

Additional Notes on Drosophilid Flies (Diptera, Drosophilidae) in the Bonin Islands, with Descriptions of Two New Species

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Abstract Additional information on drosophilid taxonomy and ecology in the Bonin Islands is given, based on unpublished data accumulated since 1979. Two new species are described. The recent history of drosophilid faunal changes in the Bonins, including speculation on colonization and extinction, is sketched by compiling all collection records obtained so far. In accordance with the MACARTHUR-WILSON "equilibrium theory of island biogeography", the numbers of drosophilid species in Chichijima and Hahajima are regarded as being in a dynamic equilibrium at the level of 16 or 17 with considerable rates of turnover, which are estimated to be 1.11% to 1.72% per year. This equilibrium level is much lower than those in mainland local faunae, as predicted from the theory. The ecological structure of the drosophilid community in the Bonins is compared with those of mainland communities. It is characterized by the lack of some elements due to the reduced habitat diversity and the niche expansion of component species.

As mentioned by MACARTHUR and WILSON (1967), island biogeography has contributed a major part of evolutionary theory. The biota of the Bonin Islands has also attracted the special attention of many taxonomists and ecologists (*e.g.* HATTORI, 1908; GRESSITT, 1954; TUYAMA & ASAMI, 1970). Several reports have been published on drosophilid flies from the taxonomical standpoint (KIKKAWA & PENG, 1938; WHEELER & TAKADA, 1964; OKADA, 1971, 1973; 1986) or from the ecological standpoint (TODA, 1976; FUYAMA *et al.*, 1980; FUYAMA & WATADA, 1981; YAMAMOTO *et al.*, 1985). This paper adds some information to our knowledge on the taxonomy and ecology of drosophilid flies in the Bonins, based on new data accumulated since 1979. Finally, compiling the information so far obtained, we sketch the recent history of faunal changes in drosophilids and the ecological structure of the drosophilid community in the Bonins.

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Material and Methods

The material used in this study was obtained by the following collections.

In 1979, one of us, M. J. TODA (M.J.T.), made collections of drosophilid flies living in the forest canopy layer and at streamsides from October 23 to November 13. To survey the vertical microdistribution of drosophilids in a forest, four "retainer" type I traps (TODA, 1977 a) baited with fermenting banana were set out at different heights from the ground to the canopy. The upper two traps were suspended by a rope hung from a bough of the canopy. Two stations were selected at Mt. Yoake in Chichijima and at Okimura in Hahajima. Vegetation, trap heights and collecting period at each station are as follows. Mt. Yoake Station: evergreen broad-leaved secondary forest with mixture of pine (*Pinus lutchuensis*) trees (tops of broad-leaved trees *ca.* 15–16 m high, pine trees *ca.* 20–25 m high), floor vegetation sparse, dominated by ferns; trap heights—12.8, 6.8, 1.5, 0.1 m; October 23 to November 6. Okimura Station: evergreen broad-leaved secondary forest dominated by *Calophyllum inophyllum* (tree tops *ca.* 15–16 m high), floor vegetation sparse; trap heights—12.7, 6.7, 1.5, 0.1 m; November 9 to 13. Collections at streamsides were also made by using four "retainer" type I traps at each of the following three places during the period shown in parentheses: the River Yatsuse (October 23 to 30) and a small mountain stream at Mt. Yoake (October 31 to November 7) in Chichijima, and a rocky stream at Okimura (November 9 to 13) in Hahajima. In addition to the trap collections, sweeping collections with an insect net were made at various sites, *e.g.* forest floor vegetation, fallen fruits and fleshy fungi.

In December, 1980, Y. FUYAMA (Y.F.) and his colleagues made trap collections in Chichijima with an aim to study the habitat selection of two sibling species, *Drosophila melanogaster* and *D. simulans*. The collecting methods and the body of the results have already been reported by YAMAMOTO *et al.* (1985). This paper reports all the collection data, including other species than *D. melanogaster* and *D. simulans*.

In 1984, Y.F. and his colleague made trap collections during December 7 to 14 in Chichijima for the same purpose as in 1980. Since the quantitative collection data have been unfortunately lost, only the list of species collected is available, along with a few numerical data for some rare species.

In 1985, A. RIIHIMAA (A.R.) made a collection trip to the Islands from November 2 to 10. He made trap collections with fermenting banana, papaya, apple and malt as bait and sweeping collections on various fallen fruits in Chichijima and Hahajima. Furthermore, he brought some fallen fruits and fleshy fungi from Hahajima and confirmed by laboratory rearing that some drosophilid species bred on such substrates.

Drosophila (Hirtodrosophila) paiviae TODA et RIIHIMAA, sp. nov.

(Figs. 1–8)

Diagnosis. Mesoscutum brownish grey, with 4 indistinct, dark, longitudinal

stripes; outer pair running along line of dorsocentrals (Fig. 1). Third to 6th abdominal tergites each medially with large, posteriorly expanding, black patch (Figs. 2, 3). Aedeagus apically bilobed, finely serrate on margin, curved dorsad, pointed at tip (Fig. 6).

♂, ♀. Body length, ♂ *ca.* 1.9 mm (range: 1.70–2.08), ♀ *ca.* 2.3 mm (2.02–2.49). Thorax length (including scutellum), ♂ *ca.* 1.0 mm (0.91–1.05), ♀ *ca.* 1.1 mm (1.06–1.23).

Head: Eye dark red, with sparse, fine pile. Antenna with 2nd joint greyish yellow, 3rd dark grey. Arista with *ca.* 6 (5–7) upper and *ca.* 2 (1–2) lower branches in addition to small terminal fork. Frons slightly narrower than 1/2 of head width (mean=0.48, 0.46–0.50, measured at level of anterior ocellus), yellowish grey, anteriorly pale and with a few frontal hairs. Ocellar triangle black. Periorbits narrow, dark grey, posteriorly black. Anterior reclinate orbital *ca.* 3/8 (0.37, 0.30–0.52) length of posterior reclinate; proclinate *ca.* 3/4 (0.76, 0.69–0.90) length of posterior reclinate. Face yellow; carina high, broad. Clypeus brownish yellow. Cheek yellow, with dark grey patch below eye, *ca.* 1/5 (0.20, 0.16–0.25) as broad as maximum diameter of eye. Vibrissa prominent; 2nd oral minute. Palpus yellowish grey, flattened, apically with 1 prominent seta.

