

THE EVOLUTIONARY STATUS OF *DROSOPHILA SERRATA*

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One of the peculiarities of the genus *Drosophila* is the abundance in it of pairs, and of groups of several, sibling species. Siblings are species morphologically similar enough to be practically indistinguishable by inspection, and yet having attained complete or almost complete reproductive isolation. It is tempting to speculate that the evolution of morphological features has reached, in this genus, a high degree of perfection, and that the adaptive evolution is directed largely in physiological channels (Dobzhansky, 1956). Species being so often morphologically close, it is not surprising that geographic races of *Drosophila* species are as a general rule morphologically indistinguishable (cf. Patterson and Stone, 1952; see, however, Stalker and Carson, 1947, and Prevosti, 1954, 1955). In fact, the taxonomic category of subspecies has been seldom made use of in *Drosophila*, at least as compared to other groups of animals the systematics of which has achieved an "advanced" stage. In *Drosophila*, geographic populations, or races, of a species differ more often in such "recondite" traits as the gene arrangements in their chromosomes, which must, however, be regarded as connoting physiological differentiations. Instances of conspicuous variation in visible traits are, to be sure, known among *Drosophila*, but they usually represent intrapopulation balanced polymorphisms. The best studied case of this sort is the variation of the coloration of the abdomen in *Drosophila polymorpha* (da Cunha, 1949); the case of *Drosophila montium* is alleged to be similar (Freire-Maia, 1949), but the published data are inconclusive.

Drosophila serrata Malloch (1927) is a species belonging to the *melanogaster* species group of the subgenus *Sophophora*, described from a locality (Eidsvold) in

Queensland, Australia. A redescription, in the form now accepted in *Drosophila* systematics, can be found in Mather, 1955. We have collected strains belonging to this species from several localities in eastern Queensland, in New South Wales, in New Guinea, and New Britain. Two morphologically distinguishable subspecies can be recognized among these strains. Incipient reproductive isolation, particularly sexual isolation and some hybrid sterility, is also observed among these strains. Interestingly enough, the limits of the morphological subspecies do not coincide, however, with those of the reproductively isolated groups of populations. Observations and experiments bearing on the evolutionary status of this remarkable species are reported below.

GEOGRAPHIC DISTRIBUTION

We have in our laboratories living strains of *Drosophila serrata* descended from mass-cultured founders collected in the localities shown in fig. 1. In more detail, these localities are: Bulahdelah, some 130 miles north of Sydney, New South Wales (this population is referred to below as "Sydney"); Moggill Farm, Brisbane, Queensland (referred to as "Brisbane"); Mundubbera, Queensland; Burnett River, Queensland; Proserpine, Queensland; Crystal Cascade, near Cairns, Queensland (referred to as "Cairns"); Bisianumu Plantation, Sogeri Plateau, north of Port Moresby, Territory of Papua (referred to as "Moresby"); Bulolo Gorge, between Bulolo and Wau, Territory of New Guinea (referred to as "Bulolo"); Keravat, near Rabaul, New Britain (referred to as "Rabaul"). The species has also been found at Gordonvale, near Cairns, and at Lake Barrine, Atherton Plateau, Queensland; in the valley of Musgrave River, Territory of Papua; for more

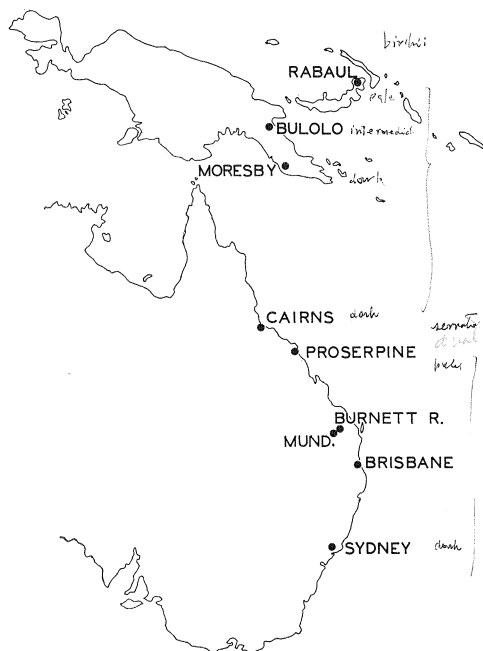


FIG. 1. Geographic origin of the strains of *Drosophila serrata* which served as material for the present investigation.

