostomal sclerite; hp, hypopharyngeal sclerite; mh, mouth hook. Scale: 0.1 mm.

Sterno-index 0.8. Legs yellow, femora darkened. Fore leg with metatarsus at basal 2/3 swollen and black; 2nd tarsal joint ventroapically elongate, ending in 4 stout black bristles. Wing hyaline, veins yellow. C reaching M. R_{4+5} and M slightly convergent. R_{2+3} nearly straight. C-index 2.0; 4V-index 2.0; 5x-index 1.5; Ac-index 2.5; C1-bristles 2; C3-fringe 2/5. Haltere yellow. Abdominal tergites glossy brownish black; 6th sternite with bifurcate outgrowth.

Periphallic organs black. Hypandrium: ventrocaudal corner triangular, with small surstylus. Cercus broad but short. Phallic organs black; aedeagus elongate; ventral fragma narrow; vertical rod strong. Ovipositor blade-like, parallel-sided. Epiproct and hypoproct of female triangular. Mouth hook (mh, Fig. 1) without ventral teeth in 1st instar larva, with about 6 teeth in 2nd, and about 13 in 3rd; hypostomal (hs), epistomal (es), and hypopharyngeal (hp) sclerites as usual in the family Drosophilidae. Other features including internal organs and puparium are as described in the previous paper (OKADA, 1975) under the name *colocasiae*.

Holotype ♂, allotype ♀, and 9 ♂, 2 ♀ paratypes, Yonehara, Ishigaki Is., Okinawa, 14 VI 1973, collected ex flowers of *Alocasia* by N. WATANABE. Other specimens examined: many ♂ and ♀, Shuri, Okinawa, 11 I 1975 (M. YAFUSO); many ♂ and ♀, Wulai, Taiwan, 2 VIII 1974 (N. WATANABE): all ex flowers of the same plant. Holotype (No. 11348. 1) is deposited at the National Science Museum, Tokyo.

Relationships. Closely related to *D. pistilicola* CARSON and OKADA from Papua New Guinea, having in common a bifurcated outgrowth of 6th abdominal sternite, distally not narrowing blade-like ovipositor, long divergent posterior spiracles of larvae and puparium, and as reported by YAFUSO (1979, read at the Joint Ann. Meet. Ent. Soc. Jap. and Jap. Soc. appl. Ent. Zool., Fukuoka), larval breeding site radically confined to the pistillate flower area of the host plant, the staminate flower area being occupied by the larvae of *D. alocasiae* OKADA.

2. Synhospitalic Evolution of *Drosophilella* Species

"Synhospitalic pertains to two or more related parasitic species occurring together on the same host species, even the same host individual, regardless of whether their microhabitat (*e. g.*, plumage region) may be different" (EICHLER, 1966). Although this term was originally used by EICHLER for speciation in parasitic animals

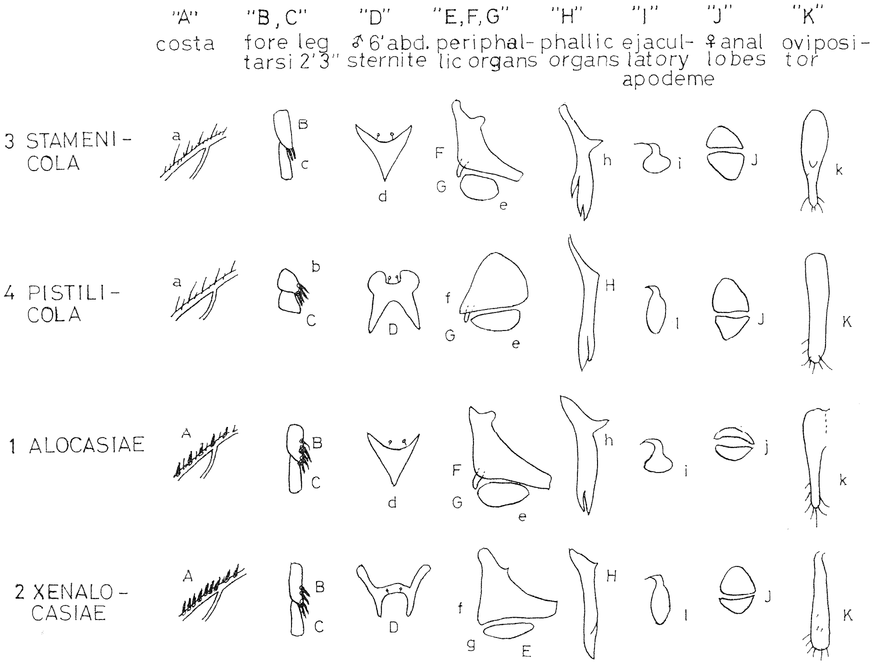

Fig. 2. Comparison of 4 species of *Drosophilella* (1–4) with diagnostic characters of external structures ("A"–"D") and of genital armatures ("E"–"K"). Capital letters attached to figures, plesiomorphs; small letters, apomorphs.

such as Mallophaga and Anoplura, it can be applied to plant-living species and not only for speciation but also for distribution, as exemplified here by *Drosophilella* species.

