THE *DROSOPHILA ANANASSAE* COMPLEX
WITH DESCRIPTION OF A NEW SPECIES FROM
FRENCH POLYNESIA (*DIPTERA: DROSOPHILIDAE*)

Shane F. McEVEY (*), J.R. DAVID (*) (**), L. TSACAS (*)

(*) Laboratoire de Biologie et Génétique Évoluées, Centre National de la Recherche Scientifique, F-91190 Gif-sur-Yvette.
(**) Centre de l'environnement d'Opunohu, BP 1013, Papetoai, Moorea, Polynésie française.

**Keywords:** *Drosophilidae*, taxonomy, *D. monieri*, *D. ananassae*, French Polynesia, wing indices, flower-breeding, island speciation, genetic species.


Summary. — *Drosophila (Sophophora) monieri*, n. sp. is described from French Polynesia. This new species breeds in the rotting flowers of *Hibiscus tiliaeus*, inter alia, while *D. ananassae* apparently does not. At altitudes above 800 m on Tahiti only *D. monieri* was present whereas at low elevations *D. ananassae* was more abundant. *D. monieri* is a member of the *ananassae* complex of the *ananassae* subgroup. The complex now includes ten species many of which are insular endemics in the South Pacific. Three occur in southeast Asia, four on isolated Pacific islands, one in northern Australia and New Guinea, one in the Afrotropical region and *D. ananassae* itself, as a result of its association with man, is circumtropical; it is probably indigenous to southeast Asia. A number of these species are very similar, but some diagnostic details of the metatarsal sexcombs and male genitalia are known and are presented here. The complex of several cryptic island species provides a useful model for research into the process of speciation.

The occurrence of species endemic to oceanic islands is convincing evidence that speciation occurs in allopatri; island faunas thus provide good models for evolutionary studies. In the drosophilid family the most interesting evolutionary radiation has occurred on the Hawaiian islands, which harbor over 500 endemic species. In a recent survey of drosophilids of Pacific Oceania, Hardy and Kaneshiro (1981) pointed out that, with the exclusion of Hawaii, the Polynesian fauna was largely unknown, with only 43 endemic species, 33 of which were from Samoa and only two from the Society Islands.

During the present survey of Drosophilidae in Moorea and Tahiti (Society Islands, French Polynesia), about 20 species were collected, among which were found several new taxa to be described elsewhere. It thus appears that, by contrast with Hawaii, the drosophilid fauna of French Polynesia is quite depauperate. A newly discovered species, described here, is especially interesting since it is a close relative of the widespread and domestic species, *D. ananassae*. Morphological and ecological data are provided below, as well as a general overview of the nine other species now included in the *D. ananassae* complex.

The new species is described below in a format similar to that used by Bock and Wheeler (1972) and the description is therefore comparable to those of *D. pallidosa*, *D. phaeopleura*, *D. nesoetes*, *D. atripex* and *D. varians*. The wing indices used here are calculated with the formulae given by Sturtevant (1942) and Bock (1976) (1).

**Drosophila (Sophophora) monieri**, n. sp. McEvey & Tsacas


**Types**: all from the iso-female type-culture. **Holotype** male: Moorea Fr Polynesia, type-culture no. 271, 11-1986, J.R. David; Muséum National d'Histoire Naturelle, Paris; 3224 (specimen number corresponding to McEvey's register). **Paratypes**: same data as holotype with numbers: 3014-26, 3216-23, 3225-53, 3494-543; held in Muséum National d'Histoire Naturelle, Paris (25 males, 25 females); National Science Museum, Tokyo (5 males, 5 females); British Museum of Natural History, London (5 males, 5 females); Bishop Museum, Hawaii (5 males, 5 females); the Australian National Insect Collection, Canberra (5 males, 5 females) and the Australian Museum, Sydney (5 males, 5 females).

**Diagnosis**: Phallus with anterior paramere short, broad, and pointed, without sensilla; submedian spines on caudal margin of hypandrium close together. Spermathecae not distinctively blackened apically (cf. *D. ananassae*).

