

## XIV. Evolutionary Implications of the Mating Behavior of the Species of *Antopocerus* (Drosophilidae) in Hawaii<sup>1</sup>

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The genus *Antopocerus*, as delimited by Hardy (1965), consists of a group of nine closely related Hawaiian species physically characterized by their unique antennae, especially those of the males (Fig. 1). The female antennae (Fig. 2) are much less modified although the first segment is somewhat enlarged and the arisal rays are shorter and more numerous when compared to those of the genus *Drosophila*. The *Antopocerus* species are moderately large, ranging in body length from 4.6 mm. (*A. orthopterus*) to 6.4 mm. (*A. longiseta*) and with wing lengths of 4.8 mm. (*A. orthopterus*) to 6.75 mm. (*A. longiseta*).

### FIELD BEHAVIOR

All species of the genus are denizens of dense forests of Hawaii in areas where the rainfall is typically more than 100 inches per annum. The adults are shy and secretive, restricting their activities during the day to areas of high humidity and low light intensity, typically within three or four feet of the ground, preferring the dense sub-layer of ferns and small shrubs. The adults can often be observed sitting singly on the undersides of fern fronds, on the frond stems of large tree ferns, and on horizontally oriented shrub or tree branches. During the late afternoon as the light intensity decreases and the relative humidity increases they may move somewhat higher up in the vegetation. They have been observed in the early morning, when a steady precipitation is occurring, to be at considerable distances from their preferred daytime sites. They possess the ability to fly rapidly and vigorously; apparently during the dawn period, if a heavy cloud cover exists and rain is falling, they do move about considerably.

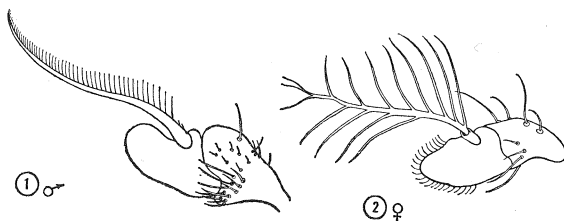


FIG. 1. *Antopocerus aduncus*, antenna of male; FIG 2: *Antopocerus diamphidiopodus*, antenna of female.

<sup>1</sup> This investigation was supported, in part, by Public Health Service Research Grants GM-10640 and GM-11609 from the National Institutes of Health, and by Research Grant GB-711 from the National Science Foundation.

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They are never found in gregarious assemblages, but appear to be solitary in their behavior. As any collector can testify, they possess high ability to detect movement, and are quick to take flight and dive into denser, less well lighted vegetation.

Few data are available concerning the feeding habits of the adults. Infrequently they visit fermenting baits used by collectors. *A. cognatus* was observed feeding upon the surface of rotting *Heimerliodendron bruonianum* leaves but individuals of the *Antopocerus* species do not seem attracted to substances such as bleeding and fermenting tree fern stumps, decomposing lobeliad flowers, fruits and leaves or fungi all of which attract numerous individuals of other species of Hawaiian drosophilids.

Heed (this Bulletin) has shown that most of the *Antopocerus* females lay their eggs only in the fallen decomposing leaves of *Cheirodendron gaudichaudii*. *Cheirodendron* trees never form dense stands, but rather are scattered throughout forests dominated typically by *Metrosideros polymorpha* and *Cibotium* spp. *A. tanythrix* also uses decaying leaves of *Tetraplasandra* sp., and *A. cognatus* to date has been reared only from *Ilex anomala*. All of the larvae feed and mature within the decaying leaves and eventually pupate in the soil.

#### ADVERTISING

Males of many species of Hawaiian drosophilids select particular sites within the forest and advertise their presence to other individuals, either visually by utilizing specific movements or presumably by pheromones (Spieth, 1966). Neither field nor laboratory studies have yielded any evidences that the *Antopocerus* males engage in such activities. Apparently the individuals of the two sexes of *Antopocerus* meet by chance as a result of their normal activities in flying about and sitting on the vegetation.

#### AGONISTIC BEHAVIOR

Many Hawaiian drosophilids exhibit aggressive behavior toward other individuals, including not only other members of their own species but also those of other species and in a few instances of other genera and orders; ritualized aggressive movements and postures have been evolved by many species (see Spieth, 1966). *Antopocerus* species rarely exhibit any such aggressive behavior although occasionally, under the confined conditions of the laboratory, curling has been observed. Such behavior has not been seen in the field, but it should be noted that the finding of two *Antopocerus* adults in close proximity is extremely rare due to their solitary behavior.