The first evolutionary step of synhospitalism should be the establishment of a synhospitalic couple from one or more ancestral species. This event, however, is not considered here. The further differentiation in time and disperasl in space of the synhospitalic species will be treated and discussed in this report.

Drosophilella pistilicola and *D. stamenicola* breed microallopatrically (or synhospitalically in the sense presently defined) on the same spadix of *Colocasia esculenta* in Papua New Guinea (Carson and Okada, 1980). Similarly, *D. xenalocasiae* and *D. alocasiae* share the same spadix of *Alocasia odora* in Taiwan and Okinawa (Okada, 1975; Yafuso, *op. cit.*). The "phyletic" relationships among these four *Drosophilella* species are analysed taximetrically, using 20 diagnostic characters ("A"—"T") as listed below. They concern external structures (4 characters), genital armatures (7), internal structures (4), early stages (3), and ethological features (2), each divided into two states, coded 0 and 1 according to presumed plesiomorphism and presumed apomorphism, respectively (Table 1, Figs. 2, 3).

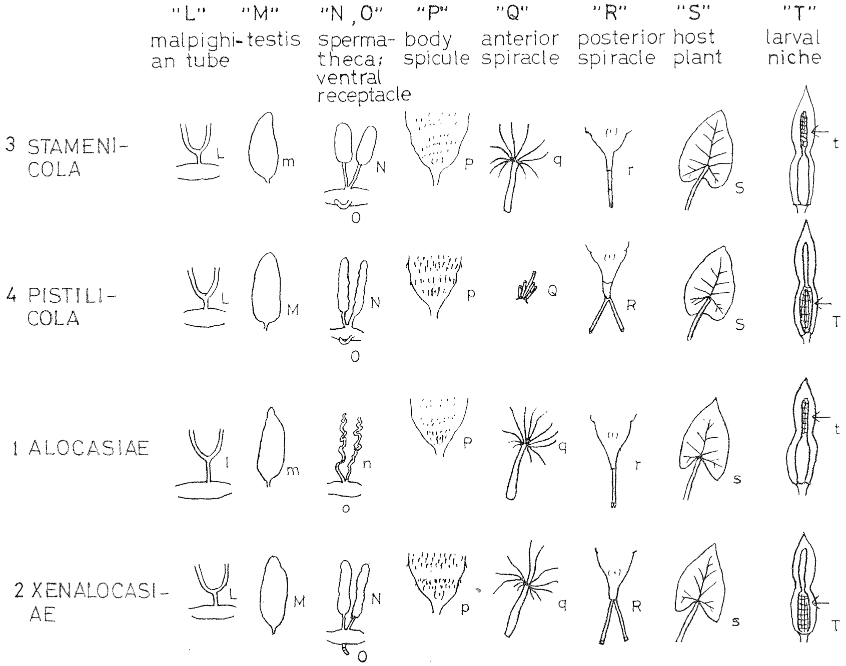

Fig. 3. Comparison of 4 species of *Drosophilella* (1–4) with diagnostic characters of internal structures ("L"–"O"), early stages ("P"–"R"), and of ethological features ("S"–"T"). Other signs as in Fig. 2.

External structures

"A" Costal bristles strong at least partially (A=0), or fine (a=1).
"B" Tarsal joints of fore legs elongate (B=0), or compressed (b=1).
"C" Stout teeth of 2nd tarsal joint of fore legs four or more (C=0), or two (c=1).
"D" Sternal process of male abdomen bifurcate (D=0), or conical (d=1).

Genital armatures

"E" Male cercus oblong (E=0), or oval (e=1).
"F" Caudoventral corner of epandrium rectangular (F=0), or acute-angular (f=1).
"G" Surstylus present (G=0), or absent (g=1).
"H" Basal process of aedeagus absent (H=0), or present (h=1).
"I" Ejaculatory apodeme longer than broad (I=0), or broader than long (i=1).
"J" Female anal lobe triangular (J=0), or crescent (j=1).
"K" Ovipositor broad, blade-like (K=0), or narrow especially distally (k=1).