**Etymology**: Dedicated to Professor Roger Monier, former Scientific Director of Life Sciences at the CNRS who instituted the RCP «Polynesia» grant 806 which made this study possible.

**Body length**: 3.0 mm (holotype); 2.6 - 3.3 mm (paratype range); females generally larger.

**Head**. male and female: Arista with 4-5 straight rays above and 3 below plus terminal fork. Frons narrow anteriorly, broad posteriorly, breadth in middle equal to length; tan with slight pollinosity when viewed at acute angle to the front. Orbitals in the ratio 9:4:9; equidistant; anterior two slightly closer to eye margin. Carina prominent, with very narrow ridge dorsally. 2nd antennal segment tan, concolorous with front; 3rd segment dusky tan, finely hirsute. Greatest width of cheek 0.1 times greatest diameter of eye. 1st and 2nd oral bristles subequal. Eye with very dense short dark pile. Inner and outer verticals subequal, about 1.3 times longer than posterior reclinate.

**Thorax**. male and female: Brown. Acrostichal hairs in 8 rows in front of dorsoventral bristles, 6 irregular rows (regular rows in some paratypes) between dorsoventrals. Ratio anterior/posterior dorsoventrals 0.8. Sterno-index 0.6-0.7. Preapical bristles on all tibiae; apical

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(1) The 4V and 4C wing indices in all drosophilid descriptions by Tsacas, prior to this one, have been calculated in error in the following manner: the 4V-index has been the inverse of the standard 4V-index (Sturtevant 1942) and the 4C-index has been derived using the length of the ultimate — instead of the penultimate (Sturtevant 1942) — section of the fourth vein. All measures used here in the derivation of wing indices are straight-line distances.
bristle strongly developed ventrally on mid-tibia and barely developed on fore-tibia. Sex-comb of male in transverse rows of stout black bristles; in holotype male: 3 metatarsal rows (from above down) 4-5, 6, and 7 teeth; 3 rows on the second tarsal segment of (from above down) 3-4 irregularly placed, 5 and 6-7 teeth; and one tooth near the apex of the third and fourth tarsal segments. Figure 1 shows a leg of a male from the type-culture 271 and Table 1 shows the paratype range of teeth-numbers on the sex-comb.

TABLE 1

The number of teeth in each row of the male sex-comb (fore-legs) of seven closely related species of the anassae species complex. ana, D. anassae; atr, D. atripex; mon, D. monieri, n. sp.; nes, D. nesoeote; pal, D. pallidosa; pha, D. phaeopleura and var, D. varians. D. tronensis has no sex-comb; the descriptions of the tarsal setation of the other taxa are cursory.

<table>
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</table>

Wings. holotype male: Hyaline. Costal-index = 1.7; 4V-index = 2.3; 4C-index = 1.5; 5X-index = 2.0; third costal section with heavy setation on basal 0.6 (the range of these wing indices, in 13 male paratypes, is given in Table 2). Wing lengths: male 2.3 mm; female 2.6 mm.

Abdomen, male and female: Tergites of male, tan and darker in female, darkened slightly with age. Tergites of both sexes with diffuse, dark bands posteriorly, fainter posterolaterally and uniform in width.

Periphalic organs (Figures 2 and 3). Genital arch (epandrium) narrow dorsally and broad laterally; toe (ventral epandrial lobe) elongate as in D. phaeopleura but with only about 6 bristles. Primary and secondary claspers present. Primary clasper (surstylus) large, with two sets of teeth (prensistae) — a median row of five strongly pointed teeth (cf. three in D. phaeopleura) and a ventromedial cluster of five to six strongly pointed teeth (one of which is greatly elongated); and a lateral row of thicker and shorter blunt black teeth in two portions, an upper of three and a lower of four to five teeth. The secondary clasper (ventral cercal lobe) is very small with a very large curved black medial tooth, and with two medial and three lateral bristles.

