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Drosophilidae Associated with Flowers in Papua New Guinea

I. *Colocasia esculenta*

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Synopsis Inflorescences of the plant species serve as a breeding site for two very similar new species of *Drosophilella*, which are described in this paper. During a brief coexistence within the young inflorescence, females of both species oviposit and then depart. Although *stamenicola* oviposits among both staminate and pistillate flowers, *pistilicola* oviposits exclusively among the pistillate flowers at the base of the inflorescence. By the time the staminate portion has deliquesced and dropped off, it contains exclusively *stamenicola* larvae and puparia; conversely, pistillate sections remain on the plant as the berries are formed; they yield only *pistilicola* adults. Thus the strict subdivision of the floral niche is seen between the two species. *Styloptera repletoides* sp. n. oviposits on the inflorescences only after the decay processes are well advanced.

Introduction

Over the last forty years, flies of the family Drosophilidae have received ever increasing attention because of their usefulness in the study of genetics and evolution. As a result, the fauna of most of the world is now reasonably well known. A conspicuous exception is the great tropical island of New Guinea. Although a few species have served as objects of special population studies, neither basic systematic nor ecological surveys of the fauna of this region have been made.

In an attempt to rectify this deficiency, we made intensive collections of Drosophilidae in the Morobe District, Papua New Guinea, between July and December 1977. Starting at the summit of Mt. Kaindi (2,200 m) we sampled populations from the different altitudinal ecosystems, extending to sea level near the city of Lae. Specimens were obtained in a variety of ways. Fruit and mushroom baits were used as well as general sweeping and collecting at night near lights. Of particular interest, however, is the discovery of a diverse fauna specifically associated with fresh or wilted flowers, from which the insects may be aspirated directly.

Many of these flower species complete their life cycles on the inflorescences of specific plants. In this paper we describe three new species and give an account of their ecology and development within the inflorescences of the common taro, *Colocasia esculenta*.

Material and Methods

Colocasia esculenta (L.) SCHOTT is grown abundantly for food in many parts on the tropical world. Although it is a characteristic food plant of Pacific Polynesia, where it is known as taro, it is widely grown in India, Southeast Asia, the Philippines and New Guinea as well. YEN and WHEELER (1968) shows that two chromosomal types of this plant (2n=28, 2n=42) are very widespread in the western Pacific and India. Like others before them, they consider the plant to be of Indo-Malaysian origin.

In the Morobe District of Papua New Guinea the plant was found growing in gardens, and, sparsely, along roadsides, from an altitude of about 1,515m on Mt. Kaindi to near sea level south of Lae in marshes near the Markham River. When inflorescences were discovered, specimens of associated Drosophilidae were aspirated from them directly. Inflorescences were collected in plastic bags and returned to the laboratory where searches of the staminate and pistillate flowers for young stages of Drosophilidae were carried out. In order to study later development, pupation and emergence, the inflorescences were placed in vials of water under a glass cylinder or on top of sterile damp sand in a clean container with a mesh cover. Emerging flies were aspirated and identified. Development of individual inflorescences and their fauna in the field were studied during repeated visits to the same area, using bags of fine nylon mesh to exclude flies at certain stages.

Holotypes and allotypes of the 3 new species are deposited at the Bernice P. Bishop Museum, Honolulu.

Descriptions of New Species

1. *Drosophilella stamenicola* sp. n.

(Fig. 1)

♂, ♀. Body about 1.5 mm in length. Eye purplish black, almost bare. Antenna greyish brown, 3rd joint paler. Arista as long as antenna, merely finely pubescent. Palpus greyish brown, with a stout apical seta. Ocellar triangle and periorbit subshining greyish black. Frons mat brownish black, anteriorly yellowish brown and 1.5 times as broad as median length. Cheek grey, half as broad as the greatest diameter of eye. Face grey, broadened below. Carina large and long, yellowish brown. Clypeus mat brown. Anterior reclinate orbital minute, nearer to proclinate than to posterior reclinate, which is as long as proclinate. Vibrissa strong, other orals fine.

Mesoscutum mat brownish black, scutellum paler. Thoracic pleura dark brown. Humerals 2, lower shorter. Acrostichal hairs in 4 rows. Anterior dorsocentrals 2/3 as long as posteriors, slightly nearer to posteriors than to each other. Sternoindex 0.5. Anterior scutellars parallel, 2/3 as long as posteriors. Legs (Fig. 1: B, C) brown; 2nd tarsal joint of fore leg in both sexes prolonged apically below, ending