#### BASIC MALE COURTSHIP BEHAVIOR

The male mating behavior of each of the species displays a basic pattern intimately related to their unique and aberrant antennae. The behavioral elements shared by all are as follows:

The male orients upon a female, apparently by visual means alone, and quickly assumes the head-under-wings posture at the rear of the female. Simul-

taneously he depresses his head and elevates his abdomen with the result that the body slants forward at an angle of about  $15^{\circ}$ – $20^{\circ}$  with respect to the substrate. His fore tarsi are directed forward with the entire length of each tarsus in contact with the substrate. Immediately thereafter he drums the fore tarsi rapidly against the substrate, using each leg alternately. Such male leg drumming occurs in pulses, alternated with wing movements that are specific for each species (see individual species descriptions). After a variable period of leg drumming and wing action the male rears sharply upward and forward, thrusting his head and thorax above the female's abdomen but *under* her wing vanes. This forward and upward rearing action results in (1) the lifting of the male's forelegs from the substrate so that he is then exclusively supported by his meso- and metathoracic legs and (2) the pushing and sliding of his head along the under surface of the female's wing vanes, thus forcing her wings laterally and upward from their resting positions. The male's arista and second antennal segments serve as the articulation surfaces against the female's wing vanes. After lunging and having achieved a "forward" stance, the male then proceeds to engage in further, complex courtship behavior. (See individual species descriptions.)

Infrequently the male may interrupt his courtship at the rear of a nonreceptive female and circle about her, facing her as he moves with a rapid hopping type motion and simultaneously engaging in specific wing movements.

#### SPECIES SPECIFIC MALE COURTSHIP PATTERNS

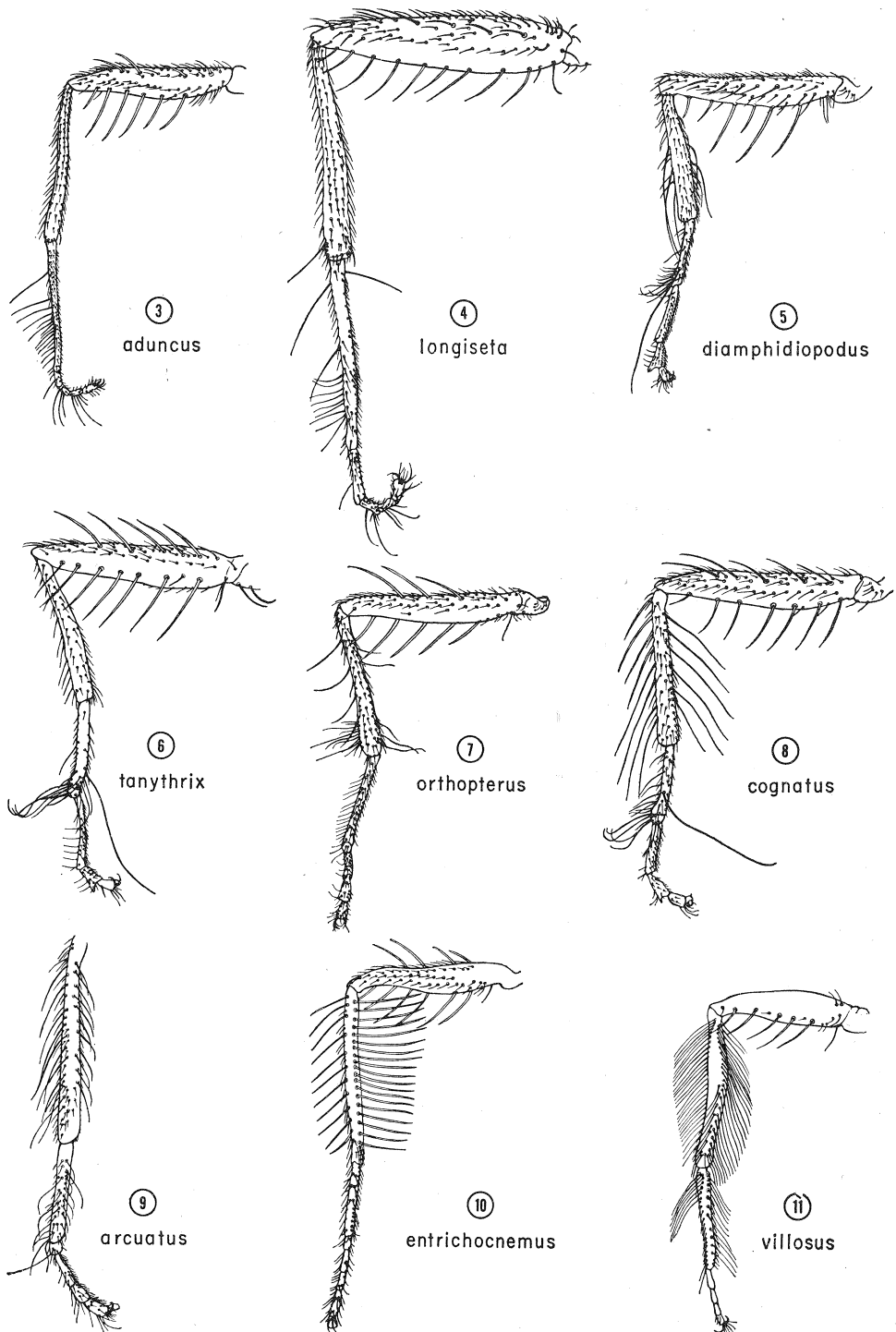
The males of each of the species of *Antopocerus* display specific courtship behaviors in addition to the basic pattern described above. These are as follows:

##### A. *aduncus* Hardy

At head-under-wing position the wings of the male are raised upward approximately  $35^{\circ}$  and forward  $80^{\circ}$  with the vanes rotated almost  $90^{\circ}$  with respect to the horizontal plane. From this extended position the wings are then simultaneously flicked forward to  $90^{\circ}$ – $110^{\circ}$  two or three times in rapid succession. After one or more bouts of wing flicking which alternate with foreleg pawing, the male rears upward and his lifted forelegs (Fig. 3) are partially folded and extended forward with the fore coxae pointing downward, the femora forward, up and outward above and beside the female's abdomen. The tibiae, which are slightly concave, point downwards and forward alongside the female's abdomen with the tarsi extended forward and inward under her abdomen. Both legs are then vibrated rapidly, but the male's wings are held stationary at the  $80^{\circ}$  extended position. After a vibratory bout he drops back to the head-under-wing posture and repeats the entire sequence.