Phallic organs (Figures 4 and 5). Aedeagus non-bifid, densely hirsute, with median indentation; slender along entire length. Anterior paramere articulated to aedeagus, very small (cf. D. phaeopleura), pointed and fin-shaped; without sensilla; branched at other end forming a small finger-like paramere with several minute sensilla and another small rounded protruberance lacking sensilla. Posterior paramere long, extending beyond aedeagus; slender, tapering gradually to a point, sheathing the aedeagus. Submedian spines on caudal margin of hypandrium close together and black.

Egg guide (Ovipositor/Oviscape) (Figure 6). Brown, with a fine subterminal hair and 16 short spines, the terminal six on the ventral side close together with an additional spine separated from the others in a dorsal, subterminal position.

Spermatrieae (Figure 7). Elongate, uniformly brown or only faintly darker apically; strongly sclerotized.

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Egg filaments. Two slender filaments flattened in upper quarter.

Pupae. Anterior spiracles with about 12 branches.

Fig. 1 to 7, Drosophila monieri, n. sp.: 1, male sex-comb; 2-3, periphallic organs: 2, posteroventral view, 3, lateral view; 4-5, phallic organs: 4, ventral view, 5, lateral view; 6, egg guide; 7, spermathecae.

Distribution. The type locality is the island of Moorea, part of the Society Islands group (French Polynesia), in the Pacific Ocean (Figure 8). Further specimens were collected from nearby Tahiti.

MORPHOLOGICAL AFFINITIES

Drosophila monieri, n. sp. is a member of the D. ananassae complex of the D. ananassae subgroup because the aedeagus is non-bifid and apically hirsute (Bock and Wheeler 1972). The complex comprises a number of morphologically very similar taxa, which are listed in Table 3. Wing indices and the configuration of teeth on the primary clasper are included in the table. The first six species listed are apparently very similar,
however *D. cornixa*, *D. ironensis*, *D. lachaisei* and *D. varians* do not closely conform. For example *D. varians* has 12 teeth in a row, medially on the primary forcep, which is not differentiated into upper and lower segments; and *D. cornixa* has an extremely large tooth on the secondary clasper, which is almost as large as the anal plate itself. Bock and Wheeler (1972:46) noted that, on purely morphological grounds, the inclusion of *variants* in the *ananassae* subgroup might be questioned. The species lacks the single-toothed secondary clasper characteristic of all members of the subgroup, and the anal plate has the lowermost bristles differentiated, a characteristic of species of the *suzukii* subgroup (Bock and Wheeler 1972). *Drosophila ironensis* has two stout bristles on the secondary clasper and only a single row of five teeth in the upper medial row of the primary clasper (Table 3). In this respect it is similar to *D. lachaisei*; however, *D. ironensis* males have no sex-comb.

### Table II

A comparison of the wing indices of *D. ananassae* and *D. monieri*, n. sp. from Polynesia, showing the variability. s.e.: standard error (n=13); b: third costal section; c: ultimate section of the fourth longitudinal vein, (see Bock 1976).

<table>
<thead>
<tr>
<th></th>
<th><em>Drosophila ananassae</em></th>
<th></th>
<th><em>Drosophila monieri</em></th>
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<tr>
<td>index</td>
<td>mean  s.e.  min  max</td>
<td>mean  s.e.  min  max</td>
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<tr>
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<td>1.79  0.02  1.63  1.97</td>
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<tr>
<td>4V</td>
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<tr>
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<tr>
<td>b/c</td>
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<td>0.62  0.01  0.57  0.66</td>
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<td>C3</td>
<td>0.58  0.01  0.53  0.61</td>
<td>0.58  0.01  0.48  0.66</td>
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</table>

Wing indices are useful diagnostically when combined with other characters. There is, however, a certain amount of variability within a taxon, as is indicated, for example, in Table 2. The range of values among a number of specimens, like the range of the *C*- and *4V*-indices of *D. ananassae* and *D. monieri* (Table 2), do not overlap at all and this affords more confidence in identification. The sex-combs of *D. monieri* and the Fijian species *D. phaephytida* Bock & Wheeler, 1972, are very similar but other morphological features are clearly different. For example, The *C*-index of these two species differ: the average *C*-index of *D. monieri* is 1.8 with a range from 1.63 to 1.97 (Table 2), while in *D. phageleafida* the index is given as 1.6 without a range. Furthermore there are clear differences in the male genitalia: *D. phageleafida* has very large anterior parameres, laterally with four well spaced minute sensilla and spines spaced far apart on the novasternum but in *D. monieri* the parameres are small and bare and the spines on the novasternum are close together.

