

X. Male Genitalia of Some Hawaiian Drosophilidae^{1,2}HARUO TAKADA³

As a part of a project of the Japan-U. S. Cooperative Science Program, an opportunity was given to the author to participate in a collecting trip to investigate the *Drosophila* fauna in the Hawaiian Islands. The following is a result of the collections made from July 15 to August 14, 1964. In addition to the author's collections, examples of many species of endemic Drosophilidae were available from the laboratory stocks and the wild collections of Drs. Lynn Throckmorton, W. B. Heed, Hampton Carson, Herman T. Spieth, Frances Clayton, Marshall R. Wheeler, and D. Elmo Hardy.

Sturtevant (1919) mentioned the importance of the male genitalia as an auxiliary tool to separate the two closely related species, *Drosophila melanogaster* and *D. simulans*. Since that time the main parts of the genitalia, especially the external genital apparatus and the copulatory organs of *Drosophila* have been investigated by many workers, especially Hsu (1949) and Okada (1954). In recent times modern taxonomists have realized the importance of characteristics of the male genitalia to systematics, and to phylogeny.

The present paper is a survey of the male genitalia of 55 species of the endemic Hawaiian Drosophilidae, studied from a comparative point of view. These are illustrated in Figures 1 through 4. Finally, an attempt has been made to show the phylogenetic relationships among the Hawaiian Drosophilidae; this is done in Figures 5 and 6.

SPECIES LIST

The species used in this investigation have come from the five main Hawaiian Islands: Hawaii, Maui, Oahu, Molokai, and Kauai. Table 1 lists the species, both the named ones and the undescribed (or unidentified) ones and also shows the collection locality or the collection number and the numbers of the male genitalia figures in Figures 1 to 4. In Figures 1 to 3, the standard bristle patterns of the anal plates are abbreviated or omitted.

DESCRIPTIONS OF MALE GENITALIA

Idiomyia species 1, from Hawaii.

External genital apparatus (Figure 1.1): Genital arch convex at anterior margin, with about 17-18 bristles on lower portion; toe prominent, covering a part of the clasper; upper portion without bristles; heel pointed downward. Anal

¹ This paper is dedicated to Professor Sajiro Makino, Zoological Institute, Hokkaido University, Sapporo, Japan, in honor of his sixtieth birthday, June 21, 1966.

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TABLE 1

List of the species used in this study, with their geographic origins, and the corresponding drawings in Figures 1 through 4