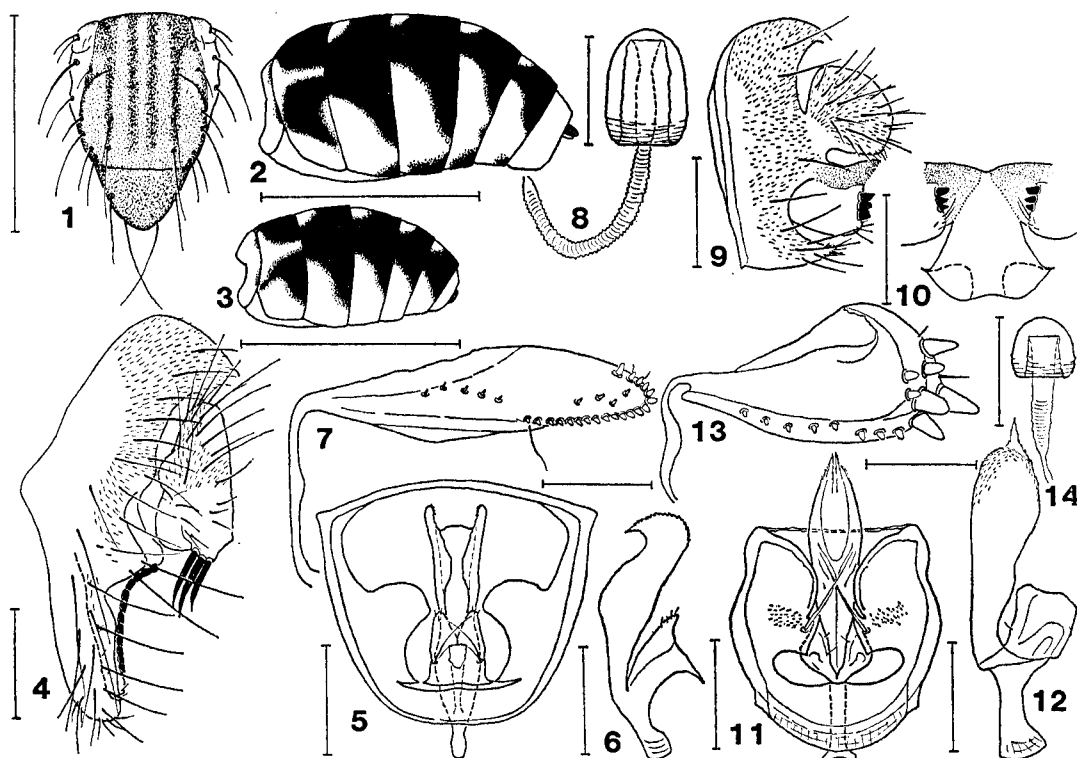
Thorax (Fig. 1): Scutellum dark brownish grey. Thoracic pleura whitish pale brown. Humerus pale brown, anteriorly slightly greyish; humerals 2, upper one longer. Acrostichal hairs in 6 rows. Anterior dorsocentrals *ca.* 2/3 (0.66, 0.53–0.71) length of posteriors; cross distance of dorsocentrals *ca.* 2.3 (1.92–2.87) length distance. Prescutellars absent. Anterior scutellars *ca.* 7/10 (0.70, 0.67–0.79) length of posteriors. Sterno-index *ca.* 0.8 (0.70–0.94).

Legs pale brown; ultimate tarsal joints dark. Preapicals on mid and hind tibiae; apicals on mid tibia. Fore metatarsus as long as 2 succeeding tarsal joints together; mid and hind metatarsi as long as 3 succeedings together.

Wing hyaline. Veins dark grey; cross veins clear. R_{2+3} slightly curved to costa at tip; R_{4+5} and M nearly parallel. Cl-bristles 2. Wing indices: C *ca.* 2.5 (2.12–2.74), 4V *ca.* 2.3 (1.96–2.56), 4C *ca.* 1.2 (1.03–1.43), 5x *ca.* 2.1 (1.87–2.32), Ac *ca.* 2.6 (2.07–2.92), C3-fringe *ca.* 0.5 (0.42–0.58). Halteres pale brown.

Abdomen (Figs. 2, 3): Tergites pale yellow; 1st tergite with faint, narrow, medially interrupted, grey, caudal band; 2nd tergite with 1 pair of large, black patches; ♀ 3rd to 6th tergites each often with 1 pair of black patches on lateral margins; ♀ 5th tergite sometimes with 1 small greyish patch between median and lateral patches; 7th tergite entirely yellow.

Periphallic organs (Fig. 4): Epandrium pubescent in mediocaudal to upper part, much elongate below, triangularly projected on caudal margin near base of surstylus, with *ca.* 6 (5–7) bristles in upper part, *ca.* 10 in middle part, *ca.* 11 or 12 in lower part. Surstylus much elongate below, with *ca.* 12 short, somewhat quadrate primary teeth in concave row on inner margin and several small setae in lower to outer part. Cercus submedially pubescent, with tuft of 3 or 4 long, stout, black



Figs. 1-14. 1-8, *Drosophila (Hirtodrosophila) paiviae* TODA et RIIHIMAA, sp. nov. 9-14, *Nesiodrosophila ogasawarensis* TODA, sp. nov. 1: thorax; 2: ♀ abdomen; 3: ♂ abdomen; 4, 9: peripheral organs; 10: decasternum and surstylus; 5, 11: phallic organs (ventral view); 6, 12: aedeagus (lateral view); 7, 13: ovipositor; 8, 14: spermatheca. (Scale-line = 1 mm in 1-3, 0.1 mm in 4-14).

spines at caudoventral apex, knob on lateral margin and *ca.* 15 (14-16) long bristles.

Phallic organs (Figs. 5, 6): Anterior paramere small, narrowly triangular, apically with *ca.* 4 sensilla. Posterior paramere forming transverse bar connecting caudolateral corners of novasternum. Novasternum with 1 pair of submedian spines near bases of anterior parameres.

♀ reproductive organs: Ovipositor (Fig. 7) distally elliptical, with *ca.* 4 discal and *ca.* 25 marginal teeth; *ca.* 5 proximal marginal teeth small, somewhat separate from others; subterminal hair located *ca.* 2/3 distad on ventral margin; basal ithmus long, narrow. Spermatheca (Fig. 8) elongate; introvert deep; outer capsule and introvert basally wrinkled; duct distally expanded.