localities in eastern Queensland, see Mather, 1955. It may be worth while to note that the species has *not* been encountered in samples of *Drosophila* from the vicinities of Sydney; in the valley of Brown River, near Port Moresby; near Goroka and on the road to Daulo Pass, eastern Highlands of New Guinea; and only a few specimens were encountered in the vicinity of Lae, New Guinea, and none of them produced viable progenies. It remains to be discovered whether our species extends its distribution to central and western Queensland and the territories beyond.

MORPHOLOGY

One of the traits which permits division of the strains at our disposal into two clear-cut subspecies, the southern one, *Drosophila serrata serrata*, and the northern one, *Drosophila serrata birchii*, is found in the male genitalia. The difference can easily be seen in both living and dried male specimens under a moderate to high magnifica-

tion of a dissecting microscope. The strains of *serrata serrata* (Sydney, Brisbane, Mundingubbera, Burnett River, and Proserpine) all have two pairs of strong bristles on the genital arch (fig. 2). Males from the Greenslope, Queensland, strain used by Mather also had two pairs of bristles (fig. 9A, in Mather, 1955). The males of *serrata birchii* (Cairns, Moresby, Bulolo, and Rabaul) have three pairs of bristles on the genital arches (fig. 3). At least 20 males have been examined from every strain, without finding a single exception to the rule.

The strains fall into the same two groups also on the basis of a quite different trait—the coloration of the dorsal part of the abdomen in the females. This trait is easily visible in females several days old after the hatching from pupae, but not in young females which are not fully hardened. The subspecies *serrata serrata* has females with dark abdomens. The dark brown bands along the posterior borders of the abdominal

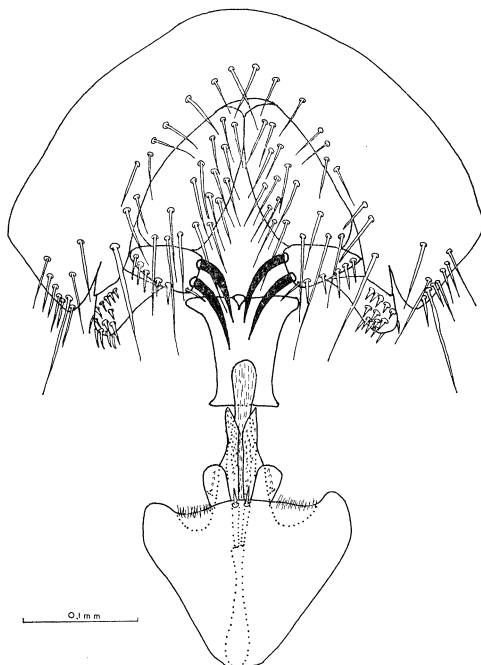


FIG. 2. Male genitalia of *Drosophila serrata serrata* Malloch.

Secondary clasper
or subclasper

n. subsp.

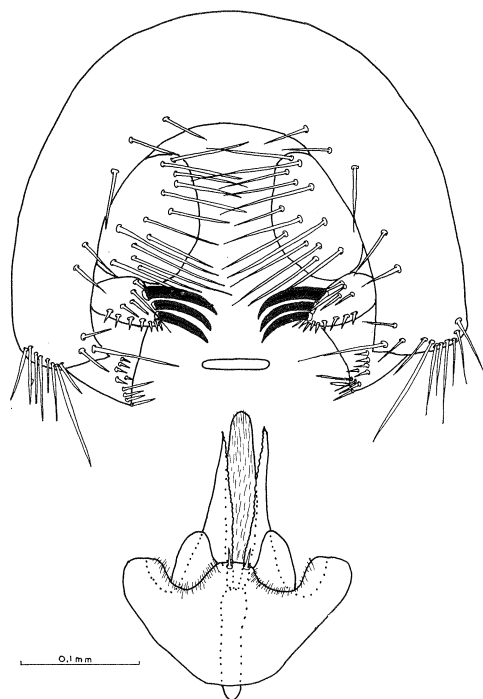


FIG. 3. Male genitalia of *Drosophila serrata birchii* subsp. nov.

tergites are expanded laterally towards the antero-lateral angles of the tergites. The outlines of these bands are not sharp, making the whole abdomen seem fuscous-brown in color; the lighter parts are the middles of the anterior parts and the posterior lateral angles of the tergites. Females of *serrata birchii* have lighter abdomens. In most females, the dark bands are found only on the posterior margins of the 2nd to 5th tergites. These bands are narrowing, rather than expanding laterally, as a rule not reaching the lateral margins. They are more or less sharply delineated, dark brown to black, but leaving most of the tergite brownish yellow.