Species	Locality	No. in Fig. 1-4
<i>Idiomya</i> species 1	HH10.7	1
<i>Idiomya perkinsi</i>	Puu Kolekole, Molokai	2
<i>Antopocerus cognatus</i>	Kipuka Puauulu, Hawaii	3
<i>Antopocerus longiseta</i>	Puu Kolekole, Molokai	4
<i>Antopocerus diamphidiopodus</i>	Puu Kolekole, Molokai	5
<i>Nudidrosophila</i> species 2	Kipuka Ki, Hawaii	6
<i>Nudidrosophila amita</i>	Kipuka Ki, Hawaii	7
<i>Drosophila</i> (<i>Drosophila</i>) <i>disticha</i>	Puu Kolekole, Molokai	8
<i>Drosophila</i> (<i>Drosophila</i>) species 3	Kipuka Ki, Hawaii	9
<i>Drosophila</i> (<i>Drosophila</i>) <i>basimacula</i>	Mohihi, Kauai	10
<i>Drosophila</i> (<i>Drosophila</i>) <i>quasianomalipes</i>	Kokee, Kauai	11
<i>Drosophila</i> (<i>Drosophila</i>) <i>mimica</i>	Kipuka Puauulu, Hawaii	12
<i>Drosophila</i> (<i>Drosophila</i>) <i>olaae?</i>	Paliku, Maui	13
<i>Drosophila</i> (<i>Drosophila</i>) <i>scolostoma</i>	Paliku, Maui	14
<i>Drosophila</i> (<i>Drosophila</i>) species 4	Alakai Swamp, Kauai	15
<i>Drosophila</i> (<i>Drosophila</i>) <i>hirticoxa</i>	Paliku, Maui	16
<i>Drosophila</i> (<i>Trichotobregma</i>) <i>petalopeza</i>	Paliku, Maui	17
<i>Drosophila</i> (<i>Drosophila</i>) <i>fungicola</i>	Kipuka Puauulu, Hawaii	18
<i>Drosophila</i> (<i>Drosophila</i>) <i>incompleta</i>	Paliku, Maui	19
<i>Drosophila</i> (<i>Drosophila</i>) <i>parva</i>	Kipuka Puauulu, Hawaii	20
<i>Drosophila</i> (<i>Drosophila</i>) <i>villosipedis</i>	C99.3	21
<i>Drosophila</i> (<i>Drosophila</i>) <i>pilimana</i>	West Maui, Maui	22
<i>Drosophila</i> (<i>Drosophila</i>) <i>engyochracea</i>	Kipuka Puauulu, Hawaii	23
<i>Drosophila</i> (<i>Drosophila</i>) <i>grimshawi</i>	Molokai	24
<i>Drosophila</i> (<i>Drosophila</i>) <i>crucigera</i>	C63.4	25
<i>Drosophila</i> (<i>Drosophila</i>) <i>adiastola</i>	Waikamoi, Maui	26
<i>Drosophila</i> (<i>Drosophila</i>) <i>punalua</i>	Pupukea, Oahu	27
<i>Drosophila</i> (<i>Drosophila</i>) <i>picticornis</i>	Mohihi, Kauai	28
<i>Drosophila</i> (<i>Drosophila</i>) <i>nasalis</i>	Waikamoi, Maui	29
<i>Drosophila</i> (<i>Drosophila</i>) <i>crassifemur</i>	Puu Kolekole, Molokai	30
<i>Drosophila</i> (<i>Drosophila</i>) <i>crassifemur</i>	Kipuka Ki, Hawaii	31
<i>Drosophila</i> (<i>Drosophila</i>) <i>crassifemur</i>	Halemanu, Kauai	32
<i>Drosophila</i> (<i>Drosophila</i>) species X <i>Lonchoptera</i>	West Maui, Maui	38
<i>Drosophila</i> (<i>Drosophila</i>) <i>ochracea</i>	Hawaii	55
<i>Dettopsomyia nigrovittata</i>	Mt. Tantalus, Oahu	34
<i>Titanochaeta contestata</i>	Pupukea, Oahu	35
<i>Scaptomyza</i> (<i>Exalloscaptomyza</i>) <i>mauiensis</i>	Mt. Tantalus, Oahu	36
<i>Scaptomyza</i> (<i>Tantalia</i>) <i>albovittata</i>	Pupukea	33
<i>Scaptomyza</i> species 5	Kipuka Puauulu, Hawaii	37
<i>Scaptomyza</i> species 6	Paliku, Maui	39
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 7	West Maui, Maui	40
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 8	Paliku, Maui	41
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 9	Mohihi, Kauai	42
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 10	Paliku, Maui	43
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 11	Paliku, Maui	44
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 12	Mohihi, Kauai	45
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 13	Paliku, Maui	46
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) <i>photophilia</i>	Paliku, Maui	47
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) species 14	Paliku, Maui	48
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) <i>longipecten</i>	Paliku, Maui	49
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) <i>cryptoloba</i>	Pupukea, Oahu	50
<i>Scaptomyza</i> (<i>Trogloscaptomyza</i>) <i>latitergum</i>	Haleakala, Maui	51
<i>Scaptomyza</i> (<i>Bunostoma</i>) <i>anomala</i>	Alakai Trail, Kauai	52
<i>Scaptomyza</i> (<i>Bunostoma</i>) <i>cnecosoma</i>	Manoa Valley, Oahu	53
<i>Scaptomyza</i> (<i>Bunostoma</i>) <i>palmae</i>	Kamuela, Hawaii	54

plate fused with genital arch at middle; without tip and rear angle, and with about 8 short bristles at under margin.