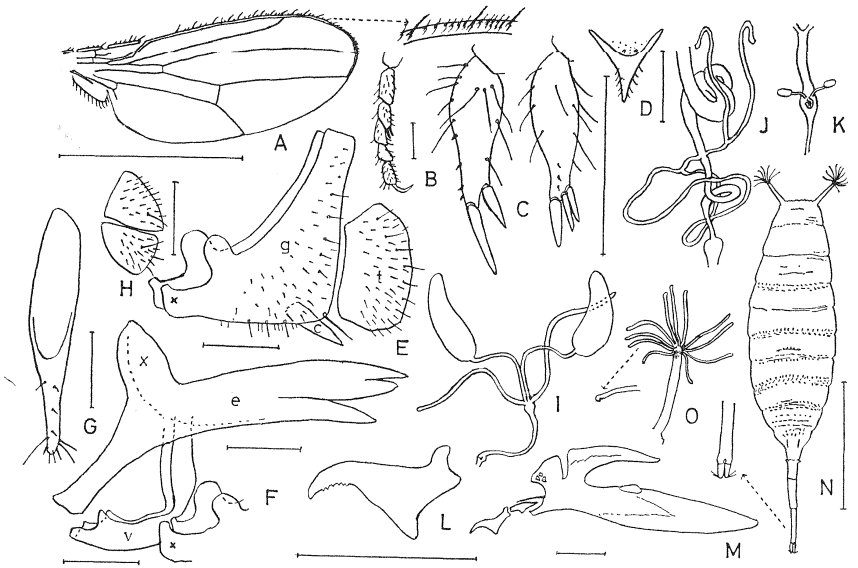

Fig. 1. *Drosophilella stamenicola* sp. n. A: Wing; B: fore tarsi; C: ibid., 2nd joint; D: process of male 6th abdominal sternite; E: periphallic organs; F: phallic organs; G: ovipositor; H: female epiproct and hypoproct; I: male internal reproductive organs; J: digestive system; K: female internal reproductive organs; L: mouth hook of 3rd instar larva; M: cephalopharyngeal skeleton of 3rd instar larva; N: puparium; O: anterior spiracle of puparium; c, surstylus; e, aedeagus; g, epandrium; t, cercus; v, ventral fragma; x, subbasal conical process of aedeagus. Scale 1 mm in A and M; 0.1 mm in other figures.

in 2 stout black teeth. Tarsal joints thick and short, fore metatarsus shorter than succeeding 2 tarsal joints; mid and hind metatarsi as long as or longer than succeeding 3 tarsal joints. Wing (Fig. 1: A) hyaline; C reaching M; R_{2+3} weakly curved to C at apex. C-index 1.8; 4V-index 2.0; 4C-index 1.0; 5x-index 1.4; Ac-index 3.0. C1-bristles 1; C3-fringe sparse, 2/5. Haltere brown, apically dark. Abdominal tergites mat brownish black, grey pruinose. Male 6th sternite with a caudally pointed rod-like process (Fig. 1: D).

Periphallic organs (Fig. 1: E) black. Epandrium triangular in lateral aspect, with ventrocaudal corner rectangular. Surstylus vestigial. Cercus quadrate. Phallic organs (Fig. 1: F): aedeagus black, elongate, apically trilobed in lateral aspect, and subbasally with a large conical process. Ventral fragma as long as vertical rod. Ovipositor (Fig. 1: G) yellowish brown, elongate, distally pointed, with a few long setae. Female epiproct and hypoproct triangular (Fig. 1: H). Mid-intestine twice coiled. Malpighian tubules with common stalks short, posterior branches completely fused at apices (Fig. 1: J). Testis (Fig. 1: I) orange brown, elongate oval. Paragonia slender. Spermatheca (Fig. 1: K) hyaline, elliptical. Parovaria absent.

Ventral receptacle small, with a small fold.

Mouth hook of the 3rd instar larva (Fig. 1: L, M) ventrally dentate. Puparium (Fig. 1: N, O): anterior spiracle with about 10 long branches in a whorl; stalk longer than branches. Caudal abdominal segments much elongate, ending in paired short posterior spiracles.

Type-series: Bulolo, ♂ holotype (No. 90604.1), ♀ allotype (No. 90604.2), 5 ♂ paratypes, 6 XI 1977; Lae, 7 ♂, 7 ♀ paratypes, 30 VIII 1977; Garagos River, 1 ♂, 4 ♀ paratypes, 28 IX 1977. All collected by CARSON and OKADA ex flowers of *Colocasia esculenta*.

Relationships. Resembles *D. alocasiae* OKADA in having the rod-like ventral process of male 6th abdominal sternite, subbasal conical process of aedeagus, distally much narrowing ovipositor, and much elongate caudal segments of puparium with short spiracle. It differs from *alocasiae*, however, in having only 2 stout teeth on the 2nd tarsal joint of fore leg (4 in *alocasiae*), and female epiproct and hypoproct triangular (crescent in *alocasiae*).

2. ***Drosophilella pistilicola*** sp. n.

(Fig. 2)

♂, ♀. Body about 1.5 mm in length. Eye purplish black, finely pubescent. Antenna dark brown, grey pruinose. Arista nearly bare, straight, slightly longer than antenna. Palpus slender, black, with a long apical seta. Ocellar triangle and periorbits subshining black. Cheek mat black, broad, 1/3 as broad as the greatest diameter of eye. Clypeus mat black. Face grey; carina long, grey. Anterior reclinate orbital minute, nearer to proclinate than to posterior reclinate, which is nearly as long as proclinate. Vibrissa long; 2nd oral 1/4 as long as vibrissa.

Thorax mat black, pteropleura yellowish brown. Humerals 3, median one longest. Acrostichal hairs in 2 or 4 rows. Anterior dorsocentrals half as long as posteriors; cross distance of dorsocentrals slightly longer than or subequal to the length distance. Anterior scutellars convergent, slightly shorter than posteriors. Legs black; 2nd tarsal joint of fore leg in both sexes (Fig. 2: B) elongate apically below, ending in 4 stout black teeth; 3rd and 4th tarsal joints much broader than long. Wing (Fig. 2: A) hyaline, C reaching M. Costal fringe sparse, weak. C-index 1.8; 4V-index 1.8; 4C-index 1.1; 5x-index 1.3; Ac-index 2.8. C1-bristles 1; C-3 fringe 3/5. Haltere black. Abdominal tergites mat black; 1st tergite velvety black; 6th sternite with a large black distally bifurcated process (Fig. 2: C).