Holotype ♂, Bonin Is.: Hahajima, emerged from fleshy fungi collected on 8. XI. 1985 (A. RIIHIMAA); deposited in the Entomological Institute, Hokkaido University, Sapporo, Japan (EHU).

Paratypes, Bonin Is.: 15 ♂, 15 ♀, same data as holotype; in EHU and the collection of M.J.T.

Distribution. Bonin Is.: Hahajima.

Relationships. This species belongs to the *trivittata* species-subgroup of the *quadrivittata* species-group, and is closely related to *D. trivittata* STROBL, 1893 and *D. trilineata* CHUNG, 1960 in having similar ♂ genitalia but clearly distinguishable from the latter two species in the coloration of mesoscutum and abdomen.

Remarks. The species name is dedicated to Miss Paivi KARVONEN, the fiancée of the junior author (A.R.).

Nesiodrosophila ogasawarensis TODA, sp. nov.

(Figs. 9–14)

Nesiodrosophila sp.: OKADA, 1971: 69; TODA, 1976: 343.

Diagnosis. Thoracic pleura yellow, with 1 longitudinal, broad, dark brown stripe from propleurite to base of halteres. Surstylus with 3 stout primary teeth (Fig. 9). Cercus fused to epandrium (Fig. 9). Aedeagus distally bilobed, apically with 1 pair of membranous, acute projections and numerous fine serrations, dorsomedially without any processes (Figs. 11, 12).

♂, ♀. Body length, ♂ *ca.* 1.8 mm (1.58–1.92), ♀ *ca.* 2.1 mm (1.92–2.24). Thorax length, ♂, *ca.* 0.7 mm (0.57–0.80), ♀ *ca.* 0.8 mm (0.68–0.82).

Head slightly broader than thorax. Eye red, oblique to body axis, with thick pile. Antenna with 2nd joint orange brown, 3rd yellowish grey, broad, fan-shaped in frontal view. Arista with *ca.* 5 (4–6) upper and *ca.* 2 (1–2) lower branches in addition to terminal fork. Frons flat, slightly narrower than 1/2 of head width (0.47, 0.45–0.50), yellowish brown, anteriorly with a few frontal hairs. Ocellar triangle brown, especially dark on inside margins of ocelli; ocellars inserted well outside ocellar triangle. Periorbits yellow, long, anteriorly broader and ending near anterior margin of frons. Anterior reclinate orbital *ca.* 4/5 (0.81, 0.72–1.03) length of posterior reclinate, inserted outside and slightly anteriorly to proclinate; proclinate as long as posterior reclinate (1.05, 0.95–1.15). Face flat, upper 3/4 orange yellow, lower 1/4 brown; carina indistinct. Clypeus dark brown. Cheek yellow, *ca.* 1/7 (0.15, 0.11–0.20) as broad as maximum diameter of eye. Vibrissa stout, long; 2nd oral fine. Palpus yellow, club-shaped, subapically with 1 prominent seta.

Thorax: Mesoscutum and scutellum dark yellow; humerus paler. Humerals 2, subequal. Acrostichal hairs in 6 irregular rows. Anterior dorsocentrals *ca.* 2/3 (0.68, 0.44–0.84) length of posteriors; cross distance of dorsocentrals *ca.* 1.8 (1.47–2.06) length distance. Prescutellars absent. Anterior scutellars as long as posteriors (1.07, 0.78–1.18); posterior scutellars nearer to each other than to anteriors. Stern-index *ca.* 0.4 (0.37–0.52).

Legs yellow. Preapicals on all tibiae; apicals on mid tibia. Fore metatarsus as long as 2 succeeding tarsal joints together; mid metatarsus slightly longer than, hind metatarsus as long as 3 succeedings together.

Wing somewhat fuscous. Veins brown; cross veins clear. R_{2+3} gently curved to costa at tip; R_{4+5} and M nearly parallel. C1-bristles 2. Wing indices: C *ca.* 2.4 (2.18–2.77), 4V *ca.* 2.6 (2.26–2.96), 4C *ca.* 1.3 (1.13–1.51), 5x *ca.* 3.2 (2.81–4.04), Ac *ca.* 2.7 (2.45–3.03), C3-fringe *ca.* 0.6 (0.52–0.67).

Abdomen: Tergites yellow; 2nd to 6th tergites each with nearly straight, dark brown, caudal band. Sternites pale yellow.

Periphallalic organs (Figs. 9, 10): Epandrium nearly entirely pubescent, deeply concave on lower caudal margin, with *ca.* 2 bristles in upper part, *ca.* 1 in middle part, *ca.* 10 in lower part; heel prominent; toe pointed. Surstylus somewhat quadrate, caudoventrally with several setae; upper part fused basally to epandrium, distally to decasternum. Decasternum broad, basally with 1 pair of dorsad recurved flaps. Cercus small, elliptical, entirely pubescent, with *ca.* 20 long bristles.

Phallic organs (Figs. 11, 12): Anterior paramere somewhat quadrate in lateral view, with *ca.* 2 minute sensilla on inner margin. Posterior paramere forming weak transverse bar connecting caudolateral corners of novasternum. Novasternum submedially pubescent, with 1 pair of submedian spines.

♀ reproductive organs: Ovipositor (Fig. 13) broad, robust, with 1 large, 1 medial, 2 small discal teeth and 3 apical large, 8 proximal small marginal teeth; basal ithmus long, narrow. Spermatheca (Fig. 14) small, hemispherical; outer capsule and introvert basally wrinkled; duct broad.

Holotype ♂, Bonin Is.: Chichijima, 31. X. 1979, by sweeping on forest floor (M. J. TODA); in EHU.

Paratypes, Bonin Is.: 390 ♂, 377 ♀, Chichijima, 22. X-7. XI. 1979, ex fallen fruits, fleshy fungi, banana baits of traps and by sweeping on forest floor and tree trunks (M. J. TODA); 1 ♂, 3 ♀, Hahajima, 9, 13. XI. 1979, ex fallen fruits and by sweeping on forest floor (M. J. TODA); in EHU and the collection of M.J.T.

Distribution. Bonin Is.: Chichijima, Hahajima.