Phallic organs (Figure 4.1): Penis slender, subapically with a medio-dorsal process in lateral aspect. Anterior gonapophyses slender, with a sensillum at tip;

apex of anterior gonapophyses not reaching the level of insertion of the paramedian spines of the hypandrium. Posterior gonapophyses absent. Hypandrium apically flat and with paramedian spines. Phallosomal index (P.I.) = 4.0.

Idiomyia perkinsi Grimshaw.

External genital apparatus (Figure 1.2): Similar to *Idiomyia* sp. 1, with the following differences. Genital arch with 20–22 bristles on under margin. Anal plate with rear angle and with dense bristles.

Phallic organs (Figure 4.2): As in *Idiomyia* sp. 1, with the following differences. Anterior gonapophyses rather long, the tip extending beyond the level of insertion of the paramedian spines of the hypandrium. P.I. = 5.0.

Antopocerus cognatus (Grimshaw).

External genital apparatus (Figure 1.3): Genital arch broad below, with about 12 bristles on the lower portion. Anal plate separated from genital arch, the tip and rear angle absent. Primary teeth of clasper about 7–8.

Phallic organs (Figure 4.3): Like *Idiomyia perkinsi*, with the following differences. Upper half of anterior gonapophyses with many tiny sensilla. P.I. = 5.0.

Antopocerus longiseta (Grimshaw).

External genital apparatus (Figure 1.4): Genital arch narrow above, broad below, with a bristle at the middle and about 10 bristles on the lower portion. With about 6 primary teeth on clasper.

Phallic organs (Figure 4.4): Penis and anterior gonapophyses rather slender; apex of anterior gonapophyses at almost the same level as the point of insertion of the paramedian spines of the hypandrium. P.I. = 5.0.

Antopocerus diamphidiopodus Hardy.

External genital apparatus (Figure 1.5): Like *Antopocerus longiseta*, but with the following differences. Rear angle of anal plate present. Genital arch weakly sclerotized on upper posterior portion, and with about 12 bristles on lower portion.

Phallic organs (Figure 4.5): Similar to those of *Antopocerus cognatus*, with the following differences. Middle portion of penis convex dorsally; P. I. = 5.0.

Nudidrosophila species 2, from Hawaii.

External genital apparatus (Figure 1.6): Genital arch uniformly broad, the anterior margin nearly straight; with 6 bristles along the posterior margin and about 10 on the under margin; toe slightly higher.

Phallic organs (Figure 4.6): Penis broad apically, pointed dorso-apically. Paramedian spines of hypandrium rather long. P.I. = 5.0.

Nudidrosophila amita Hardy.

External genital apparatus (Figure 1.7): Posterior margin of genital arch nearly straight; with about 8 bristles on the lower portion. Anal plate semi-circular.

Phallic organs (Figure 4.7): Penis bow-shaped and with a hook-like process on the dorso-apical portion. P.I. = 6.0.

Drosophila disticha Hardy.