Periphallic organs (Fig. 2: D): epandrium caudoventrally pointed. Surstylus vestigial. Cercus large fusiform in lateral aspect. Phallic organs (Fig. 2: E): aedeagus elongate, apically bilobed in lateral aspect, subbasally without conical process. Penis envelope paired, slender. Ovipositor (Fig. 2: F) oblong, distally not markedly narrowing. Epiproct and hypoproct of female (Fig. 2: G) triangular. Malpighian tubules (Fig. 2: I) with common stalks comparatively long; posterior branches completely fused at apices. Testis (Fig. 2: H) elongate oval; paragonia slender. Spermatheca (Fig. 2: J) oblong; ventral receptacle small, once folded.

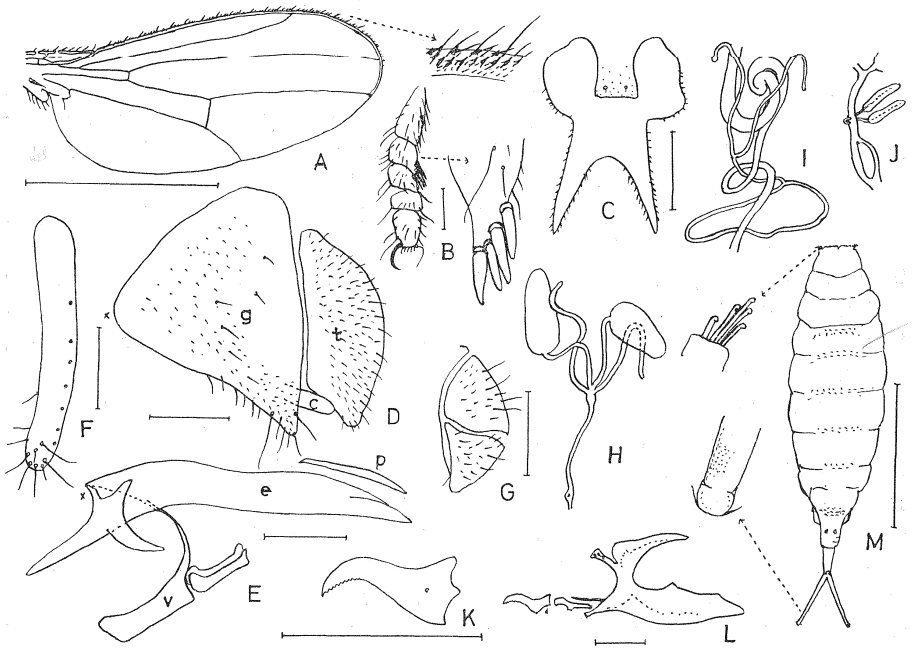

Fig. 2. *Drosophilella pistilicola* sp. n. A: Wing; B: fore tarsi; C: process of male 6th abdominal sternite; D: periphallic organs; E: phallic organs; F: ovipositor; G: female epiproct and hypoproct; H: male internal reproductive organs; I: digestive system; J: female internal reproductive organs; K: mouth hook of 3rd instar larva; L: cephalopharyngeal skeleton of 3rd instar larva; M: puparium; p, penis envelope; other signs and scale as in Fig. 1.

Mouth hook of the 3rd instar larva (Fig. 2: K, L) with fine dentation ventrally. Anterior spiracle of puparium (Fig. 2: M) with about 5 short branches; posterior spiracles with long divergent stalks.

Type-series: Bulolo, ♂ holotype (No. 90603.1), ♀ allotype (No. 90603.2), 3 ♀ paratypes, 6 IX 1977; Garagos River, 1 ♂, 4 ♀ paratypes, 28 IX 1977; Lae, 2 ♂, 4 ♀ paratypes, 30 VIII 1977. All collected by CARSON and OKADA from the flowers of *Colocasia esculenta* together with the foregoing species.

Relationships. Resembles *D. colocasiae* DUDA from Okinawa Is. in having 4 stout teeth on the 2nd tarsal joint of fore leg, bifurcate process of the 6th abdominal sternite, broad and almost parallel-sided ovipositor, oblong spermatheca and triangular epiproct and hypoproct of female, smooth subbasal part of aedeagus, and long divergent stalks of puparial posterior spiracles. It differs from *colocasiae* in having the costal fringe sparse, process of the 6th abdominal sternite H-shaped (V-shaped in *colocasiae*), and branches of the anterior spiracles of puparium short.

3. *Styloptera repletoides* sp. n.

(Fig. 3)

♂, ♀. Body about 1.5 mm in length. Head somewhat broader than thorax. Eye dark red, with thick pile. Antenna with 2nd joint yellow, anteriorly black; 3rd black. Arista with 4 upper and 2 lower long branches and a small fork. Palpus black, with a long apical seta. Cheek 1/3 as broad as the greatest diameter of eye. Ocellar triangle black; ocellars inserted outside ocellar triangle. Periorbit greyish white, black at anterior end. Frons white, with 2 broad anteriorly convergent black longitudinal stripes, and anteriorly as broad as median length. Face greyish white; carina well developed. Clypeus black, laterally pale. Anterior reclinate orbital before proclinate, half as long as proclinate, which is shorter than posterior reclinate. Vibrissa strong, other orals fine.