##### A. *diamphidiopodus* Hardy

At head-under-wings posture the male repeatedly flicks both wings upward  $45^{\circ}$  and forward  $90^{\circ}$ . After several bouts of wing flicking, alternating with foreleg pawing, he rears upward with his lifted forelegs (Fig. 5) folded and extended forward with the fore coxae pointing downward, the femora upward and forward, and the tibiae and tarsi hanging directly downward. His wings are then vibrated



Figs 3-11. Fore legs of males of the *Antopocerus* species.

at *extremely* high speed forward and backward in long sweeps of about  $170^\circ$  arc. Immediately after the wing vibrations start, the male curls the tip of his abdomen upward and forward and extrudes a droplet of fluid from the anal papillae. Simultaneously he draws his fore tarsi with a cleaning (moistening?) type motion between his labellar lobes and then repositions the folded forelegs so that the downward directed tibial-tarsal elements are so placed that the tips of large tufts of setae on the distal end of the first tarsal segment and the short second (Fig. 5) are in contact with the posterior end of the tip of the female's abdomen, and the three distal tarsal segments of each leg as a unit are turned laterally away from the median plane. The forelegs are then rapidly vibrated with the result that the tibial-tarsal elements move up and down in small amplitude. After a brief burst of vibration, the forelegs are thrust slightly farther forward, and the terminal three tarsal segments are turned inward and under the tip of the female's abdomen, followed immediately by a slight upward lifting motion. After a vibratory bout of several seconds the male may drop back to the head-under-wing posture and repeat the entire sequence.

#### *A. entrichocnemus* Hardy

At head-under-wings position the male spreads both wings outward approximately  $30^\circ$ . From this extended position the wings are simultaneously flicked forward to  $170^\circ$  from the resting position three to six times. After several bouts of wing flicking alternating with foreleg pawing, he then rears upward and his lifted forelegs (Fig. 10) are folded with the coxae directed downward, the femora upward and forward over the female's abdomen, and the tibiae and tarsi directed backward and oppressed against the femora. The folded forelegs are then vibrated vertically in small amplitudes, and gradually lowered until at least the double rows of tibial setae (Fig. 10) make contact with the tip of her abdomen. Simultaneously with the leg vibrations both wings are vibrated at *extremely* high speed forward and backward in sweeps of about  $90^\circ$ - $100^\circ$  arc and also the articulating membrane surrounding the anal papillae is exposed. After a vibratory bout the male may drop back to the head-under-wing posture to repeat the entire sequence.

#### *A. longiseta* (Grimshaw)

The courtship of *A. longiseta* is essentially similar to that displayed by *A. aduncus* except for the following movements:

1. When the male's wings are flicked to their extreme forward position they are always vibrated in tiny amplitude for a fraction of a second whereas only occasionally is such vibration observed in *aduncus*.

2. When the *longiseta* male vibrates his forelegs (Fig. 4) against the abdomen of the female, he extends both wing vanes horizontally to  $90^\circ$  and vibrates them up and down in tiny amplitude. This entire movement is lacking in *aduncus*.

#### *A. orthopterus* Hardy

The courtship of *A. orthopterus* is essentially similar to that displayed by *A. diamphidiopodus* except for the following:

1. The wing flicks involve slightly less raising of the male's wing vanes, and a somewhat larger forward movement. This is a quantitative difference which is difficult to measure accurately.

2. The foreleg setal ornaments of *orthopterus* are located on the distal end of the tibia as well as on the first tarsal segments (Fig. 7). When the male thrusts his forelegs forward for vibrating at the tip of the female's abdomen, they are lowered so that the tibial setae are in close proximity with the tip of the female's abdomen while the terminal three tarsal segments are turned directly outward 90° from the median plane and parallel with the substrate. If this were not done the spatial relations of the downward pointed tibial-tarsal section of the legs would cause the fore tarsi to be jammed against the substrate as he assumes the vibratory posture.

#### *A. tanythrix* Hardy

The courtship of *A. tanythrix* is essentially similar to that displayed by *A. diamphidiopodus* and *A. orthopterus*. Details of how the forelegs are utilized in vibration against the female have not been ascertained but the peculiar structure of the fore tarsi is quite similar to that of *diamphidiopodus*. (Compare Figs. 5 and 6).