Internal structures

"L" Common Malpighian tubes short (L=0), or relatively long (l=1).
"M" Testis oval (M=0), or rather conical (m=1).
"N" Spermatheca oblong (N=0), or coiled (n=1).

Table 1. Character (n) × Species (t) matrix. AL, *Drosophilella alocasiae*; X, *D. xenalocasiae*; ST, *D. stamenicola*; PI, *D. pistilicola*; CO, *D. colocasiae*. 0, plesiomorph; 1, apomorph.

Characters (n)	Species (t)				
	1 AL	2 X	3 ST	4 PI	5 CO
"A"	0	0	1	1	1
"B"	0	0	0	1	0
"C"	0	0	1	0	0
"D"	1	0	1	0	NC
"E"	1	0	1	1	NC
"F"	0	1	0	1	NC
"G"	0	1	0	0	NC
"H"	1	0	1	0	NC
"I"	1	0	1	0	NC
"J"	1	0	0	0	NC
"K"	1	0	1	0	NC
"L"	1	0	0	0	NC
"M"	1	0	1	0	NC
"N"	1	0	0	0	NC
"O"	1	0	0	0	NC
"P"	0	1	0	1	NC
"Q"	1	1	1	0	NC
"R"	1	0	1	0	NC
"S"	1	1	0	0	0
"T"	1	0	1	0	NC

"O" Ventral receptacle present (O=0), or absent (o=1).

Early stages

"P" Larval body spicules weak (P=0), or strong (p=1).
"Q" Anterior spiracles of puparia short and sessile (Q=0), or long (q=1).
"R" Posterior spiracles of puparia long and divergent (R=0), or very short and with long common stalk (r=1).

Ethological features

"S" Host plant *Colocasia* (S=0), or *Alocasia* (s=1).
"T" Larval niche pistillate flowers (T=0), or mainly staminate flowers (t=1).

From the character (n)×taxon (t) table (Table 1), a t×t matrix is produced by means of proximity analysis using S_0 (similarity coefficient of OKADA, 1970).

$$S_0=\frac{2n_{JK}+n_{jk}}{n}=\frac{n_{JK}+n_{jk}}{n}+\frac{n_{JK}}{n}=S_{SM}+S_{RR}$$

where, n is number of characters, n_{jk} is number of symplesiomorphs (0 in both taxa in comparison), and n_{JK} is number of synapomorphs (1 in both taxa in comparison). Synapomorph is weighted twice the symplesiomorph, in accordance with the syn-

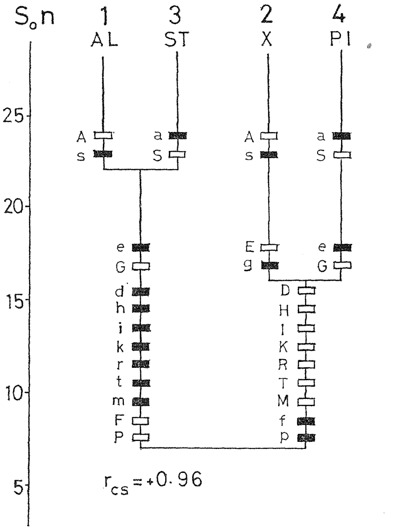

Fig. 4.

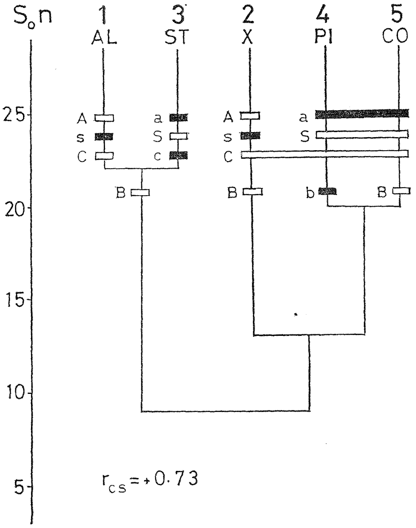

Fig. 5.

Fig. 4. A cladogram to show the relationships among 4 species of *Drosophilella*. Plesiomorphs (open bars) and apomorphs (solid bars) are selected from original n×t matrix (Table 1). r_{cs}, cophenetic correlation coefficient between original and derived n×t matrices.