External genital apparatus (Figure 1.8): Like *Antopocerus diamphidiopodus*,

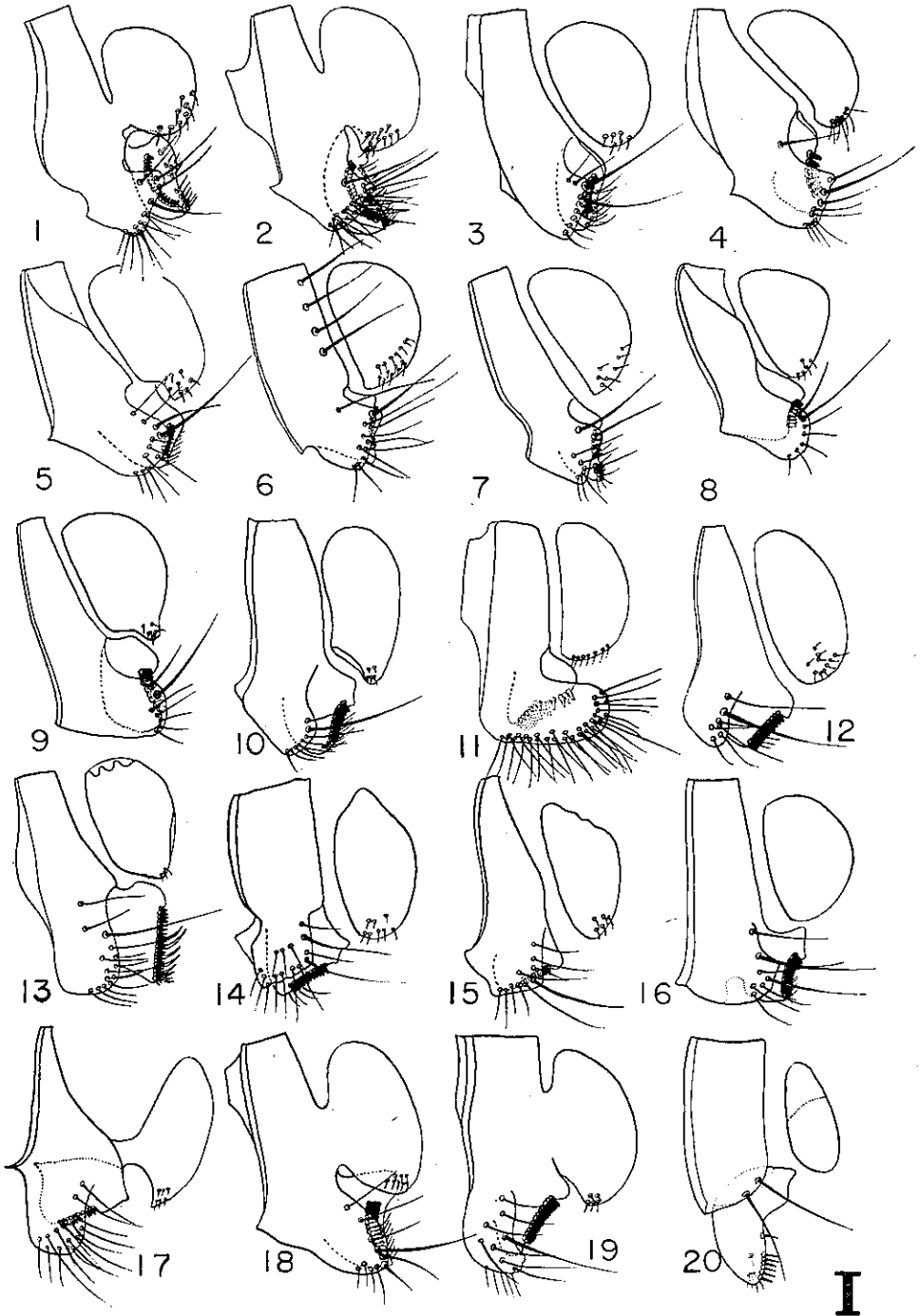


FIG. 1. Male external genital apparatus of 20 species of Hawaiian *Drosophilidae* (see Table 1).