The coloration of the abdomen varies within subspecies, as well as between the subspecies, and within as well as between strains. The Brisbane, Cairns, and Moresby strains contain some relatively dark and relatively light individuals, with a distinct suggestion of a bimodality. We have raised

separately progenies of darker and of lighter females, and they proved to be darker and lighter on the average respectively. An attempt to divide the flies into discrete classes was, however, felt to be giving untrustworthy results. Moreover, since the males show no bimodality in the abdominal coloration, the characteristics of one of the parents in every cross are uncertain, complicating the genetic analysis.

As to the interstrain but intrasubspecific variation, the situation can be described as suggesting the existence of south-north gradients in the coloration of the female abdomen within each subspecies. In either subspecies, the more southern strains tend to be darker than the more northern ones. The darkest *serrata serrata* are the Sydney strain, while Brisbane, Mundubbera, Burnett River, and Proserpine are lighter. The lightest strain of *serrata birchii* is Rabaul, and the darkest either Moresby or Cairns, Bulolo being intermediate. It should be made clear that these interstrain variations do not erase the differences between the two subspecies. We can recognize the subspecies of a single living female by the color of her abdomen. A group of females from Rabaul is also recognizable as being lighter on the average than a group of Moresby or Cairns females. Some individuals seem, however, intermediate, and would be misclassified if examined singly.

There are indications of differences between the two subspecies also in other characters. Males of *serrata birchii* are generally lighter in coloration than *serrata serrata*, but the difference is not reliable. The females of the former tend to be lighter all over than in the latter, but only the abdominal color is diagnostic. Figs. 2 and 3 suggest differences in the penis and the gonapophyses, those of *serrata birchii* being longer than in *serrata serrata*. How reliable these characters are for classification is uncertain.

Malloch's type locality of *Drosophila serrata* being very close to Mundubbera and Burnett River, it seems safe to conclude that our southern subspecies is the typical one.

TABLE 1. *Sexual preferences among strains of Drosophila serrata*
S = *Drosophila serrata serrata*, B = *Drosophila serrata birchii*

Females	Males	Females tested	Number inseminated	Per cent inseminated
Sydney (S)	Sydney (S)	19	18	95
"	Brisbane (S)	19	19	100
"	Mundubbera (S)	9	9	100
"	Burnett River (S)	10	10	100
"	Cairns (B)	38	0	0
"	Moresby (B)	49	43	88
"	Bulolo (B)	24	0	0
"	Rabaul (B)	20	0	0
Brisbane (S)	Brisbane (S)	20	18	90
"	Sydney (S)	26	24	92
"	Mundubbera (S)	9	9	100
"	Burnett River (S)	8	8	100
"	Proserpine (S)	30	28	93
"	Cairns (B)	42	1	2
"	Moresby (B)	71	44	62
"	Bulolo (B)	22	1	5
"	Rabaul (B)	25	0	0
Mundubbera (S)	Bulolo (B)	18	0	0
Cairns (B)	Cairns (B)	18	18	100
"	Sydney (S)	25	0	0
"	Brisbane (S)	35	1	3
"	Mundubbera (S)	19	1	5
"	Burnett River (S)	14	0	0
"	Proserpine (S)	19	0	0
"	Moresby (B)	104	25	24
"	Bulolo (B)	34	26	76
"	Rabaul (B)	120	59	49
Moresby (B)	Sydney (S)	33	12	36
"	Brisbane (S)	22	17	77
"	Cairns (B)	40	16	40
"	Bulolo (B)	35	2	6
"	Rabaul (B)	36	10	28
Bulolo (B)	Sydney (S)	9	0	0
"	Brisbane (S)	22	0	0
"	Mundubbera (S)	26	0	0
"	Cairns (B)	23	23	100
"	Moresby (B)	43	2	5
"	Rabaul (B)	23	22	96
Rabaul (B)	Rabaul (B)	20	18	90
"	Sydney (S)	23	1	4
"	Brisbane (S)	13	0	0
"	Cairns (B)	42	31	74
"	Moresby (B)	43	14	33
"	Bulolo (B)	23	21	91