Relationships. This species is closely related to *N. flava* NISHIHARU, 1981 but clearly distinguishable from the latter by the diagnostic characters.

Ecological Notes

1. Vertical distribution

The samples obtained at the two stations for vertical distribution were dominated by *D. simulans*, *D. pectinifera* and *D. melanogaster*. Together they made up 99.9% of the total number of individuals collected at Mt. Yoake Station, and 99.6% at Okimura Station. The vertical distribution patterns of these three species are shown in Fig. 15. Identical patterns were observed at both stations. *D. melanogaster* was almost confined to the canopy layer. *D. simulans* was distributed more or less evenly from the subarboreal layer to the canopy, but had a peak in the canopy. However, the main habitats of these two species are human habitations (TODA, 1976), especially *D. melanogaster* is found most often inside buildings (FUYAMA & WATADA,

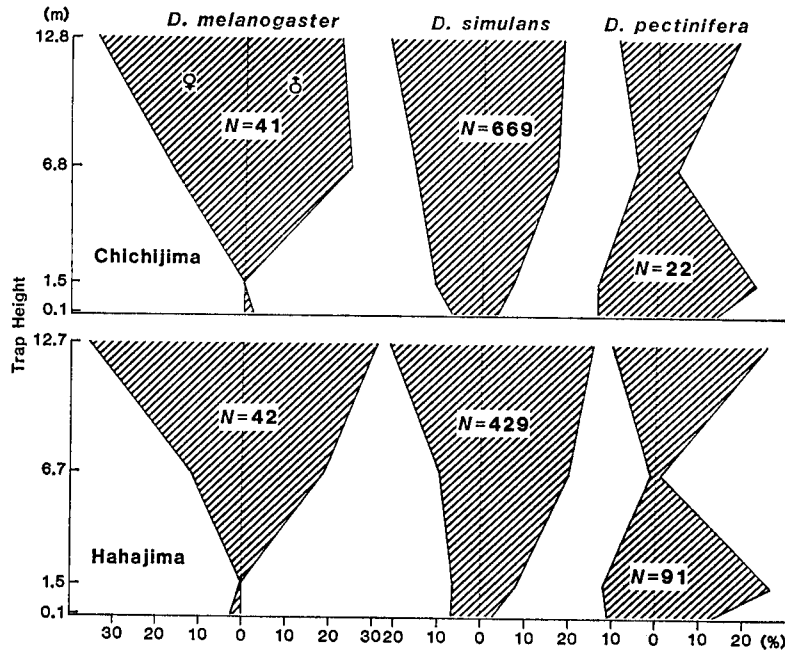


Fig. 15. Vertical distribution patterns of three predominant species in secondary forests in Chichijima and Hahajima.

1981; YAMAMOTO *et al.*, 1985). When domestic species invade natural forests, they are usually distributed mainly in upper layers (TODA, 1977 b, 1984). On the other hand, an endemic wild species, *D. pectinifera*, was distributed in two separate layers, the floor and the canopy. This pattern is relatively rare in the vertical distribution of drosophilid flies in a forest (cf. TODA, 1977 b, 1984, 1985; TODA & FUKUDA, 1985; BEPPU, 1980, 1985, 1986). Collection records of other rare species were as follows: *N. ogasawarensis* 1 ♀ at 1.5 m high (Mt. Yoake), *Chymomyza fenestrata* 1 ♀ and *D. suzukii* 1 ♂ at 12.7 m high (Okimura).

2. Collections at streamsides

The results are shown in Table 1. The composition of the samples obtained did not differ much from those in forests, also dominated by *D. simulans*, *D. pectinifera* and *D. melanogaster*. It is noteworthy that *D. daruma* was collected at the River Yatsuse.

3. Sweeping collections

Table 2 shows the numerical data of samples obtained by net sweeping at various habitats in Chichijima and Hahajima. In Chichijima, *N. ogasawarensis* nearly monopolized the samples obtained from the forest floor, decayed bark or tree sap on fallen tree trunks or stumps. However, this species was rare in Hahajima. Instead, *D. pectinifera* and *Leucophenga boninensis* were predominant on the forest floor in Hahajima. It should be noted that *D. novicia* was recollected in Hahajima for the first time since its original description based on material obtained in 1958.

Table 1. Drosophilid flies collected by traps at streamsides in Chichijima and Hahajima in October and November, 1979

Island Station	Chichijima		Hahajima	Total
	River Yatsuse	Mt. Yoake	Okimura	
<i>D. simulans</i>	115	60	393	568
<i>D. pectinifera</i>	53	8	84	145
<i>D. melanogaster</i>	39	2	36	77
<i>D. annulipes</i>	4	—	—	4
<i>D. kikkawai</i>	2	—	1	3
<i>D. daruma</i>	2	—	—	2
<i>My. serrata</i>	—	—	1	1
Total	215	70	515	800

Table 2. Drosophilid flies collected by net sweeping at various habitats in Chichijima and Hahajima in October and November, 1979

Island Habitat*	Chichijima							Hahajima				Total
	FF	DB	TT	DL	AD	FE	Total	FF	DB	DL	Total	
<i>N. ogasawarensis</i>	602	48	5	—	—	—	655	2	—	—	2	657
<i>D. pectinifera</i>	5	—	—	20	50	—	75	59	1	49	109	184
<i>L. boninensis</i>	1	—	—	3	98	—	102	54	—	7	61	163
<i>D. kikkawai</i>	—	—	—	70	—	—	70	—	—	19	19	89
<i>D. simulans</i>	—	—	—	1	—	1	2	8	2	7	17	19
<i>D. annulipes</i>	—	—	—	—	—	—	—	1	—	4	5	5
<i>Sc. hexasticha</i>	2	—	—	—	—	—	2	—	—	—	—	2
<i>Sc. pallida</i>	—	—	—	—	—	1	1	—	—	—	—	1
<i>D. novicia</i>	—	—	—	—	—	—	—	1	—	—	1	1
<i>My. serrata</i>	—	—	—	—	—	—	—	—	1	—	1	1
Total	610	48	5	94	148	2	907	125	4	86	215	1,122

* Abbreviations of habitats: FF, forest floor; DB, decayed bark, fallen tree trunks or stumps; TT, tree trunks; DL, decayed leaves and stems of herbaceous plants; AD, *Alocasia odora* C. KOCH stands; FE, forest edge herbage stands.