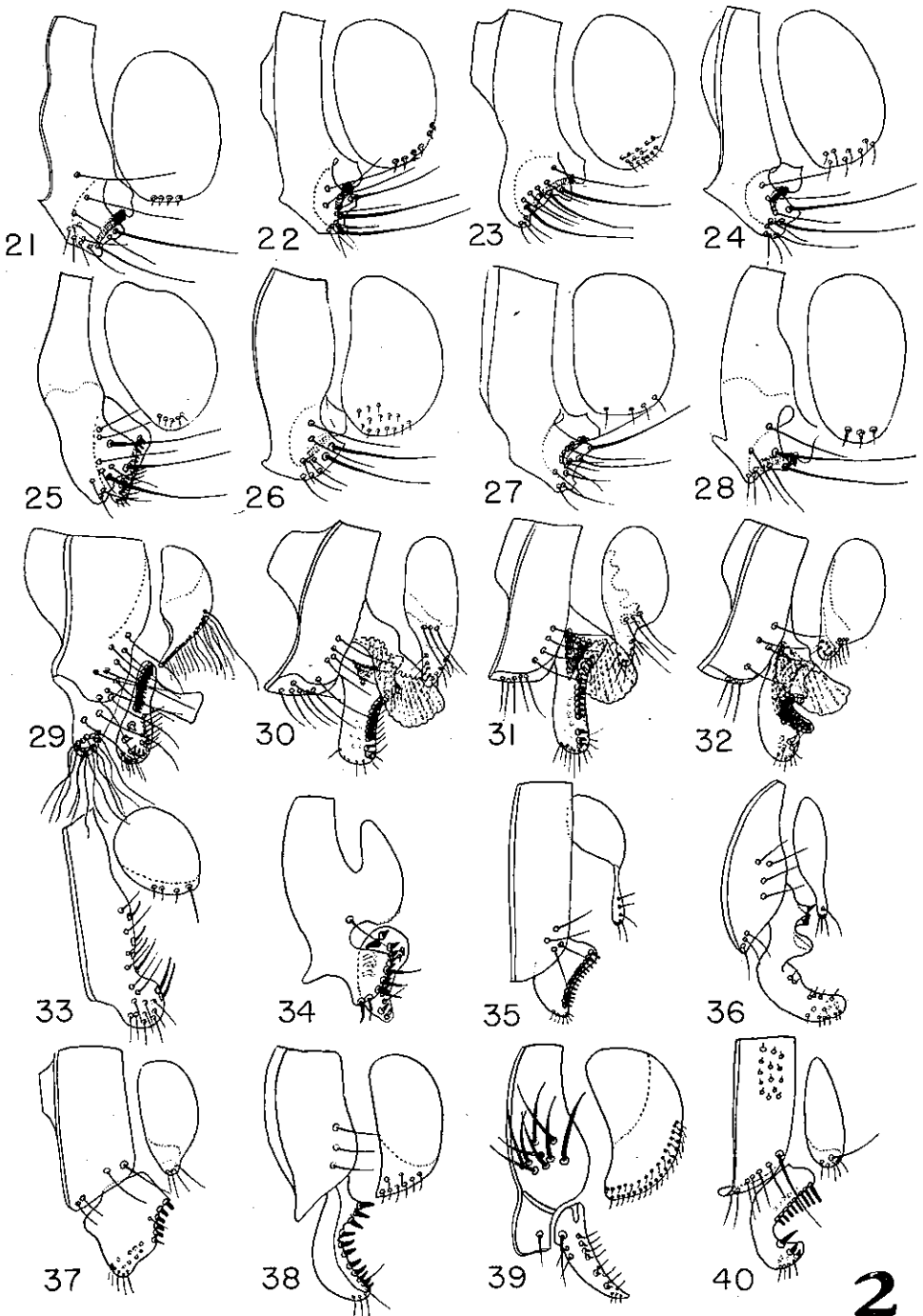


FIG. 2. Male external genital apparatus of 20 species of Hawaiian Drosophilidae (see Table 1).

with the following differences. Genital arch with about 7 bristles along the under margin. Anal plate triangular.

Phallic organs (Figure 4.8): As in *Antopocerus longiseta*, with the following differences. Penis slender, and pointed at tip. P.I. = 8.0.

Drosophila species 3, from Hawaii.

External genital apparatus (Figure 1.9): Tip of anal plate pointed and with a few short bristles. Clasper with about 8 primary teeth.

Phallic organs (Figure 4.9): Similar to *Drosophila disticha*. P.I. = 7.0.

Drosophila basimacula Hardy.

External genital apparatus (Figure 1.10): Like *Drosophila* sp. 3, with these differences. Anal plate oblong, dark brown.

Phallic organs (Figure 4.10): Paramedian spines of hypandrium stout; bridge connecting the claspers H-shaped. P.I. = 6.0.

Drosophila quasianomalipes Hardy.

External genital apparatus (Figure 1.11): Genital arch rather narrow, boot-shaped, the lower portion with about 40 bristles. Clasper fig-shaped, the primary teeth scattered along the posterior margin, about 10 in number.