Mesoscutum greyish white, with 6 irregularly demarcated black longitudinal stripes. Scutellum grey, with X-shaped black patch, and with black spots at insertion of scutellars. Thoracic pleura grey, with 3 irregular longitudinal black stripes. Humerals 2, lower longer. Acrostichal hairs in 2 rows. Dorsocentrals in 3 pairs, equal in length. Sterno-index 0.6. Anterior scutellars parallel, slightly longer than posteriors, which are somewhat nearer to each other than to anteriors. Legs yellow, with black annuli: 2 on femora, 2 on tibiae. Fore and mid metatarsi as long as succeeding 2 tarsal joints; hind metatarsus longer than succeeding 2. Wing hyaline; 1st costal section apically much swollen and black; a black patch present below R_1; R_{2+3} curved to C apically; R_{4+5} and M slightly divergent distally. C-index 1.2; 4V-index 2.0; 4C-index 2.2; 5x-index 3.0; Ac-index 3.0. C1-bristles 2, very long; C3-fringe 1/2. Haltere yellowish grey, dark at tip. Abdominal tergites yellowish grey, with caudal black bands laterally protruded and medially interrupted.

Periphallic organs (Fig. 3: A) black. Epandrium much narrowing above, broadly truncate below. Surstylus broad but short, with a row of about 10 stout black pointed teeth. Cercus pointed caudoventrally. Phallic organs (Fig. 3: B) pale brown. Aedeagus rod-like, apically pointed and black; apodeme black and

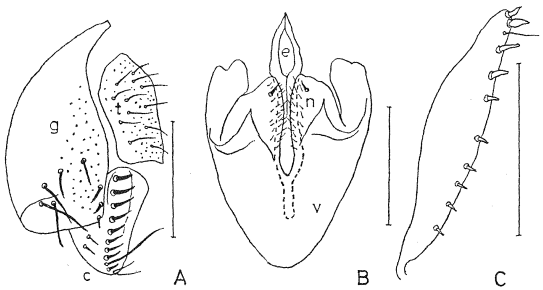

Fig. 3. *Styloptera repletoides* sp. n. A: Periphallic organs; B: phallic organs; C: ovipositor; n, hypandrium; other signs as in Fig. 1. Scale 0.1 mm.

very short. Paramere seemingly absent. Hypandrium triangular, densely pubescent; submedian spines very short. Ovipositor (Fig. 3: C) pale yellow, elongate, pointed, with about 10 stout teeth on ventral margin.

Type-series: Bulolo, ♂ holotype (No. C218.4.1), ♀ allotype (No. C218.4.2), 1 ♂, 1 ♀ paratypes, 11–18 IX 1977; Garagos River, 1 ex paratype, 29 IX 1977. All reared by CARSON ex flowers of *Colocasia esculenta*.

Relationships. Resembling *S. formosae* DUDA in having the striped mesonotum and striped thoracic pleura, but distinguished from it by the annulated legs and X-shaped patch on the scutellum (parallel patches in *formosae*).

4. *Dettopsomyia formosa* LAMB

Dettopsomyia formosa LAMB, 1914, Trans. Linn. Soc. Lond., (2) (Zool.), **16**: 350.

Specimen examined: Garagos River, 1 ex, reared by CARSON ex flowers of *Colocasia esculenta* along with the foregoing species.

Distribution. New Guinea (new record), Philippines, Micronesia, Solomon Is., Samoa, Hawaii, Seychelles, C. America.

Ecological Observation

These observations were carried out at five sites in the Morobe District between August and December, 1977 (Table 1). All locations were along the Lae–Bulolo–Wau–Edie Creek Road. At the two highest altitudes, the plants were growing in native gardens; the others were along roadsides in ditches or in one instance (Bulolo) within an *Araucaria* plantation.

a. *Adult flies*

The inflorescence of *Colocasia* emerges from the base of the plant as a vertical spike. Before the flower opens, the spathe is in a spiral configuration and is tightly

Table 1. Collections of drosophilids from *Colocasia esculenta*, Morobe District, Papua New Guinea.

Site	Altitude (m)	Number of specimens captured (C) and reared (R) from inflorescences
Markham River 1 km S. of bridge	60	*Drosophilella stamenicola* C–7; R–45 *Drosophilella pistilicola* C–8; R–4
Garagos River 49 km S. of Lae	150	*Drosophilella stamenicola* C–329; R–71 *Drosophilella pistilicola* C–320; R–97 *Styloptera repletoides* R–5 *Dettopsomyia formosa* R–1
Bulolo Back Road	730	*Drosophilella stamenicola* C–441; R–45 *Drosophilella pistilicola* C–73; R–51 *Styloptera repletoides* C–1; R–11
Wau	1,200	*Drosophilella stamenicola* C–46 *Drosophilella pistilicola* C–15
Kunai Creek, Mt. Kaindi	1,515	*Drosophilella stamenicola* R–26

appressed to the developing spadix within. At a crucial moment, the spathe relaxes very slightly, opening a slight spiral crack along its length (Fig. 4, stage 1). Such inflorescences, although not visibly open, allow access for the very small adults of the two species of *Drosophilella* described here. Unless the inflorescence is forced open, it cannot be determined from external inspection whether flies are present within or not. These two species remain within the inflorescence for only a very short time, perhaps only for a single day, after which they completely evacuate the inflorescence and are not seen visiting it at later stages.