#### *A. villosus* Hardy

At head-under-wing posture the male spreads his wings outward approximately 30°. From this extended position the wings are simultaneously flicked forward to 150° from the resting position several times. The male alternates bouts of wing flicking with foreleg pawing. The remainder of the courting sequence has not been observed but these preliminary positions correspond with those of *entrichocnemus* and, since the male foreleg ornamentation and segmental structure are basically similar to those of *entrichocnemus* (Figs. 10 and 11), it can reasonably be presumed that the remainder of the courtship will involve vibrating of the fore tibia against the dorsum of the female's abdomen.

### FEMALE COURTSHIP PATTERNS

Females utilize a variety of actions to indicate their nonreceptivity. When a male approaches and attempts to achieve the head-under-wing posture the female may rapidly decamp. If she does not flee the presence of the male, she may depress her abdomen and wing tips so that he is unable to achieve his courting stance. More often, however, the male succeeds in assuming the head-under-wing position and then the female kicks vigorously with her hind legs. If the male still persists with his courting sequence, she typically raises her abdomen thus preventing the male from engaging in his foreleg courting movements.

Receptive behavior has been observed only in the case of *A. aduncus* females. Such individuals stand immobile, a characteristic of all receptive females of the endemic Hawaiian species, and allow the male to proceed with his courtship. The *aduncus* female holds her abdomen parallel to the substrate and the visual (to the observer) elements of the acceptance response are (1) the slight spread-

ing of the female's wings and (2) the extrusion of the ovipositor. These are characteristic acceptance responses of Hawaiian drosophilids but the *aduncus* female does not drop her body against the substrate as is characteristic of many species. Further, the extrusion of the ovipositor by the *Antopocerus aduncus* females is relatively slight, approximately 1 mm. in comparison to the 2-3 mm. extension displayed by other large Hawaiian drosophilids such as the picture wings. During copulation the females may move about, fending off other individuals, a quite uncharacteristic behavior for an Hawaiian drosophilid but regularly displayed by species from other areas. The male during copulation may grasp the female's abdomen with both his fore and middle legs or alternately the foreleg tarsal claws may hold onto the dorsal surface of the female's wing vanes. The male's hind tarsi are always crossed under the tip of the female's abdomen and during the first part of the copulatory act his hind tarsi rub the lateral surface of the female's abdominal tip. Five copulations of *aduncus* have been timed and they varied in duration from 14'11" to 18'55" with an average of 15'36".

#### ANALYSIS OF MATING BEHAVIOR

Of the nine species belonging to *Antopocerus*, seven have been observed in courtship and as shown above the males display in common a basic courtship pattern. Additionally males of each species observed possess specific behavioral patterns that distinguish them from each of their relatives. Analysis of these differences show that each species, however, falls into one of three different types or patterns which are correlated particularly with the setal ornamentation and general structure of the male's fore tibia and tarsi.

##### *Male pattern I:*

The male, after he has reared upward and forced the female's wings apart, extends his forelegs forward with the tarsi under the female's abdomen and rapidly vibrates them against her venter. *A. aduncus* and *longiseta* display this type of behavior. Both species possess relatively unspecialized fore tarsi, with a long basitarsal segment and with the second and third segments undifferentiated and of decreasing length. Tarsal ornamentation is relatively simple, consisting of long setae concentrated mainly on a portion of the distal half of the first segment (Figs. 3 and 4). Neither species utilizes abdominal tip display nor high speed, large amplitude wing vibrations.

##### *Male pattern II:*

The male, after he has reared upward and forced the female's wings apart, extends his forelegs forward with the tibia and tarsi hanging directly downward just behind the tip of the female's abdomen. The legs are then vibrated rapidly with the specialized setae of the basitarsus and/or tibia striking against the female's abdominal tip. The distal three tarsal segments are divaricated away from the body of the female. After a vibratory bout the forelegs are moved farther

forward and the distal three tarsal segments are turned inward and under the tip of the female's abdomen, serving to lift upward the female's abdomen.

At the same time that these actions are occurring, both wings are vibrated at extremely high speed in long forward and backward sweeps, the tip of the male's abdomen is curled upward and a droplet of fluid extruded from the anal papillae. *A. diamphidiopodus*, *orthopterus* and *tanythrix* display this type of behavior. All three species possess male tarsi that are fundamentally similar in structure and setal ornamentation (Figs. 5, 6, and 7). The basitarsus is moderately long, somewhat enlarged at the distal tip. The second tarsal segment is short, the third longer than the fourth. A clump of elongated setae are borne on the distal end of the first segment and on the second segment of *diamphidiopodus* and *tanythrix*, while *orthopterus* has a clump of long hairs on the end of the tibia. Hardy (1966) indicates that *A. cognatus* is morphologically very similar to *diamphidiopodus*, and this includes the fore tarsal structure and ornamentation (Figs. 5 and 8). The mating behavior of *cognatus* has not been observed but the similarity of the male's forelegs to those of the other three species of Type II indicates a high probability as to the pattern of mating behavior it must display.