Phallic organs (Figure 4.11): Penis long and slender, swollen apically and pointed at the tip. Anterior gonapophyses rather small. P.I. = 7.0.

Drosophila mimica Hardy.

External genital apparatus (Figure 1.12): Genital arch with about 7 bristles on the lower portion, the toe directed downward.

Phallic organs (Figure 4.12): Penis rather short; anterior gonapophyses broad, the apices at almost the same level as the level of insertion of the paramedian spines. P.I. = 3.0.

Drosophila olaae Grimshaw (?).

External genital apparatus (Figure 1.13): Middle and lower portion of genital arch with about 15 bristles; toe rather round, the heel nearly absent. Clasper rather large, with about 20 primary teeth in a straight row and about 20 heavy spines arranged on the inside surface. Anal plate elliptical, the dorsal margin weakly sclerotized.

Phallic organs (Figure 4.13): As in *Drosophila mimica*. P.I. = 4.0.

Drosophila scolostoma Hardy.

External genital apparatus (Figure 1.14): Genital arch and anal plate heavily sclerotized, rather broad, and with about 12 bristles on the lower portion; the toe at about the same level as the heel.

Phallic organs (Figure 4.14): Posterior gonapophyses present; anterior gonapophyses not reaching to the level of the insertion of the paramedian spines. P.I. = 6.0.

Drosophila species 4, from Kauai.

External genital apparatus (Figure 1.15): Genital arch narrow above, broad below, the toe at about the same level as the heel.

Phallic organs (Figure 4.15): Sensilla of anterior gonapophyses absent. P.I. = 6.0.

Drosophila hirticoxa Hardy.

External genital apparatus (Figure 1.16): Genital arch broad below, the anterior and posterior margins straight; with about 7 bristles on the lower portion. Anal plate semicircular, the under margin without marginal bristles.

Phallic organs (Figure 4.16): Like *Drosophila disticha*, but with the following differences. Penis very long. P.I. = 8.0.

Drosophila (Trichotobregma) petalopeza Hardy.

External genital apparatus (Figure 1.17): Genital arch very narrow above, the toe and heel rounded, and with about 20 bristles on the lower portion. Anal plate oblong, the tip pointed; anal plate fused to genital arch at lower portion.

Phallic organs (Figure 4.17): Tip of anterior gonapophyses extending beyond the level of insertion of the paramedian spines. P.I. = 6.0.

Drosophila fungicola Hardy.

External genital apparatus (Figure 1.18): Genital arch and anal plates heavily sclerotized; genital arch with about 10 bristles along the lower margin; heel nearly absent; toe pointed downward and with a spine at the tip. Anal plate fused with genital arch. Clasper broad, with about 13 primary teeth.

Phallic organs (Figure 4.18): Anterior gonapophyses oval in lateral aspect; paramedian spines rather massive. P.I. = 3.0.

Drosophila scolostoma Hardy.

External genital apparatus (Figure 1.19): Anterior margin of genital arch sinuate. Anal plate fused with genital arch at middle; toe pointed downward, the heel nearly absent.

Phallic organs (Figure 4.19): Anterior gonapophyses rather long; paramedian spines of hypandrium rather long. P.I. = 5.0.

Drosophila parva Grimshaw.

External genital apparatus (Figure 1.20): Genital arch rather broad, the under margin with 2 bristles. Anal plate oblong, separated from genital arch, and divided into two parts: the primary and the secondary anal plates. One clasper, large; primary teeth in two groups: the upper one with 1-2 teeth, the lower part with about 6 teeth.

Phallic organs (Figure 4.20): Penis laterally flattened, sinuate, its basal apodeme about half as long as the penis. Paramedian spines of hypandrium short. P.I. = 1.5.

Drosophila villosipedis Hardy.

External genital apparatus (Figure 2.21): Genital arch comparatively long and narrow, with about 13 bristles on the lower portion; the heel pronounced, the toe prominent and rounded; under margin concave. Anal plate separated, large and elliptical, with 4 spines on the under margin.