When such a "fly flower" is found, it is a simple matter to collect all specimens which are harbored within. This can be done with an aspirator; with slight agitation, the flies will start coming out from under the curl of the spathe. A second and perhaps better method is to imprison the entire inflorescence within a clear plastic bag and then aspirate all flies which have emerged into the bag.

A special study of the number of flies found within the inflorescence was made of seven individual specimens collected at the Garagos River site on November 4, 1977 (Table 2). The data overall display the fact that the two species occur in approximately equal in numbers within the inflorescence and that, although there is some irregularity, the overall sex ratio slightly favors the male sex in both species. The mean number of flies per inflorescence is 92.7; 50.7% of these are *D. stamenicola*. Counts from flowers collected at Bulolo and Wau indicate that *D. stamenicola* is the more frequent species at these higher altitudes.

b. *Egg counts*

Returning to a consideration of the Garagos River site, observations were extended to include counts of eggs deposited within the inflorescence by each of the species. A clear difference between the eggs of the two species was recognized; that of *D. pistilicola* has a small "cap" of soft secretory material which covers its apex (Fig. 5).

Counts of eggs of the two species within five selected stage 1 inflorecences are

Table 2. Counts of *Drosophilella* adults aspirated from seven inflorescences of *Colocasia esculenta*, Garagos River site.

Inflorescence No.	*Drosophilella stamenicola*				*Drosophilella pistilicola*			
	♀♀	♂♂	Total	Sex ratio*	♀♀	♂♂	Total	Sex ratio*
1	30	46	76	153.3	36	47	83	130.6
2	22	19	41	86.4	6	13	19	216.7
3	20	13	33	65.0	11	15	26	136.4
4	13	13	26	100.0	11	26	37	236.4
5	38	40	78	105.3	10	23	33	230.0
6	12	2	14	16.7	18	15	33	83.3
7	23	38	61	165.2	59	30	89	50.8
Total	158	171	329	108.2	151	169	320	111.9
Mean	22.6	24.4	47	—	21.6	24.1	45.7	—

* ♂♂ per 100 ♀♀

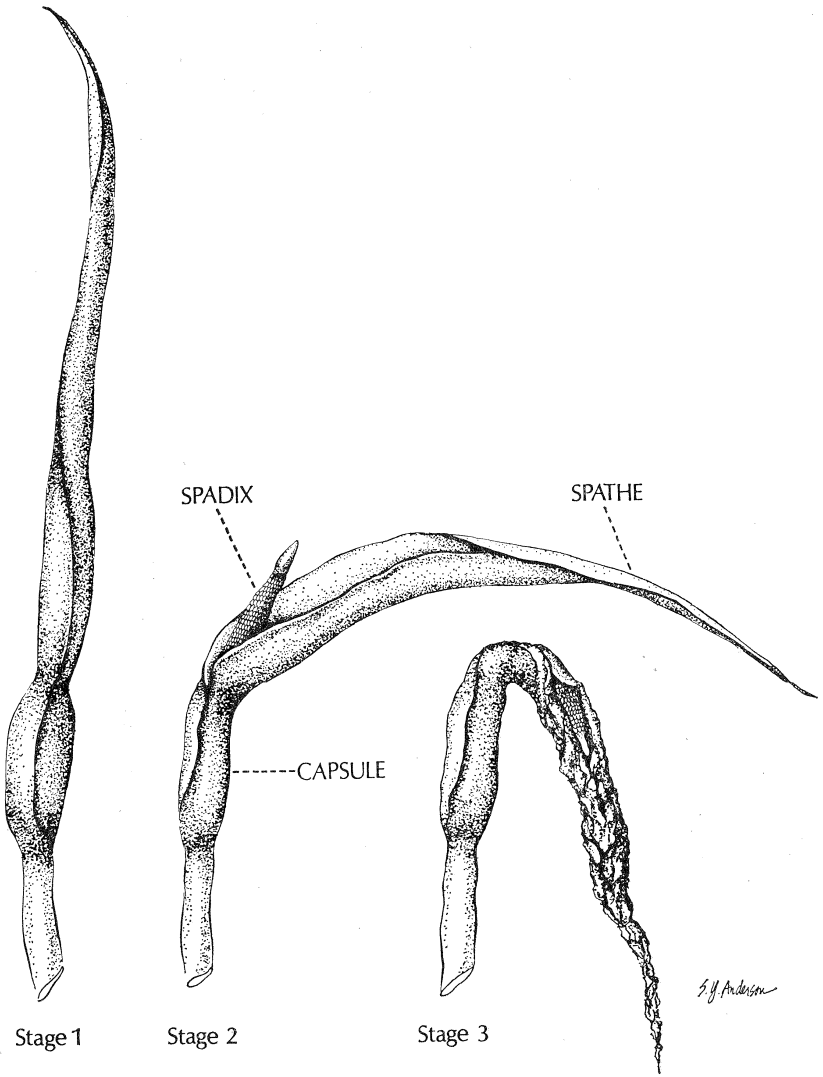

Fig. 4. Inflorescences of *Colocasia esculenta*. Stage 1 (day 0): "fly and egg" stage; Stage 2 (day 4 to 5): young larvae; Stage 3 (day 9 to 10): large larvae and puparia. In the latter, the staminate portion of the spadix and the spathe are decayed and shortly fall off, carrying along the puparia of *Drosophilella stamenicola*. Puparia of *D. pistilicola* form around the base of the berries within the fleshy green capsule and remain on the plant.