#### *Male pattern III:*

The male, after he has reared upward and forced the female's wings apart, extends his folded forelegs over the dorsum of the female's abdomen, with the tarsi and tibia oppressed against and under the femur. The folded forelegs are then vibrated rapidly in tiny amplitude, and gradually the whole leg is lowered until the two "lateral" rows of long tibial setae (Fig. 10) come into contact with the dorsum of the female. At the same time the three distal tarsal segments of each leg are curled around and under the tip of her abdomen. Simultaneously with the foreleg movements the wings are vibrated in long sweeps at an extremely rapid rate, and the articulating membrane surrounding the anal papillae and the genitalia of the male is exposed. Type III behavior is displayed by *A. entrichocnemus* and *villosus*. The final portion of the repertoire of the *villosus* behavior has not been observed but up to that point it corresponds in all details with that of *entrichocnemus*. Males of both of the species have forelegs that are similar in structure (Figs. 10 and 11), i.e., the fore tibia bear a row of long setae along each anterodorsal and posterodorsal surface, the basitarsus is long, the second segment is short but normal in shape, the third and fourth are also relatively short.

The mating behavior of the rare species *D. arcuatus* (Fig. 9) has not been observed, but the male has forelegs that are somewhat similar to those of *diamphidiopodus* and its relatives, especially *cognatus*. (See Figs. 9, 5 and 8).

#### *Phylogeny of Mating Types*

The pattern of courtship behavior displayed by the *Antopocerus* species clearly indicates the close relationship of the genus to other endemic Hawaiian members of the genus *Drosophila*. Distinctive behavioral elements which the *Antopocerus* species share in common with other Hawaiian Drosophiloids are (1) the accept-



ance responses of the female as displayed by *A. aduncus*, (2) the male's use of both wings for display, (3) the extrusion by some males of an anal droplet, and (4) the actions of the male's forelegs while he is courting at the rear of the female. The most common and widespread method by which Hawaiian *Drosophiloid* males use their forelegs during courtship is to vibrate their fore tarsi under and against the venter of the female's abdomen while they are at the rearward or head-under-wings position. This type of tarsal action obtains especially for those species whose males possess distinct and unique tarsal ornaments, i.e., the bristle tarsi, spoon tarsi, and forked tarsi groups, as well as a number of the modified mouthpart species. This seems to be the primitive method of use of the male foreleg as a courting element and is also shown by numerous other non-Hawaiian species belonging to the subgenus *Drosophila* such as the *virilis* group. As Throckmorton (1966) has shown, the Hawaiian *Drosophiloids* are more closely related to the subgenus *Drosophila* than to any other section of the genus *Drosophila*.

It is therefore reasonable to conclude that the Type I behavior is the most primitive within the genus *Antopocerus* and that the Type II and III species have been derived from Type I ancestors. Significantly males of both Type II and III do, during the terminal portion of courtship, utilize their distal three tarsomeres so that they are brought into contact with the female's venter.

#### SPECIES DISTRIBUTION

The geographical distribution of the nine *Antopocerus* species (Table 1) reveals a number of significant features, i.e.:

(1) Except for *A. diamphidiopodus* none of the species is known to exist on more than one of the islands.

(2) Five of the species live on Maui, three on Hawaii, two on Molokai and one each on Oahu and Lanai.

(3) None of the species has been found on Kauai or West Oahu.

(4) The two species which display the most primitive type of mating behavior are restricted to Maui and Molokai.

McDougall (1964) has shown that the major Hawaiian islands (Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii, Fig. 12) decrease in age from west to east with lavas from Kauai being at least 5.6 million years old while the oldest lavas from Hawaii (Kohala area) are less than a million years old. The present islands

TABLE 1

Species	Mating type	Kauai	W. Oahu	E. Oahu	Lanai	Molokai	W. Maui	E. Maui	Kohala (Haw.)	Kona (Haw.)	Volcano (Haw.)
<i>aduncus</i>	I	absent	absent	.	.	.	X	X	.	.	.
<i>longiseta</i>	I	absent	absent	.	.	X	.	.	.	.	.
<i>arcuatus</i>	II?	absent	absent	X	.	.	.	.	.	.	.
<i>cognatus</i>	II?	absent	absent	.	.	.	.	.	.	X	X
<i>diamphidiopodus</i>	II	absent	absent	.	X	X	X	X	.	X	X
<i>orthopterus</i>	II	absent	absent	.	.	.	.	X	.	.	.
<i>tanythrix</i>	.	absent	absent	.	.	.	.	.	X	X	X
<i>entrichocnemus</i>	III	absent	absent	.	.	.	X	X	.	.	.
<i>villosus</i>	III	absent	absent	.	.	.	X	X	.	.	.