The samples from decayed leaves and stems of herbaceous plants were characterized by the abundance of two species of the *montium* species-subgroup, *D. pectinifera* and *D. kikkawai*, in both islands. Sweeping at *Alocasia odora* stands in Chichijima yielded a considerable number of individuals of *L. boninensis*. This species was frequently observed resting at the edge of the underside or walking with characteristic wing waving behavior on the surface of leaves of this plant. Furthermore, copulation was sometimes observed there.

4. Collections on fallen fruits

The combined data obtained by M.J.T. in 1979 and by A.R. in 1985 on the numbers of adult flies collected on various kinds of fallen fruits are presented in

Table 3. Thirteen kinds of fruits, treated separately for Chichijima and Hahajima, were subjected to a cluster analysis (UPGMA: unweighted pair-group method using arithmetic average, SNEATH & SOKAL, 1973) to compare the similarity of their drosophilid consumers. The similarity was evaluated by HORN's (1966) measurement of overlap.

The resulting dendrogram is shown in Fig. 16. *Elaeocarpus photimiaefolius* in Chichijima was quite unique in the predominance of *N. ogasawarensis*. However, in Hahajima only 2 individuals of *D. pectinifera* were collected on fallen fruits of this plant. Therefore, this plant in Hahajima was not subjected to the cluster analysis. Wild fruits of *Ficus microcarpa* and *Terminalia catappa* were frequently used by an endemic species, *D. pectinifera*. *D. kikkawai* was relatively abundant on fallen fruits of *T. catappa* in both islands. *L. boninensis* was commonly found on those fruits in Hahajima. On the other hand, cultivated plants, orange, banana and papaya, were characterized by the predominance of *D. simulans*. This species frequently utilized also wild fruits of *F. microcarpa* and *T. catappa*. Two endemic plant species, *Pandanus boninensis* and *Morus boninensis*, resembled the cultivated plants more than the wild ones in the composition of their drosophilid consumers. It should be noted here that 1 ♀ of *Scaptomyza polygonia* was collected on fallen fruits of *F. microcarpa* in Chichijima in 1985, although it is likely that larvae of this species do not feed on fallen fruits but mine living leaves of herbs (cf. NISHIHARU, 1980). This is the first record of this species from the Bonins.

5. Collections on fleshy fungi

Since fleshy fungi were relatively scarce in October and November 1979, the collection records were poor (Table 4). In Chichijima a number of individuals of *N. ogasawarensis* were collected on Agaricales fungi, together with *L. boninensis* and *D. pectinifera*. In Hahajima 4 ♂ of *Mycodrosophila serrata* (previously cited as *My. gratiosa*), which was rarely collected by other methods as well, i.e. 1 ♀ by trap at streamside of Okimura (Table 1) and 1 ♂ on fallen fruits of *T. catappa* (Table 3), were collected on Aphyllophorales fungi. Other species, *D. pectinifera* and *D. simulans*, were collected on Agaricales.

6. Breeding records

The numbers of drosophilid flies which emerged from several kinds of substrates brought from Hahajima in November 1985 are shown in Table 5. All the flies that emerged from fruits of *F. microcarpa* and *P. boninensis* were *D. simulans*. This species also made up the majority of flies from papaya and orange. A small number of individuals of *D. busckii* emerged from the latter two cultivated fruits, and only 1 individual of *D. pectinifera* from orange. No emergence of *D. pectinifera* from *F. microcarpa* fruits, on which adult flies of this species were frequently seen, suggests differentiation between adult and larval food. Two species, *D. paiviae* and *My. serrata*, emerged from fleshy fungi.

Table 3. Drosophilid flies collected on various kinds of fallen fruits in Chichijima and Hahajima in October and November, 1979 and 1985

Island	Chichijima										Hahajima										Total
	Ep	Fm	Tc	Pp	Pb	Total	Ep	Fm	Po	Tc	Or	Bn	Pb	Pp	Mb	Total					
<i>N. ogasawarensis</i>	147	—	1	—	—	148	—	—	—	1	1	—	—	—	—	2	150				
<i>D. pectinifera</i>	3	376	151	—	—	530	2	81	9	144	15	2	119	—	16	388	918				
<i>D. kikkawai</i>	—	15	197	37	—	249	—	14	9	52	3	1	—	3	—	82	331				
<i>L. boninensis</i>	—	—	—	—	—	—	—	—	—	26	3	—	—	—	5	34	34				
<i>My. serrata</i>	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1				
<i>D. simulans</i>	1	263	187	85	23	559	—	95	36	176	713	414	2,787	1,137	130	5,488	6,047				
<i>D. suzukii</i>	—	4	—	—	—	4	—	—	—	1	7	1	5	—	—	14	18				
<i>D. melanogaster</i>	—	—	49	5	21	75	—	—	—	—	—	—	3	17	—	20	95				
<i>Ch. fenestrata</i>	—	—	—	2	—	2	—	—	—	—	—	—	—	—	—	—	2				
<i>Sc. pallida</i>	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1				
<i>Sc. polytonia</i>	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1				
Total	151	660	585	129	44	1,569	2	190	54	401	742	418	2,914	1,157	151	6,029	7,598				

* Abbreviations of kinds of fruits: Ep, *Elaeocarpus photinifolius*; Fm, *Ficus microcarpa*; Tc, *Terminalia catappa*; Pp, papaya; Pb, *Pandanus boninensis*; Po, *Pouteria obovata*; Or, orange; Bn, banana; Mb, *Morus boninensis*.

7. Recent changes in the drosophilid fauna

To demonstrate the recent history of faunal changes of drosophilids in the Bonins, all the collection records from Chichijima and Hahajima are compiled in

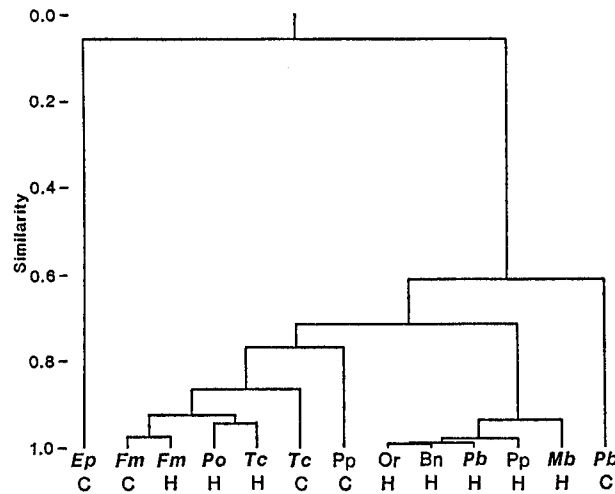


Fig. 16. Cluster analysis (UPGMA) for the similarity of drosophilid consumers in 13 kinds of fallen fruits (cf. the foot note of Table 3 for the abbreviations) treated separately for Chichijima (C) and Hahajima (H).