given in Table 3. These are the same inflorescences as are numbered 1 to 5 in Table 2 and from which adults were counted. These counts show that *D. pistilicola* lays fewer eggs per female than does *D. stamenicola*. The mean number of eggs per inflorescence, therefore, strongly favors *D. stamenicola* at the Garagos site (about 5 to 1). This is, of course, even more striking at higher altitudes (*e.g.*, Bulolo) where *D. pistilicola* is much less frequent in the adult population of the inflorescence.

c. *Position of eggs and small larvae within the inflorescence*

Oviposition by the female of both species is exclusively on the staminate (upper) and pistillate (lower) regions of the inflorescence. Figure 6 diagrams the spadix after the spathe has been removed. The first set of columns to the right of the diagram represent the frequency distribution of the eggs of the two species among the eight regions of approximately 10 mm each into which the spadix may be divided. Counts from twelve inflorescences from three sites are included. It may be seen in this figure that the eggs of *pistilicola* are laid only in the pistillate section whereas those of *stamenicola* are deposited both in the lower part of the staminate section and throughout the pistillate section.

Two slightly older inflorescences (stage 2, Fig. 4) were examined for the presence of small larvae. Even newly hatched larvae of *D. pistilicola* can be easily distinguished from *D. stamenicola* by the presence of a prominent bifurcation at the posterior end. The data show that at this later stage, the *stamenicola* larvae are distributed in the same manner as the deposition of the eggs. Although the majority of *pistilicola* larvae still occupy the pistillate section, some larvae have moved upward into the transitional region. A few have reached the staminate portion.

d. *Position of third instar larvae and puparia*

At 9 to 10 days after oviposition both the spathe and the staminate portion of the spadix deliquesce, often separating from the forming seed capsule at a point corresponding to the line between the transitional region and the first pistillate section (Fig. 4, stage 3; see also Fig. 6). Examination of the decayed staminate remnant at this time reveals many larvae working through it. Without exception these are *D. stamenicola*. All specimens of this species which were reared from the inflorescences of *C. esculenta* from all sites were reared specifically and only from this portion of the inflorescence (for details, see Table 1). The minimum time of egg to adult in the laboratory is about 18 days for this species.

Conversely, *D. pistilicola* adults emerge only from the pistillate seed capsules. This species apparently takes longer to develop; adults do not appear until approximately 30 days after oviposition. All of the *Styloptera repletoides* and *Dettopsomyia formosa* listed in Table 1 were reared from the pistillate "capsules" along with *D. pistilicola*. Many small parasitic wasps emerged from these same carpellate units. Eggs, larvae, pupae and adults of one or more species of moth flies (Psychodidae) were found at most sites. Their eggs are deposited on the surface of the individual pistillate flowers.

Examination of selected inflorescences maintained in the laboratory show that

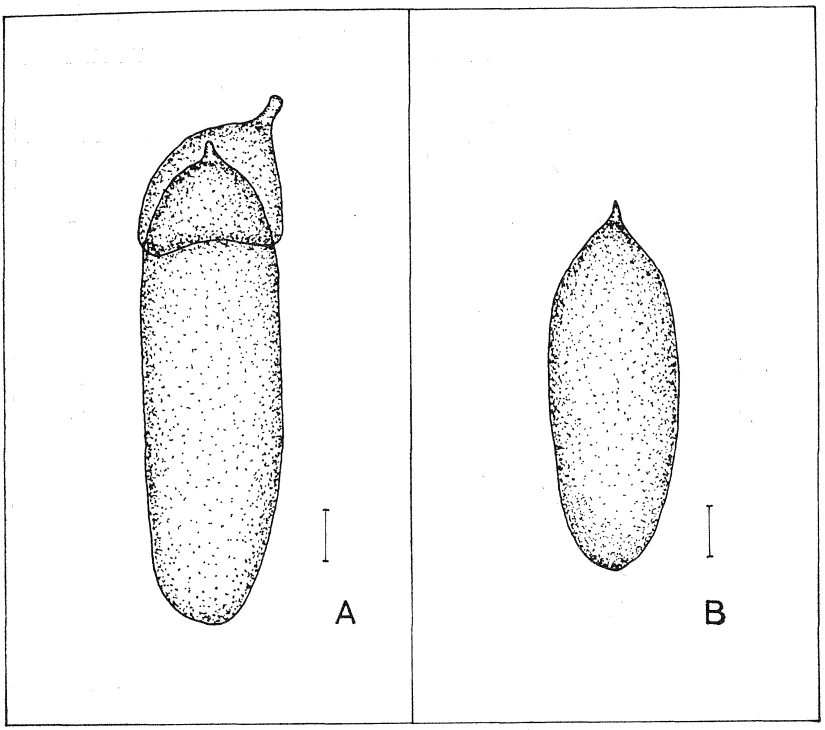

Fig. 5. Mature eggs of *Drosophilella*. A: *pistilicola*, showing the cap of secretory material at the anterior end; B: *stamenicola*. Scale 0.1 mm.