A formal description of the northern subspecies can be given as follows:

Drosophila serrata subspecies *birchii*
Dobzhansky and Mather

Differs from *Drosophila serrata serrata* Malloch (1927) in having three, instead of two, pairs of strong bristles on the genital

arch in the males. Females of *birchii* have more lightly colored abdomens, the dark bands on the posterior margins of the abdominal tergites being sharply delimited anteriorly, and narrowing, instead of expanding, towards the lateral margins of the tergites.

Type Locality—Rain forest of the Crystal Cascade Park, near Cairns, Queensland, Australia. The type deposited in the Australia Museum, Sydney, Australia.

SEXUAL ISOLATION

First attempts at crossing the two subspecies having failed, we have made a systematic study of the sexual isolation between them. Groups of 10 virgin females from various strains were placed in ordinary culture bottles with about 10 males of the same or of a different strain, and kept in a lighted constant-temperature room at 25° C. In about 5 days, the females and males were transferred, without etherization, to fresh culture bottles. About 5 days or a week later, the surviving females were dissected, and their spermathecae were examined under a microscope for the presence or absence of sperm. The data obtained are summarized in table 1. It can be seen that, with most combinations of strains, the results are practically of all-or-none kind, almost all females being either inseminated or almost all left virgin. This fact seemed to us to make unnecessary for our purposes to use the more cumbersome "male-choice" method, i.e., exposing two kinds of females to one kind of males.

Intercrosses of the strains of *serrata serrata* occur quite easily. Every one of the 9 intercrosses of this sort recorded in table 1 gives 90 to 100 per cent of the females inseminated. In the subspecies *serrata birchii* the situation is more complex. Insemination of 90 or more per cent of the females has been obtained only when females and males came from the same strain, and also in the crosses Bulolo♀ × Cairns♂, Bulolo♀ × Rabaul♂, and Rabaul♀ × Bulolo♂. Most peculiar is the behavior of the Moresby strain; although according to its morphology it belongs unambiguously to the subspecies *serrata birchii*, it intercrosses actually more easily with some *serrata serrata* strains (Sydney♀ × Moresby♂, Brisbane♀ × Moresby♂, Moresby♀ × Brisbane♂) than to other strains of *serrata birchii* Cairns♂, Moresby♀ × Bulolo♂, Moresby♀

× Rabaul♂, Bulolo♀ × Moresby♂, and Rabaul♀ × Moresby♂).

Disregarding the peculiar behavior of the Moresby strain, the crosses of *serrata serrata* with *serrata birchii* result either in a lack of insemination or in insemination of only a scattering of females.

HYBRID STERILITY

Many of the culture bottles in which the females of one strain were being tested for cross-insemination by males of other strains produced hybrid progenies. All the hybrid progenies were routinely tested for fertility of the F₁ hybrid flies. Attention was paid especially to the progenies of the crosses which, as shown in table 1, result in few cross-inseminations. The results are clear and unambiguous. Except where one of the parents of the cross came from the Rabaul strain, the F₁ hybrids are fertile, and F₂ progenies are produced easily and abundantly. The hybrids having Rabaul as one of the parents produce, on the contrary, no F₂ progenies. It is easily shown that the difficulty is due to sterility of the hybrid males; the hybrid females are fertile, and produce back-cross progenies with other males. Most remarkable of all, the hybrids of Rabaul with other strains of *serrata birchii* (Cairns, Moresby, and Bulolo) are just as sterile as are the male hybrids with *serrata serrata* (Rabaul♀ × Sydney♂, table 1).