Table 4. Drosophilid flies collected on fleshy fungi in Chichijima and Hahajima in October and November, 1979

Island	Chichijima	Hahajima	Total
<i>N. ogasawarenis</i>	78	—	78
<i>D. pectinifera</i>	4	7	11
<i>L. boninensis</i>	6	—	6
<i>My. serrata</i>	—	4	4
<i>D. simulans</i>	—	3	3
Total	88	14	102

Table 5. Drosophilid flies having emerged from several kinds of substrates (cf. the foot note of Table 3 for the abbreviations of kinds of fruits) brought from Hahajima in November, 1985

Breeding substrate	Fruits				Fleshy fungi	Total
	<i>Fm</i> 0.025	<i>Pb</i> 4	<i>Pp</i> 1	<i>Or</i> 0.25	0.05	
Weight (kg)						
<i>D. simulans</i>	29	1,764	129	234	—	2,156
<i>D. busckii</i>	—	—	5	4	—	9
<i>D. pectinifera</i>	—	—	—	1	—	1
<i>D. paiviae</i>	—	—	—	—	67	67
<i>My. serrata</i>	—	—	—	—	5	5
Total	29	1,764	134	239	72	2,238

Table 6. In the previous studies a total of 21 species belonging to 7 genera had been recorded from the Bonins. The present study adds three species, *D. paiviae*, *Sc. polygonia* and *D. hydei*, to the faunal list. The last species was newly recorded from Chichijima in December, 1984.

Based on the records compiled in Table 6, some speculations are given for colonization and extinction of drosophilid species in the Bonins. It should be, however, remarked here that in 1980 and 1984 only trap collections were made in Chichijima, and in 1985 the sweeping collections were not intensive. In addition, the records before 1958 are based on relatively small collections. Therefore, the records in these years are more or less incomplete as shown with question-marks. In spite of the absence of collection records in some years, the probable existence, which is shown with (+) in Table 6, can be speculated in some cases from later records. For example, *D. paiviae*, which is an endemic species newly discovered from Hahajima in the present study, should have been existing there continuously. The speculations from the information in Table 6 are enumerated below:

1) Two species, *D. apicohispidata* and *D. ananassae*, are regarded as having gone extinct from the Bonins. The former, an endemic species, has never been collected since the initial record of 1 ♂ from Hahajima and 1 ♀ from Chichijima in 1970 (OKADA, 1973). The latter, a domestic species, has never been recorded from the Bonins since the last record of one specimen from Chichijima in 1958 (WHEELER & TAKADA, 1964).

2) Two wild species, *Sc. elmoi* and *Sc. polygonia*, and two domestic species, *D. busckii* and *D. hydei*, colonized the Bonins after 1973. The first records of these four species are as follows: *Sc. elmoi* from Hahajima in 1979, *Sc. polygonia* from Chichijima in 1985, *D. busckii* from Hahajima in 1973, and *D. hydei* from Chichijima in 1984. *D. busckii* colonized also Chichijima between 1974 and 1979. Outside the Bonins, *Sc. elmoi* is distributed in a relatively wide geographical range, Japan, Taiwan, Hawaii and Australia, and *Sc. polygonia* is distributed in Japan and Korea (WHEELER, 1981).

3) Four cases of colonization from Hahajima to Chichijima and one case in the opposite direction are supposed to have occurred after 1973. The former cases are *Ch. fenestrata* and *N. ogasawarensis* recorded first from Chichijima in 1973, and *Sc. hexasticha* and *D. suzukii* in 1979. The latter case is *D. kikkawai* recorded first from Hahajima in 1979.

4) *Sc. boninensis* and *Sc. pallida* are supposed to have become extinct from Hahajima in 1973 and between 1974 and 1979, respectively. The latter case may or may not be the replacement by its close relative, *Sc. elmoi*, which colonized Hahajima between 1974 and 1979.

5) *D. immigrans* was recorded neither from Chichijima nor from Hahajima in November, 1985. It is, however, premature to conclude its extinction from the Bonins, because this species tends to increase its population in summer (FUYAMA *et al.*, 1980). Notwithstanding, the population of this species may have been

Table 6. *Drosophilid* collection records so far accumulated in Chichijima (C) and Hahajima (H), together with speculations for colonization and extinction. The probable existence is indicated with (+), and the uncertainty with ? Endemic species are asterisked.

Year	'58 ^{a)}		'68-72 ^{b)}		'73 ^{c)} (Apr.)		'79 ^{d)}		'80 (Dec.)		'84 (Dec.)		'85 ^{e)} (Nov.)		Speculation for colonization (C) and extinction (E)
	C	H	C	H	C	H	C	H	C	H	C	H	C	H	
Human population	129 ²⁾	0 ²⁾	285 ³⁾	0 ³⁾	965	49	1220	300	1295	305	1408	369	1459	378	
Wild species															
<i>Chymomyza fenestrata</i> *	-	(+)	-	5	10	3	3	1	?	?	?	?	?	?	? C, Chichi, 1973
<i>Scaptomyza hexasticha</i> *	-	(+)	-	4	-	4	2	1	?	?	?	?	?	?	? C, Chichi, 1974-79
<i>Sc. boninensis</i> *	(+)	(+)	1	4	(+)	-	(+)	-	(+)	-	+	-	?	-	E, Haha, 1973
<i>Nesiodrosophila ogasawarensis</i> *	-	(+)	-	2	1	(+)	882	7	(+)	?	(+)	?	7	?	? C, Chichi, 1973
<i>Drosophila pectinifera</i> *	+	+	279	559	737	180	625	1129	941	(+)	+	(+)	616	344	
<i>D. paiviae</i> *	-	(+)	-	(+)	-	(+)	-	(+)	-	(+)	-	(+)	-	67	
<i>D. apicohispida</i> *	(+)	(+)	1	1	-	-	-	-	-	-	-	-	-	-	E, Bonins, 1971-
<i>Leucophenga boninensis</i>	+	+	154	265	13	142	161	290	(+)	?	(+)	?	3	?	
<i>D. novicia</i>	-	+	-	(+)	-	(+)	-	1	-	?	-	?	-	-	?
<i>Mycodrosophila serrata</i>	?	?	53	22	14	1	4	19	4	(+)	(+)	(+)	1	5	
<i>D. daruma</i>	?	-	1236	-	(+)	-	13	-	2	-	?	-	?	-	
<i>D. annulipes</i>	+	+	10	1	9	(+)	10	7	5	?	1	?	5	?	