Table 3. Numbers of adult female *Drosophilella* of two species related to the number of eggs deposited in inflorescences of *Colocasia esculenta*, Garagos River, Papua New Guinea, November 4, 1977.

Inflorescence No.	*D. stamenicola*			*D. pistilicola*		
	No. of adult ♀♀ present	No. of eggs present	No. of eggs/ adult ♀	No. of adult ♀♀ present	No. of eggs present	No. of eggs/ adult ♀
1	30	104	3.5	36	23	0.6
2	22	105	4.8	6	9	1.5
3	20	55	2.8	11	13	1.2
4	13	67	5.2	11	24	2.2
5	38	124	3.3	10	6	0.6
Total	123	455	—	74	75	—
Mean	24.6	91	3.7	14.8	15	1.0

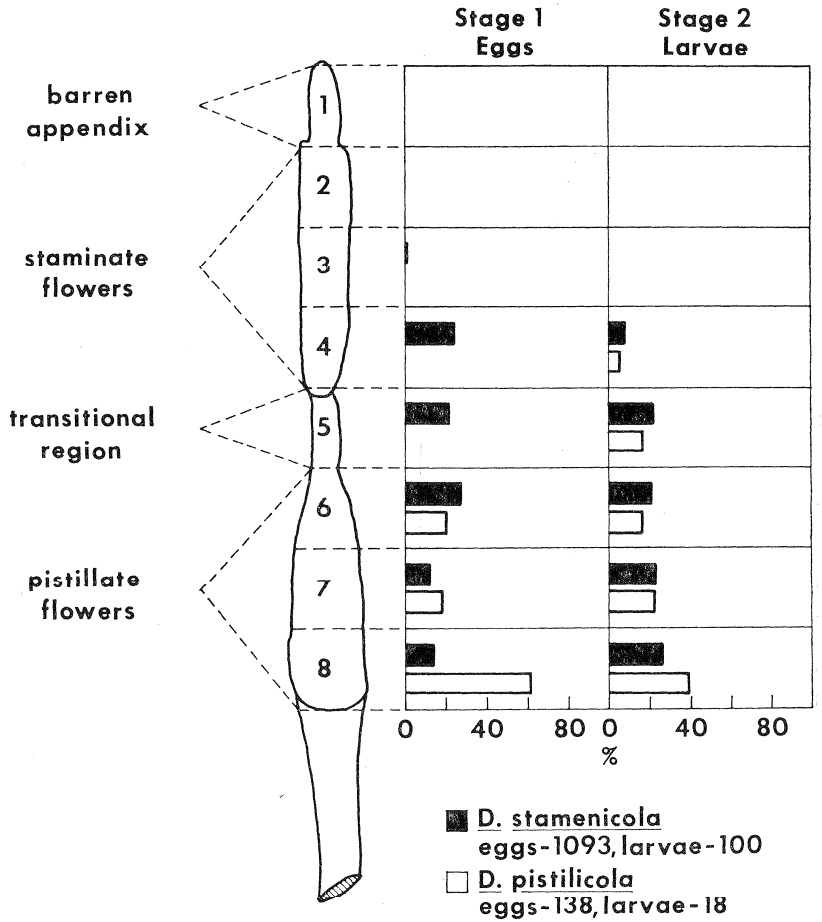

Fig. 6. Spadix of *Colocasia esculenta* with spathe removed. Columns show frequency and distribution of eggs and young larvae of the two species of *Drosophilella* in very young (Stage 1, Fig. 4) and slightly older (Stage 2, Fig. 4) inflorescences respectively.

many *stamenicola* puparia form in the drier portions of the deliquescing spathe. If the spathe and staminate spadix are very moist, however, third instar larvae will leave the plant tissues entirely. These larvae were observed to form puparia in various odd places after wandering within the enclosure in which the specimen was kept.

Upon opening the capsule by removing the heavy outer green wall, puparia of *D. pistilicola* can be found interspersed among the developing berries. At about the time of eclosion of imagines, the outer covering of the capsule partially splits back, exposing the berries within. Accordingly, adult *pistilicola* has easy access

to the open air.

In order to document the apparent movement of *stamenicola* larvae distally to the staminate portion of the flower and *pistilicola* larvae down so that they are entirely within the pistillate portion, the following observations were made. A single inflorescence between stage 2 and stage 3 (6–7 days) was selected. Starting at the extreme tip of the spathe and proceeding proximally, the entire inflorescence was searched under the binocular microscope. The time devoted to this was 1.5 hours. Most of the larvae found belonged to the second instar. A record was kept of the exact position of each larva. A total of 112 *stamenicola* larvae were found in the spathe and the male portion of the spadix. Conversely, all larvae of *pistilicola* (12) were located near the base of the inflorescence (i.e., section 8, Fig. 6). Accordingly, it appears that the separation between the species, which has been observed to be complete at stage 3 is accomplished by a very precise migration of second instar larvae.