DISCUSSION

The data presented in the foregoing pages show clearly enough that evolutionary phenomena of considerable interest can be observed in *Drosophila serrata*. It is especially evident that much more information is needed for a satisfactory understanding of these phenomena. Had our material been restricted to strains from the continent of Australia, the subspecies *serrata serrata* and *serrata birchii* would appear clearly demarcated, and would seem to be standing on the threshold of full species status. Even with these continental strains, it remains, however, unknown whether the distribution areas of the subspecies do or do not overlap,

and if they do whether hybrids or intermediates occur in nature. The only living strain of *serrata birchii* from Queensland is that from Cairns; other strains from the same region (Gordonvale, Lake Barrine) were recorded to have the same abdominal coloration in the females as in the Cairns strain, but they were, unfortunately, discarded before other tests could have been made. The nearest known locality to the south is Proserpine; the Proserpine strain, derived from a few flies hatched from garden fruit collected for another purpose, belongs clearly to *serrata serrata*. Further material from the Cairns-Proserpine region, and from the territory lying farther inland from there, is most desirable.

Crossing the Torres Strait, which separates Australia from New Guinea, discloses a very complex situation. The Moresby strain, derived from the mountains north of Port Moresby, is morphologically very similar to *serrata birchii* from Cairns. Yet the sexual preferences of the Moresby flies are unlike either those of other strains of *serrata birchii*, or of *serrata serrata*. It is to some extent sexually isolated from both, but completely isolated from neither. Crossing the Owen Stanley Mountains, we find on the northern slope of this range, at Bulolo, a population of *serrata birchii* which is actually more like that from Cairns than that from the geographically much closer Moresby. We do not know whether the species inhabits the upper reaches of the Owen Stanley; as stated above, we failed to find *D. serrata* in the highlands in the Goroka region. Moresby and Bulolo may actually be more strongly isolated than their geographic proximity would suggest.

Crossing the Vitiaz Strait, between New Guinea and New Britain, brings a new complication. The Rabaul strain is morphologically *serrata birchii*, and its sexual preferences are accordingly for other strains of the same subspecies (except, as stated above, the Moresby strain), and against *serrata serrata*. And yet, Rabaul produces sterile male hybrids with all other strains at our disposal. It would be most interesting

to discover the behavior of the populations from other islands of the Bismarck Archipelago, and from the Solomons, if the species lives there.

If we were to take hybrid sterility as the criterion of subspecific differentiation, the limits of the subspecies would be different from those drawn on the basis of morphology. We would place Rabaul in one subspecies, and all other strains in the second. If sexual preferences were used as the criterion, the division would be still different, at least tripartite rather than bipartite (compare the behavior of the Moresby strain). This is the sort of situation which has led some authors to declare the subspecies category invalid. We find it, however, convenient to have short names to refer to the easily recognizable groups of populations. Now, a certain arbitrariness of the intraspecific divisions is not an accident but a reflection of the biologically meaningful fact that populations, races, or subspecies are genetically open systems, contrasting with species which are genetically closed systems. The genetic closure is, indeed, the essence of speciation.

The incipient speciation in *D. serrata* may be compared with that in the tropical American *D. paulistorum* (Dobzhansky and Spassky, 1959; Ehrman, 1960). In the former the subspecies have become morphologically distinguishable, while in the latter they are not. In both species there appeared reproductive isolation between the subspecies; yet in *D. paulistorum* the isolation has attained the stage when some of the incipient species coexist sympatrically without mixing. One wonders whether these differences may be related to *D. paulistorum* being an essentially continental species, while *D. serrata* crosses some important water barriers. Further study of *D. serrata*, particularly a comparison of the situation on the continent of Australia with that on the adjacent islands, may shed new light on this situation.

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SUMMARY

Strains of *Drosophila serrata* have been collected and studied from Australia (coastal Queensland and New South Wales), New Guinea, and New Britain. Two subspecies, *serrata serrata* and *serrata birchii* *noya*, have been distinguished on the basis of their external appearance and genital structures. A strong sexual isolation is observed between some of the strains, but this isolation does not coincide with the limits of the morphological subspecies. The behavior of a population from the mountains north of Port Moresby (Territory of Papua) is particularly interesting—this population shows pronounced but incomplete isolation both from *serrata serrata* and *serrata birchii*, although morphologically it belongs to the latter. The population of Rabaul (New

Britain) is morphologically also *serrata birchii*, but it produces sterile male hybrids with all strains at our disposal, of *serrata serrata* as well as *serrata birchii*.

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