*Drosophila pallidosa* and *D. ananassae* are perhaps the most difficult species to distinguish in the *ananassae* complex. Bock and Wheeler (1972) suggest that, apart from the difference in abdominal pigmentation in Samoan specimens, the single morphological difference is «the reduced number of rows of the sex-comb of *D. pallidosa* in comparison with *D. ananassae»». It is perhaps less equivocal to compare the total number of teeth in the metatarsal rows. Thus Table 1 shows that *D. pallidosa* has between 11 and 18 teeth in 3 to 4 rows on the metatarsus, this barely overlaps with the range of 18 to 28 found in
D. ananassae. The possibility that the pale iso-female lines from Moorea are D. pallidosa has been rejected by a careful examination of the sex-combs; none were found to have less than 19 teeth on the metatarsus. Thus the material collected in French Polynesia does conform to the description of D. ananassae even though it is polymorphic for abdominal pigmentation.

*Drosophila monieri* is superficially similar to the pale form of *D. ananassae*. Consistent differentiation of these two species requires reference to a number of details. Firstly, the spermathecae of *D. monieri* females are uniformly brown whereas in *D. ananassae* the pigment in the spermathecae is clearly concentrated apically giving it a distinctive black tip. In ten randomly examined isofemale lines of *D. ananassae* from Moorea, all the spermathecae are distinctively blackened apically while in *D. monieri* they are uniformly brown or only faintly darkened apically. Secondly, the C and 4V wing indices mentioned above, differ (Table 2). Thirdly there are fewer rows of teeth on the sex-comb (Table 1) and lastly, and perhaps most distinctively, there are differences in the genitalia (Table 3). Indeed most species of the whole subgroup — apart from the cryptic pair *D. ananassae* and *D. pallidosa* — may be clearly distinguished by reference to the male genitalia. Sex-comb configuration, wing indices and genitalia are the important diagnostic characters for the *ananassae* complex. *Drosophila ironensis*, in fact, lacks a sex-comb altogether.

### TABLE III

Meristic characters of the wings and primary forceps of the ten species of the *D. ananassae* complex. The number of teeth on the primary forceps are in four sets: umr, upper medial row; lmr, lower medial row; ulr, upper lateral row; and llr, lower lateral row. The first six species are very similar.

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<th>species</th>
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Some reciprocal crosses were made between iso-female lines of *D. ananassae* and *D. monieri* from Moorea. No F1 progeny were produced.

**ECOLOGY**

Collections, using banana traps on the island of Moorea, yielded large numbers of *D. ananassae* adults. The initial expectation was to find there the « dark » abdominal form which is considered typical of Polynesia, for example on the Cook Islands, Niue Island, Palmyra Island and Samoa (Futch 1966, Figure 9). Interestingly, however, both dark and light forms were found. This appeared to be the situation that was observed by Futch (1966) on Samoa and which led Bock and Wheeler (1972) to the description of the cryptic species *D. pallidosa*. But a study of the abdominal pigmentation, in the various isofemale lines of *D. ananassae* from Moorea, rapidly led to the conclusion that this population was
polymorphic; specifically, light females could produce a mixture of light and dark offspring and vice versa.

On Samoa, *D. pallidosa* and *D. ananassae* apparently do not occupy exactly the same habitats. Futch (1966:109) reports that «large numbers of dark *D. ananassae*... were encountered in and around the small seaside native villages». While none, or very few, were found at a shaded inland site despite the presence there of large numbers of *D. pallidosa*. Note that Futch (1966) treated *D. pallidosa* as a light form of *D. ananassae*.