<i>Dettopsomyia nigrovittata</i>	—	?	—	79	—	(+)	—	5	—	?	—	?	—	?	
<i>Sc. pallida</i>	+	+	1	1	44	2	—	1	(+)	—	(+)	—	1	—	E, Haha, 1974-'79
<i>Sc. elmoi</i>	—	—	—	—	—	—	—	1	—	?	—	?	—	?	C, Bonins (Haha), 1974-'79
<i>Sc. polygonia</i>	—	—	—	—	—	—	—	—	—	—	—	—	1	—	C, Bonins (Chichi), 1985
Semi-domestic species															
<i>D. suzukii</i>	—	?	—	9	—	(+)	4	107	2	(+)	1	(+)	27	38	C, Chichi, 1974-'79
<i>D. kikkawai</i>	?	—	44	—	2	—	644	182	1192	(+)	+	(+)	11	1	C, Haha, 1974-'79
Domestic species															
<i>D. simulans</i>	+	+	2139	813	2722	418	11901	10215	18802	(+)	+	(+)	9324	12462	
<i>D. immigrans</i>	?	+	2077	1688	326	535	232	3	(+)	?	14	?	?	?	
<i>D. ananassae</i>	+	+	—	—	—	—	—	—	—	—	—	—	—	—	E, Bonins, 1959—
<i>D. melanogaster</i>	+	+	13	(+)	149	1	2664	606	2749	?	+	?	34	?	
<i>D. busckii</i>	—	—	—	—	—	9	2	(+)	?	(+)	?	(+)	?	9	C, Bonins (Haha), 1973; Chichi, 1974-'79
<i>D. hydei</i>	—	—	—	—	—	—	—	—	—	—	11	—	?	—	C, Bonins (Chichi), 1981— '84
<hr/>															
Total no. of individuals	—	—	6008	3442	4027	1295	17150	12574	23695	—	—	—	10030	12926	
Total no. of spp. collected	7	9	12	14	11	10	15	15	7	—	8	—	11	7	
Total no. of spp. estimated	?	?	12	17	13	16	16	17	?	?	?	?	?	?	

1) Including the data of breeding records (Table 5). 2) In 1946. 3) In 1968. Authority: a) KIKKAWA & PENG, 1938; WHEELER & TAKADA, 1964; b) OKADA, 1971, 1973; c) TODA, 1976; d) partly, FUYAMA *et al.*, 1980.

decreased in the Bonins.

Although some of these speculations may be mistaken due to sampling errors, the faunal changes in recent years are certainly related to the rapid increase of human population after the retrocession of the Islands in 1968 from the United States to Japan. Especially, Hahajima had been uninhabited for more than twenty years until the retrocession. The increasing urbanization and traffic between Chichijima and Hahajima should have facilitated the colonization by domestic species and the faunal exchange between the two islands. TODA (1976) predicted that these artificial environmental changes would cause the extinction of wild endemic species. However, we can say little about the fates of endemic species at the present stage, because no intensive surveys in wild environment have been made since 1979.

Finally, total numbers of drosophilid species in Chichijima and Hahajima were estimated, separately for each of three periods, 1968 to 1972, 1973, and 1979, when relatively intensive surveys were made. The value increased from 12 to 16 in Chichijima, while it was nearly constant, 16 or 17, in Hahajima. Of the four species added to the fauna in Chichijima during this period, three are endemic species, *Ch. fenestrata*, *N. ogasawarensis* and *Sc. hexasticha*, which are speculated to have colonized Chichijima from Hahajima. It is more likely, however, that these speculations are mistaken due to sampling errors, i.e., these endemic species have been inhabiting Chichijima from ancient times. If it is true, the estimated total number of species in Chichijima is changed as follows: 15 in 1968 to 1972, 14 in 1973, and 16 in 1979. These relatively constant values may indicate a state of equilibrium between immigration and extinction in the "equilibrium model" for insular biota by MACARTHUR and WILSON (1963). These estimated equilibrium numbers of species are much smaller than the values in mainland faunae (cf. TODA, 1984), but not so different between the two islands similar in size, Chichijima (23.95 km²) and Hahajima (20.80 km²), which is consistent with the predictions from the model. The faunal turnover rate per year at equilibrium was calculated by the following formula:

$$T = \frac{I + E}{(s_1 + s_2)t},$$

where *I* and *E* are numbers of species having colonized and become extinct, respectively, *s*₁ and *s*₂ are numbers of species at census 1 and 2, respectively, and *t* is the interval (years) between the two censuses. The rates calculated from the faunal differences between 1973 and 1979 were 0.0172 or 0.0111 (if assuming the existence of *Sc. hexasticha* in 1973) in Chichijima and 0.0152 in Hahajima.