e. *Experimental bagging of the inflorescence*

This experiment was performed to see the effect of excluding adult flies from the inflorescence. Thus, on September 9, 1977, two young but still unopened inflorescences (about one day prior to stage 1) at the Bulolo site were covered with long slender nylon-mesh bags. These were closed about the base of the pedicel by draw strings. Simultaneously, two inflorescences at a similar stage were marked as controls. When examined six days later, all four inflorescences were in stage 2; the ones within the bags appeared to be normal. No flies were present in either bagged or unbagged flowers. At the end of nine days, all four inflorescences were in stage 3 and were collected. The material was returned to the laboratory and all floral parts were searched for developmental stages of *Drosophilella* under the binocular microscope. No young stage of any insect was found within the inflorescenses which had been bagged. Nonetheless, when the young carpels were opened an ample set of seeds could be discerned throughout the carpellate section of the inflorescence. Both control inflorescences displayed ample larvae of *D. stamenicola* working the deliquescing spathe and staminate portion of the spadix. Around the pistillate flowers, furthermore, the usual number of *D. pistilicola* were found. There appeared to be no difference in seed set in individual florets between bagged and unbagged flowers. Nevertheless, there was a slightly larger number of aborting flowers (at first white in color, then turning brown as decay sets in) in the inflorescences to which the flies had access.

One may conclude that the presence of the flies is not necessary for full pollination of the flowers, although their role in possible cross fertilization mechanisms cannot be discerned from this experiment.

Discussion

The inflorescence of *Colocasia esculenta* is a complex microcosm with four

members of the family Drosophilidae of three genera breeding in it in the Morobe District of Papua New Guinea. The most thoroughly adapted for life in this specific type of inflorescence are the two species of *Drosophilella*. Large numbers of adults of both species enter the fresh flower just as it is opening. They remain within for one day. Already at oviposition, there is some niche separation between the species, with *D. pistilicola* selectively ovipositing at the pistillate base. As the inflorescence ages, the larvae eventually move to quite separate positions with large larvae and puparia of *stamenicola* remaining with the staminate spadix and the spathe as these parts decay and fall off. *D. pistilicola* puparia are exclusively formed within the capsule around the developing berries.

Clearly, these two species share the inflorescence niche in an extraordinarily precise manner. This reflects a set of highly refined adaptations in the case of the *Drosophilella* species; indeed, these species are apparently highly restricted to their host plant, *Colocasia esculenta*. As will be reported in a later paper in this series, they do not visit even the quite similar inflorescences of other species of Araceae growing in very close proximity of *Colocasia*.

Although *Drosophilella* species appear to be highly adapted to the specific inflorescence, this is apparently not equally true for the other two species which have been reared, *Styloptera repletoides* and *Dettopsomyia formosa*; the latter is recorded from a single specimen only. In neither species does the adult fly enter the very young flower; they apparently come to the inflorescence and lay their eggs only at the time when the inflorescence is beginning to wilt and decline and after the *Drosophilella* have left. Like *D. pistilicola*, both species apparently pupate among the berries of the ovoid fleshy base of the inflorescence.

OKADA (1975) has reported *Drosophilella colocasiae* DUDA and *D. alocasiae* OKADA from Taiwan, Ishigaki Is., and Okinawa Is., where they breed in the inflorescences of *Alocasia*. The association between *D. colocasiae* and *D. alocasiae* apparently resembles that described for the two species of *Drosophilella* in this paper. None of these flies appears to function as an important pollinating agent for *Colocasia esculenta*.

Although there are very strong similarities between *D. stamenicola* and *D. pistilicola*, they should not be described as sibling species. Any one of a number of specific morphological differences can be used to separate them. Furthermore, strong morphological similarities are found between *stamenicola* and *alocasiae* and between *pistilicola* and *colocasiae*. The systematic and ecological relationships of these new species to others found in closely related hosts should serve as an interesting topic for further study in this series of papers. Further investigation of the insect associates of *Colocasia esculenta* may aid in an estimation of the ancestral home of this important food plant.

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Postscript. Examination of the lectotype female of *Drosophilella colocasiae* DUDA from Java which was recently borrowed from the Zoological Museum, University of Amsterdam, through the courtesy of Drs. Th. VAN LEEUWEN and B. BRUGGE revealed that it differs from what was recorded by OKADA (1975) from Taiwan, Ishigaki Is., and Okinawa Is. The latter will be published as a new species later.

Carson 北川 杉浦 大羽 戸塚 杉山 寺沢 西沢 Krishnamurthy
100部?
Hardy 今立 Leeuwen Lemeunier Prevosti Bächli Hackman Frydenberg
Tracaos Baeder Shorrocks Frota-Pessoa Brncic Throckmorton Townsend Steffan
Spieth Pipkin Head (Kaneshiro Montgomery) Gressitt Bock Krishnamurthy
Gupta Lin Pilt Harrison Delfinado Steyskal Wirth Hoenigsberg Lachaise
Cobben Lakovaara Máca Lastovka Herskowitz Ray-Chaudhuri Papp
高田 木村 久田 羽木 尾高祖 Salvosley Parsons 金子 平山 小林
加崎 小林 若林 渡辺 酒井 倉橋 長谷川 安富 黒佐 今立 井上 上野
加納 近藤 渡辺 新島 蒲生 鈴木 渡辺 Barrios Knecht
Zettler Cordeiro Chvala ~~Ray-Chaudhuri~~ Reddy Mather Wirth Papp
Val Starmer 大木 Ebert (Brazil) 金 Johnston Vilela 小林 吉田 内山
森本 Turner 石田 渡辺 白石 池田 尾高祖 若原 加藤
Parkash 菅野 Univ Cambridge 甘 頼 Osella (Italy) 高橋 Iskandar
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