By sweeping over fallen, rotting flowers of *Hibiscus tiliaeus* — a very abundant plant in Polynesia — it was discovered that only *D. monieri* was present. Furthermore, it was the only species reared from the same rotting flowers. The discovery of this specific breeding site permitted the establishment of a number of cultures because at sea level *D. monieri* was vastly outnumbered by *D. ananassae* and the females of these two are almost identical. Some other records of association between *D. ananassae* and flowers may now warrant closer examination. Further cryptic species may be found by the application of more refined collecting techniques. Okada and Carson (1982) report the collection of «*D. ananassae*» from the inflorescence of Torch Ginger flowers (*Nicolaia elatior*) in Papua New Guinea and McEvey and Bock (1982) swept «*D. ananassae*» over flowers at Iron Range in northern Queensland.

An altitudinal transect using banana traps between sea level and 1200 m on the island of Tahiti also yielded *D. monieri*. The proportion of that species increased with altitude, in spite of the fact that *Hibiscus tiliaeus* — the plant with which it seems to be associated — is more abundant at sea level. Above 800 m only *D. monieri* was present. From these data we may conclude that *D. monieri* occupies a different ecological niche or at least it finds suitable resources where *D. ananassae* cannot; it can breed in rotting flowers, although this association is probably facultative given that it survives well on standard corn meal/agar medium and it is attracted to banana baits. *Drosophila ananassae* seems to breed mostly in decaying fruits and is mainly found at low elevations while *D. monieri* is relatively more abundant at several hundred meters; for other species, very little has been published about breeding sites.

**BIOGEOGRAPHY**

At present water and low coral reefs and atolls separate the remote, high, forested islands in the south Pacific. However, it is known that such high volcanic islands have been emerging and subsiding over millions of years in the same region. It has also been known for a long time that coral reefs and atolls are their remnants (Darwin 1842). Therefore numerous opportunities have existed in the past for small insects, like drosophilids, to be carried, by wind for example, to the localities where they are now found (Hardy and Kaneshiro 1981). Such dispersal, followed by physical isolation, may account for the present distribution of the species: *D. phaeopleura*, *D. pallidosa*, *D. nesoetes* and *D. monieri* which are endemic to single or several close islands (Figure 8). New Guinea and the islands around it to the west and southeast have not been properly surveyed and it is likely that other closely related species will be found, particularly since New Guinea has a very rich drosophilid fauna and it is the probable source of most wind-dispersed "propagules".

The present distribution of *D. ananassae* appears to be man-assisted. This is a circumtropical species frequently found in close association with humans (Futch 1966, David and Tsacas 1981). It occurs on low exposed islands in the Pacific (Figure 9) where the only suitable habitats are incidentally provided by the activities of man. In this respect the biogeography of abdominal-pigment polymorphism is of interest. Numerous *Drosophila* species are genetically variable and polymorphic with respect to body colour and a complete survey would be beyond the scope of this paper. The case of *D. ananassae* seems, however, quite unique since it exhibits consistent geographic differentiation. The fact that the widespread cosmopolitan form is light while South Pacific populations are dark is like the situation in other species (e.g., *D. malerkotliana* and *D. pseudoananassae*).
Lemeunier et al. 1986), which is difficult to explain in terms of adaptation. The difference observed over a fairly short distance in Polynesia between a population from an atoll and from an elevated and forested island could, on the other hand, be explained by natural selection as in the following case. In several species including D. melanogaster (David et al. 1985) darker forms are more common in cooler and in more humid habitats while light forms predominate in dry and sunny climates. Homogeneous, darkly pigmented populations are found on Samoa, Niue and Rarotonga (Figure 9). But other places, like

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**Fig. 8.** Distribution of the species of the Drosophila ananassae complex. The occurrence of D. atripex, or a taxon very close to it, from New Caledonia, has not previously been reported. A precise identification of the material requires further investigation.