8. Structure of the drosophilid community

In Fig. 17, the ecological structure of the drosophilid community in the Bonins is compared with those of two mainland communities in Morioka and Kiyosumi (TODA, 1984). Morioka is situated in the cool temperate deciduous broad-leaved forest zone, and Kiyosumi in the warm temperate laurel forest zone. Within a two-dimensional niche space with regard to habitat and food, each component species,

shown with its code number or the abbreviation of its species name, was located at an area corresponding to its niche. The niche position of each species was inferred from the ecological information obtained in the present and previous studies (TODA,

		MORIOKA							KIYOSUMI							BONIN Is.								
Habitat	Food	fc	ff	fe	gl	hh	sh	ss	fc	ff	fe	gl	hh	sh	ss	fc	ff	fe	gl	hh	sh	ss		
	T	4						70	40						70								Dd?	
	F	44 87	47 78		45				44				44			Cf?		No						
	G						76 (68) (49)						47 50											
	Bd						80		60				60											
	M																							
	Ld																							
	LI																							
	Fd																							
	(Tf)	(3) (13)							88	(5)			88											
	(S)																							

Fig. 17. Ecological structure of the drosophilid community in the Bonin Islands, in comparison with those in Morioka and Kiyosumi. Food types are classified into 8 categories: tree sap (T), fruits (F), garbage (G), decayed stems of herb-like plants such as banana (Bd), fleshy fungi (M), decayed herbage (Ld), living herbage (LI) and decayed fallen flowers (Fd). (Tf) means fruit trap collection and (S) sweeping collection. Habitats are classified into 7 categories: forest canopy (fc), forest floor (ff), forest edge (fe), grassland (gl), human habitation (hh), hygrophilous herbage stand often existing beside streams (sh) and streamside (ss). Abbreviations and code numbers of component species: Lb, *L. boninensis*; Cf, *Ch. fenestrata*; Sh, *Sc. hexasticha*; Sb, *Sc. boninensis*; No, *N. ogasawarenensis*; Ms, *My. serrata*; Dan, *D. ananassae*; Dpe, *D. pectinifera*; Dk, *D. kikkawai*; Dpa, *D. paiviae*; Dap, *D. apicohispida*; Dn, *D. novicia*; Dd, *D. daruma*; 24, *De. nigrovittata*; 26, *Sc. polygonia*; 27, *Sc. pallida*; 28, *Sc. elmoi*; 44, *D. suzukii*; 48, *D. melanogaster*; 49, *D. simulans*; 60, *D. busckii*; 76, *D. hydei*; 77, *D. immigrans*; 79, *D. annulipes* (cf. TODA, 1984 for other code numbers in Morioka and Kiyosumi). Probably extinct species are indicated with †.

1976; FUYAMA *et al.*, 1980). Species for which the information was insufficient for determining accurately their niche positions were indicated by attaching a question-mark.

It is immediately apparent that some guilds representing essential parts of the mainland communities are completely lacking from the Islands. Streamside environment (sh and ss) is not inhabited by any characteristic guilds. This may reflect an insular condition, i.e. the scarcity of streams. *D. daruma* which belongs to the *polychaeta* species-group derived from the Old World *virilis-repleta* radiation (THROCKMORTON, 1975) may perhaps correspond to the streamside tree sap feeding (T-ss) guild represented by species of the *robusta* species-group, which is derived from the same radiation, in the mainland communities. However, OKADA (1971) found this species in a large swarm on a bird nest, and FUYAMA *et al.* (1980) reported that a number of individuals of this species were collected by a trap set in a garden beside a house and the distribution of this species within the Bonins was restricted to the southern part of Chichijima. Another instance is the lack of tree sap feeding guilds from forests. This may reflect a general trend of southward decline in tree sap feeders, which was suggested by TODA (1984) in the comparison of community characteristics between Morioka and Kiyosumi. This vacant niche is partially compensated by *N. ogasawarensis* (No), *D. pectinifera* (Dpe) and probably *Ch. fenestrata* (Cf).

Another characteristic of the community structure in the Bonins is the niche expansion of some species, especially in the food dimension. *D. pectinifera* utilizes four kinds of food resources; mainly fruits (F), and subsidiarily fleshy fungi (M), decayed herbage (Ld) and tree sap (T). Direct counterparts in the mainland communities may be *D. rufa* (No. 55) in Kiyosumi and *D. biauraria* (No. 53) and *D. triauraria* (No. 54) in Morioka. All these species belong to the same *montium* species-subgroup. In addition, *D. pectinifera* corresponds partially to more species in the mainland communities, e.g. *D. sternopleuralis* (No. 87), *D. curviceps* (No. 78), *D. bizonata* (No. 81) and *D. angularis* (No. 83) in Kiyosumi, and *D. nigromaculata* (No. 85), *D. collinella* (No. 58) and *D. nipponica* (No. 51) in Morioka. Another species having a much broader food niche is *N. ogasawarensis*. This species utilizes mainly fleshy fungi, and subsidiarily fruits and tree sap, corresponding directly to a congeneric species, *N. delicata* (No. 31) in Kiyosumi. In spite of the fact that *N. ogasawarensis* utilizes some kinds of fallen wild fruits at least as adult food, this species is less attracted to fermenting banana bait. Similar feeding habit is seen in *Liodrosophila aerea* (No. 23). Furthermore, as mentioned above, *N. ogasawarensis* may partially use the vacant niche which is occupied by *D. subtilis* (No. 41) in Kiyosumi. Similar food niche expansions, though not so conspicuous, are observed for *D. kikkawai*, *L. boninensis* and *My. serrata*. Although the last species strongly prefers Aphyllophorales fungi as mainland congeners (Nos. 32 to 39) do (cf. NISHIHARU, 1980; TODA, 1984), the relatively frequent occurrence of adult flies on artificial fruit baits of traps or fallen wild fruits may indicate food niche expansion as suggested by

TODA (1976). In addition to food niche expansion, habitat niche expansion was also suggested for *D. pectinifera* and *L. boninensis* by TODA (1976). It is understandable that niche expansion was not observed in recently introduced domestic species but in wild, especially endemic species which have had enough time to adapt to insular environmental conditions. These cases of niche expansion give indirect evidence for "ecological release", a tendency to niche expansion evolved under insular conditions with fewer competitors (MACARTHUR & WILSON, 1967). Due to this polyphagous and eurytopic nature, some wild species, e.g. *D. pectinifera* and *L. boninensis*, seem to be quite tolerant to the recent disturbance of native environment and to the invasion of domestic species. SHIMIZU (1984) reported a similar phenomenon, i.e. "ecological release", in woody plant species by comparing vegetations between the Bonins (species-poor oceanic islands) and the Ryukyus (species-rich continental ones).

Of the domestic species, *D. simulans* (No. 49) and *D. immigrans* (No. 77) have invaded the wild environment and even primary forests to a considerable degree (TODA, 1976). However, population of the latter species has been decreasing in recent years. This density decrease may have been compensated by the density increase of the former species, so that *D. simulans* has become most predominant all over the Bonins.

In conclusion, the drosophilid community in the Bonins exhibits an ecological structure characteristic of an insular community with a depauperate fauna, with the lack of some elements due to the reduced habitat diversity and the niche expansion of component species.

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