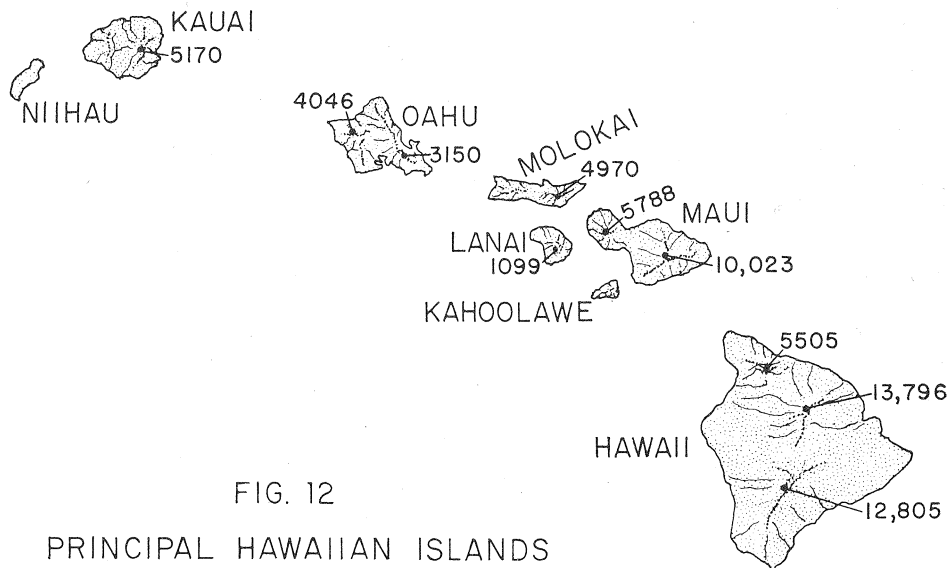


FIG. 12

## PRINCIPAL HAWAIIAN ISLANDS

of Oahu, Molokai and Maui have each been created by the fusion of two major shield volcanoes, i.e., a western and an eastern one. In all three islands the western shields are approximately 300,000 years older than the eastern shields. The islands of Maui, Molokai, and Lanai are unique also in that during their existence they have at three different times been fused together into a single land mass for considerable periods. Each of the periods of island fusion was due to the level of the sea retreating, probably as a result of extensive glaciation and the concomitant withdrawal of vast amounts of water from the ocean basins. Stearns (1966) believes that during these periods of sea level retreat the climate of the islands was cooler than normal, the rainfall increased, and the rain belts moved lower on the islands with the results that the forests moved down the slopes of the mountains. This would, of course, affect the distribution of the *Drosophiloid* fauna on the various land masses. However, Kauai, Oahu and Hawaii are surrounded by such deep oceanic waters that the changing oceanic levels that occurred during the Pleistocene would not have resulted in land connections being created between each of these three islands and any of the other islands. Thus the present distribution of the species complex has in part at least involved colonization across reaches of open ocean (Table 2).

Since the developmental stages (eggs and larvae) occur in the leaves of *Cheirodendron*, and rarely in those of *Tetraplasandra* and *Ilex*, it is difficult to conceive that migrations of the immature stages could have occurred by seaborne means. Presumably the adult flies must have been transported by aerial means in at least some instances.

The lack of any records of the genus from West Oahu and Kauai is not due either to inadequate collecting efforts or to unsuitable habitats. Numerous experienced collectors (beginning with Perkins in the last century and including during the last two decades especially Hardy and his colleagues) have diligently collected in these areas without discovering a single individual of *Antopocerus*. Further-

TABLE 2  
Estimated ages of Hawaiian Island areas\*

	Million years
Kauai	5.6-3.8
West Oahu (Waianae Mts.)	3.4-2.7
East Oahu (Koolau Mts.)	2.2-2.5
West Molokai	1.8
East Molokai	1.5-1.3
West Maui (Wailuku Mts.)	1.3-1.15
East Maui (Haleohala)	0.8
Hawaii (Kohala Mts.)	< 1.0
Hawaii (Mauna Kea)	0.6
Hawaii (Mauna Loa)	< 0.5
Hawaii (Puu Waawaa)	0.4

\* From Stearns 1966. The data were derived by employment of the K-Ar technique. Although the samples are relatively few in number the results are of real significance in showing the relative ages of the island landmasses.

more both areas not only have a rich fauna of endemic *Drosophiloids*, equivalent to that of any of the other Hawaiian areas or islands, but also the food sources of *Antopocerus* (i.e., *Cheirodendron*, *Tetraplasandra* and *Ilex*) are abundant, especially on Kauai. The conclusion is, therefore, that the genus *Antopocerus* is not now represented on West Oahu and Kauai and in all probability never was present in these areas.

#### DISCUSSION

A striking feature of the genus *Antopocerus* is the adaptive relationship of the structure of the male's antennae to his mating behavior. When the courting male lunges forward and upward over the abdomen of the female, he forcibly spreads her wings apart 45° and up 15°-20°. His erected and forward directed antennae bear the force of the lunge as they slide against the under surface of the female's wing vanes. The antennae (Fig. 1) are physically adapted for this function: (1) the first antennae segments are elongated and also enlarged in diameter; (2) the arista are elongated, enlarged and whiplike, and (3) the aristal setae are short but numerous, restricted to the dorsal surface except for an occasional short ventral seta near the distal tip in the primitive species. When the male lunges,

TABLE 3

Approximate distances between (I) Hawaiian Islands and (II) native rain forest areas of Hawaiian Islands

	I (miles)	II (miles)
Kauai—Oahu	70	90
Oahu—W. Molokai	25	..
Oahu—E. Molokai	..	50
Molokai—W. Maui	8.5	19
Molokai—Lanai	9	20
W. Maui—Lanai	9	19
E. Maui—Hawaii	30	40

his erected antennae are so positioned that the aristae are directed forward with the setose dorsal edge turned latero-ventrally and the median surface of the third segment facing upward. Thus the bare medioventral surfaces of the basal three-fourths of the aristae and the distal, "velvety" median surface of the third segment serve as the articulating elements against the female's wing vanes. Further, the elongated first segment which extends upward and forward prevents the female wing vane from pressing against the dorsal surface of the male's vertex, thus protecting the large setae located on it. Clearly the normal *Drosophiloid* antenna would be poorly adapted for such vigorous lunging movements as the *Antopocerus* males display. Selection pressure for the evolution of the Antopocerid type of antennae could not have arisen, however, until the ancestral stock first developed the peculiar male lunging behavior. *Antopocerus* thus provides a clear instance of how behavior may evolve before structural evolution can occur.