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**Fig. 9.** Localities where Drosophila ananassae has been collected in the Australasian and Pacific regions, showing the distribution and extent of abdominal pigmentation (Bock, 1984; Futch, 1966; Curran, 1936; McEvey, 1981; McEvey and Bock, 1982; Harrisson 1954; Wheeler and Takada, 1964).
New Guinea, Truk Island, Palmyra and Hawaii, harbor populations with intermediate pigmentation (Futch 1966). The Moorea and Tahiti populations seem for the moment to be unique in this respect because they are polymorphic. Interestingly, another population from French Polynesia, collected on the Takapofo atoll (in contrast to the high volcanic islands of Moorea and Tahiti) was uniformly light.

Acknowledgments

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LITERATURE CITED


ANALYSES D'OUVRAGES

Fauna of New Zealand, n° 9, Protura (Insecta) by S.L. TUXEN, 1986, Wellington, New Zealand, (DSIR, PO Box 9741), 50 pp.

Cet excellent travail publié après le décès du Professeur S.L. TUXEN, est une contribution à la connaissance des Protouras de la Nouvelle-Zélande, peu connus jusqu'à ce jour.

Après un bref historique, l'auteur présente une analyse des caractères morphologiques étudiés, des considérations sur le cycle de vie et la biologie, ainsi que les méthodes de récolte et préparation de ces petits animaux. Une clé des familles et des espèces précède les descriptions précises et bien illustrées de 16 taxons examinés, inclus dans 10 genres dont 2 genres et 7 espèces sont nouveaux pour la science.

Une très belle planche de photos réalisée au microscope électronique à balayage montre les détails de certains caractères morphologiques. Le travail inclut aussi, des considérations phylogéniques et zoogéographiques.

J. NAJT


Dans le cadre de l'étude de la Faune de Nouvelle-Zélande, L.A. Mound et A.K. Walker viennent de publier un important travail (n° 10 : Tubulifera), suite à un précédent ouvrage (n° 1 : Terebrantia).

Les deux auteurs sont d'éminents spécialistes de cet Ordre d'Insectes ; le premier du British Museum (Natural History), le second du Department of Scientific and Industrial Research de Nouvelle-Zélande.

L'ordre des Thysanoptères étant peu connu et assez rarement étudié, ce nouvel ouvrage, fruit de recherches conduites avec beaucoup de soin et de méthode représente une contribution remarquable à la connaissance de la faune néozélandaise. Si l'isolement géographique de cet archipel d'îles pouvait laisser croire à une presque totale originalité de la faune, les auteurs ont montré que les vents provenant d'Australie ainsi que l'action de l'homme ont introduit un certain nombre d'espèces. Soixante-huit taxa de Tubulifera groupés en 29 genres sont cités. Dix-sept espèces proviennent d'Australie et huit d'autres parties du monde. Par contre, deux espèces néozélandaises seulement ont été signalé. Deux sous-familles sont admises, les Idolothripinae et les Phlaeothripinae. L'actuelle division en tribus de ce deuxième groupe est discutée, et différée jusqu'à une étude plus complète de cette faune.

Une table d'identification des espèces nouvelles néozélandaises précède la description complète de toutes celles-ci et une revue des espèces introduites. Pour chacune d'elles on trouve la distribution, la biologie, le cycle biologique. La phylogénie et la morphologie d'une espèce-type guident le lecteur non spécialiste ; quant aux techniques de capture, de préparation et de montage elles figurent en rapprocheau premier volume (n° 1 : Terebrantia) rédigé par les mêmes auteurs.

Ajoutons que cet ouvrage est remarquablement présenté quant à la rédaction et la typographie ; les dessins guident le lecteur et traduisent avec précision les descriptions graphiques.

Ce nouveau volume sera un auxiliaire précieux pour les chercheurs qui sont appelés à explorer ce domaine tant au niveau des connaissances fondamentales qu'à celui de leurs applications pratiques.

J.-P. BOURNIER

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