Fig. 5. A cladogram to show the relationships among 5 species of *Drosophilella*. Signs as in Fig. 4.

apomorphy theory of HENNIG (1953). In another aspect, S_0 is a compromise of S_{SM} (simple matching coefficient of SOKAL and MICHENER) and S_{RR} (Similarity coefficient of RUSSEL and RAO) (SOKAL and SNEATH, 1963). From this $t \times t$ matrix a "cladogram" (because the plesiomorph and apomorph are presumed) is established by means of usual cluster analysis of UPGMA.

The resulting cladogram (Fig. 4) shows that *alocasiae* and *stamenicola* are most closely related, having in common 7 synapomorphic and 2 symplesiomorphic character states (d, h, i, k, m, r, t and F, P, respectively), by which they can be distinguished from the two other closely related species, *xenalocasiae* and *pistilicola*. The latter two species have in common 7 symplesiomorphic and 2 synapomorphic character states (D, H, I, K, M, R, T and f, p, respectively). It should be noticed that *alocasiae*, a member of the Oriental synhospitalic couple, is closely related to *stamenicola*, a member of Papuan synhospitalic couple. Likewise, *xenalocasiae*, the other member of the Oriental couple, is very close to *pistilicola*, the other member of the Papuan couple. These comparisons are clear both morphologically and ethologically. The two members of the Oriental and Papuan couples can be distinguished from each other by only 2 characters ("A" and "S").

Only 4 characters ("A", "B", "C", and "S") out of 20 under consideration have been determined from *colocasiae* from Java. If, however, this species is combined with the 4 species, a cladogram (Fig. 5) may be constructed which shows that *colocasiae* is closest to *pistilicola*. It may be plausibly predicted that another species will be found in Java which is synhospitalic with *colocasiae* and closely related to *stamenicola* (discussed also in OKADA, in preparation).

The following evolutionary scheme is suggested. It may be supposed that a

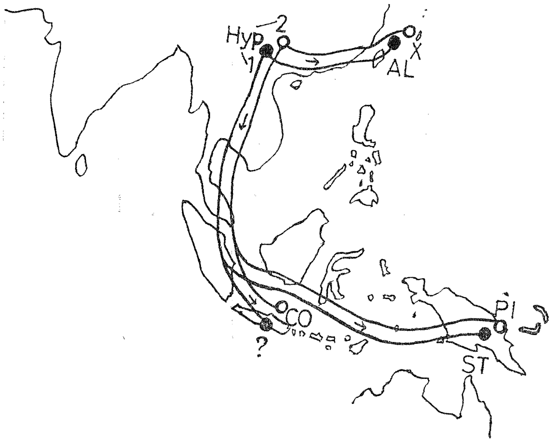

Fig. 6. Presumed processes of synhospitalic evolution and dispersal of *Drosophilella* species. AL, *alocasiae*; CO, *colocasiae*; $Hyp_{1,2}$, hypothetical species; PI, *pistilicola*; ST, *stamenicola*; X, *xenalocasiae*; ?, unknown species.

couple of ancestral species of *Drosophilella* had established synhospitalism on a certain plant of Araceae in a certain area of the Oriental Region, probably the southern part of Angaraland. Tightly keeping synhospitalism, they then evolved into *alocasiae* and *xenalocasiae* and dispersed in the direction of Taiwan and Okinawa on the one hand and into *colocasiae* and an unknown species in Java as well as into *stamenicola* and *pistilicola* in New Guinea in the other more easterly direction (Fig. 6). The process of synhospitalic evolution and dispersal of *Drosophilella* should have retained an intimate association with the evolution and dispersal of the host plants. Furthermore, the process might be well correlated with land elevation in the southern islands through eustatic movement of the sea level during the early Neogene.

Establishment of the present status of the distribution of these species was probably not much concerned with vicariance of primarily widely distributed ancestral species as stressed by CROIZAT, NELSON and ROSEN (1974). Rather this case appears to have been a more simple dispersal from a certain center of origin towards geologically newer lands.

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Hardy 許 Lin Gupta Krishnamurthy Ray-Chaudhuri Bock Harrison
Gressitt Montgomery Kaneshiro Hecd Hershkovitz Colfmade Pipkin Spieth
Steffan Steyskal Townsend Throckmorton Wirth Hoeningsberg Brncic
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Papp Laštovka Maca Lakovaara Hackman Bächli Rito
Prevosti Lemeunier Leeuwen (オランダ) 高田. 木村 戸田 別府 尾高祖
Sabrosky 金子. 中嶋 中村紀. 岩崎 小野鈴. 若林 黒川 倉橋
大羽. 北川 戸張. 森山 森脇. 酒井 長谷川仁 林孝美 高富. 黒佐2. 上野俊 加納
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