As shown above, three unique types of mating behavior are displayed by the various species within the genus. Those species whose mating behaviors have not been studied (i.e., *cognatus* and *arcuatus*, see Figs. 8 and 9) display sexually dimorphic male characters so similar to those of the other species which have been studied that they can tentatively be placed as to type of mating behavior. An analysis of the distribution of the species displaying each of the types of mating behavior, combined with a consideration of the total distribution of the species, provides an insight into the origin and historical development of the genus.

The Type I mating behavior which is considered the primitive type (see above) is displayed by only two allopatric species, i.e., *aduncus* which is restricted to Maui and *longiseta* which is restricted to Molokai. Their mating behaviors indicate that these two species are closely related.

The islands of Maui and Molokai are deemed to be less than two million years old (Table 2). During the Pleistocene these two islands plus Lanai were fused into a single landmass at least three times (i.e., during early, middle and late Pleistocene) due to the retreat of the sea level. At present Maui and Molokai are separated by a narrow channel (8.5 miles). Likewise both islands are separated from Lanai by about the same distance (9.0 miles). Nevertheless neither species, i.e., *aduncus* or *longiseta*, has been found on Lanai and neither seems to have been able to invade and establish itself on both Molokai and Maui, nor have they been able to invade Oahu and Hawaii. Thus it seems logical to conclude that the ancestral stock of *Antopocerus* arose in the Molokai-Maui-Lanai area. The most primitive descendants of the ancestral stock are now represented by two allopatric species which display low colonizing ability and are restricted to Maui and Molokai.

The Type II mating behavior is known to be displayed by three species, i.e., *diamphidiopodus*, *orthopterus*, and *tanythrix*, and presumably by *cognatus* and possibly by *arcuatus*. *A. diamphidiopodus* has the widest distribution of any of the species, being found on Molokai, East and West Maui, Lanai, and Hawaii. The distribution of this species on the first three islands can be attributed perhaps to the fact just noted that during the Pleistocene these islands were repeatedly joined into a single landmass. Hawaii, however, has always been separated from

the other islands by an ocean barrier and the presence of *diamphidiopodus* on this island clearly indicates that the species has been able to cross the ocean barrier. Further its widespread distribution indicates that it is probably the most ecologically tolerant of all the species, a conclusion further supported by its presence on Lanai which is a relatively low island with only a relict montane forest of the kind that the *Antopocerus* species need. Perhaps other species previously inhabited Lanai but have been exterminated as the island has eroded and the climatic conditions have changed thus reducing the montane forest. In addition to *diamphidiopodus*, two other species, *cognatus* and *tanythrix*, are found on the island of Hawaii and both are restricted solely to Hawaii.

The overall structure of *tanythrix* and especially the male's foreleg (Fig. 6) indicates that it may well have evolved from a *diamphidiopodus* type ancestor that invaded Hawaii.

Hardy (1966) notes the close morphological relationship of *cognatus* and *diamphidiopodus*. The structure of the male foreleg (Figs. 5 and 8) indicates that these two species must have a quite similar courtship behavior. Further Kenneth Kaneshiro (personal communication) notes that in the Kilauea area near Volcano and the Saddle Road areas above Hilo three populations have been collected conforming respectively to *cognatus*, *diamphidiopodus* and an intermediate population between the two species. In sum, parsimony would suggest (1) that *diamphidiopodus* originally evolved in the Maui-Molokai-Lanai area and (2) that the species has colonized Hawaii at least three times with the first successful colonizers evolving into *tanythrix* and a later second invasion evolving into *cognatus*. A still later invasion of *diamphidiopodus* has not only established the species itself on Hawaii but the isolating mechanisms of *cognatus* have not as yet evolved to the level that gene flow is prevented between the two species.

*A. orthopterus* is known only from East Maui. Its mating behavior is the most specialized of the Type II species. Since it is restricted to East Maui it appears to be a poor colonizer when compared to *diamphidiopodus*. It is plausible to suggest that *diamphidiopodus* and *orthopterus* diverged from a common ancestor. As noted above West and East Maui arose as separate islands with East Maui about 300,000 years younger than West Maui; these islands fused during the early Pleistocene and then were separated for a period of time and again fused from the middle Pleistocene to the present. It is an attractive hypothesis that during the first period of fusion an ancestral Type II species inhabited the entire area—then during the separation this stock evolved into *diamphidiopodus* on West Maui and *orthopterus* on East Maui.

*A. diamphidiopodus* evolved into an ecologically tolerant, aggressive species that later was able to colonize not only Molokai, East Maui, and Lanai but also Hawaii while *orthopterus* remained restricted to East Maui.

The Type III mating behavior is known to be displayed by *entrichocnemus* and *villosus*, two species known only from West and East Maui. Additionally, Kenneth Kaneshiro (personal communication) informs me that an undescribed species with ciliation on the entire male fore tibia and with a few ciliae at the apex of the basitarsus has been collected from Molokai and East Maui. The structure of the male foreleg of this new species would suggest relationship to the

Type III flies. Present data are insufficient to deduce any relationships between the species of Type III other than the fact that the extraordinary ciliation of the male *villosus* foreleg indicates a high level of specialization.

The question can be posed as to evolutionary relationships of the three mating types. Thus if Type I represents the primitive *Antopocerus* behavior, have both other types been derived independently from Type I or sequentially? If sequentially which of the two, Types II or III, is intermediate? As noted above, when the Type I male vibrates his forelegs during courtship, the femora are extended forward, upward and slightly outward above and beside the posterior portion of the female's abdomen. The fore tibiae extend downward and forward alongside the female's abdomen. The tibiae are slightly concave on their "inner" surface which enables them to "fit" against the rounded sides of the female's abdomen. Significantly the tarsi of both Type II and III males are also slightly concave even though they are employed in quite a different manner when courting. The males of Type I lack any long setae along the sides of the fore tibia and the second tarsomere is longer than the third (Figs. 3 and 4). Type II and Type III males, excepting *tanythrix*, all possess some long setae along the sides of the tibia which give them the appearance of having a row on each side (Figs. 5, 7, 8, 9, 10, 11). *A. villosus* has the greatest number and *orthopterus* the fewest. Further, males of both types have second tarsomeres that are shorter than the third tarsomeres but those of Type II are clearly shorter and more specialized than are those of the Type III males. The Type II tarsi as a unit are clearly more modified from the primitive type than are the Type III tarsi but both types might well have diverged from an ancestral stock not too different from *arcuatus*.

On the island of Kauai the food plants used by *Antopocerus* are abundant but intensive collecting has resulted in no known representatives of the species being found, which indicates that the genus most probably never has existed on Kauai. Since Kauai is the oldest of the major Hawaiian islands that currently are inhabited by the endemic Drosophiloid fauna, it can logically be suggested that the genus *Antopocerus* must be younger than Kauai. The age of Western Oahu (which to date has not been shown to be inhabited by any representative of *Antopocerus*) has been estimated by McDougall (1964) to be from 3.4 to 2.7 million years (Table 2). There remains the possibility that *Antopocerus* will eventually be found on Western Oahu since one species, *arcuatus*, is found on Eastern Oahu and the only separation between the two areas of Oahu is the low, flat valley between the two major volcanic shield mountains, the eastern Koolau range and the western Waianae range. These ranges lie roughly parallel to each other, the distance between the crests of the respective ranges being approximately 15 miles. East Oahu appears to have a maximum age of 2.5 to 2.2 million years and if *arcuatus* has not been able to cross to Western Oahu this reduces the maximum possible age of the genus to less than 2.5 million years. However, as shown above, *A. arcuatus* which is found on East Oahu is a specialized species while *A. aduncus* and *A. longiseta* (the primitive members of the genus) are restricted to Maui and Molokai respectively. Since other more specialized species also live on these two islands (see Table 1) it appears that ecologically the two primitive species are able to compete with the more specialized ones and thus the

deduction can be made that the primitive stock has not been able to colonize across expanses of ocean. Further this would indicate that, since Molokai has a maximum age of 1.8 million years and Maui 1.3 million years, the genus *Antopocerus* must be less than 1.8 million years old.

Throckmorton (1966) in his study of the relationships of the Hawaiian Drosophilidae noted that *Antopocerus* species share characteristics of the ovipositor, ejaculatory bulb, and ejaculatory apodeme with other species groups whose males possess tarsal ornaments, i.e., the bristle tarsi, the spoon tarsi and the forked tarsi. In other respects *Antopocerus* seems neutral. The mating behavior is also neutral, but it in no way presents any evidence that would contravene Throckmorton's phylogeny.

#### SUMMARY

In sum, *Antopocerus* appears to be a monophyletic genus that arose as the result of a behavioral change in the mating behavior which sufficed to create the selection pressure resulting in the evolution of structural modifications that differentiate the genus. The genus evolved in the Molokai-Maui-Lanai portion of the Hawaiian islands and therefore must be less than 1.8 million years old. The primitive species are still restricted to this area but subsequent evolution has produced more specialized species which have been able to colonize Oahu and Hawaii. All evidence indicates that speciation within the genus has occurred as a result of geographical isolation. With respect to number of species and to the distribution of its species, *Antopocerus* appears to be the "simplest" of the major species groups of the endemic Hawaiian Drosophiloids. It therefore can serve perhaps as a paradigm for the understanding and analysis of the other more complex species groups. Unfortunately as yet it is impossible to rear the species under laboratory conditions. Whenever this becomes possible the *Antopocerus* species should serve as ideal material for further analysis of the basic pattern of Drosophiloid evolution in the Hawaiian islands.

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