Phallic organs (Figure 4.21): Similar to *Antopocerus longiseta*, with the following differences. Anterior gonapophyses broad in lateral aspect. P.I. = 6.0.

Drosophila pilimana Grimshaw.

External genital apparatus (Figure 2.22): Like *Drosophila villosipedis*, with these differences. Genital arch narrow and straight.

Phallic organs (Figure 4.22): Penis apically swollen; anterior gonapophyses long. P.I. = 5.0.

Drosophila engyochracea Hardy.

External genital apparatus (Figure 2.23): Genital arch rather broad, the under margin strongly concave; with about 11 bristles. Anal plate with numerous short bristles on the under margin.

Phallic organs (Figure 4.23): Penis slender. Anterior gonapophyses very long. P.I. = 8.0.

Drosophila grimshawi Oldenberg.

External genital apparatus (Figure 2.24): Genital arch narrow, with about 10 bristles on the lower portion. Clasper concave at middle, with about 12 primary teeth.

Phallic organs (Figure 4.24): Like *Drosophila engyochracea*, but with these differences. Anterior gonapophyses rather short. P.I. = 5.5.

Drosophila crucigera Grimshaw.

External genital apparatus (Figure 2.25): Genital arch narrow above, wider below. Clasper rather large, with about 10 primary teeth.

Phallic organs (Figure 4.25): Similar to *Drosophila villosipedis*, with the following differences. Anterior gonapophyses rather broad in lateral aspect. P.I. = 6.0.

Drosophila adiastrata Hardy.

External genital apparatus (Figure 2.26): Genital arch broad at middle, with about 10 bristles on the lower portion; toe pointed; under margin convex. Anal plate large and oblong, with about 15 tiny bristles scattered on the under margin. Clasper rather small.

Phallic organs (Figure 4.26): Tip of anterior gonapophyses pointed, with well developed sensillum. P.I. = 7.0.

Drosophila punalua Bryan.

External genital apparatus (Figure 2.27): Like *Drosophila grimshawi*, with the following differences. Genital arch rather broad, the under margin zigzag; toe high and pointed; with about 11 bristles on the lower portion of the arch. Anal plate rounded.

Phallic organs (Figure 4.27): Like *Drosophila pilimana*, but with the following differences. Tip of anterior gonapophyses pointed. Paramedian spines stout. P.I. = 6.0.

Drosophila picticornis Grimshaw.

External genital apparatus (Figure 2.28): Genital arch with about 8 bristles on the lower margin, and tiny hairs present on the whole area; posterior margin sinuate. Anal plate large and elliptical, with 3 spines on the under margin.

Phallic organs (Figure 4.28): Anterior gonapophyses large, their apices extending beyond the level of insertion of the paramedian spines. Lateral process of hypandrium elongate. P.I. = 7.0.

Drosophila nasalis Grimshaw.

External genital apparatus (Figure 2.29): Genital arch broad above and nar-

rower below; heel pronounced, toe a finger-like outgrowth, pointed downward. Bristles along the posterior margin and on the lower portion of the genital arch, especially dense on the toe. Anal plate separated, composed of two parts: primary and secondary anal plates; anal plates slightly triangular, the tip rather finger-shaped, with dense hairs along the under margin. Clasper crescent-shaped, with about 12 teeth on the upper half. Bridge connecting the claspers well sclerotized.

Phallic organs (Figure 4.29): Penis flask-shaped. Anterior gonapophyses broad but short, with 3 minute apical sensilla. Posterior gonapophyses appear to be absent. Hypandrium without paramedian spines. P.I. = 2.0.

Drosophila crassifemur Grimshaw, from Molokai.

External genital apparatus (Figure 2.30): Genital arch with a large semi-membranous lobe at about the middle of the posterior margin (see Hardy, 1965). Lower portion of genital arch with 4 bristles near the posterior margin just above the clasper; toe rounded; heel pronounced, with about 7 bristles on the under margin. Anal plate oblong, separated, the tip elongated and with about 10 short bristles and 3 long bristles at the middle. Anal plate composed of two parts: the primary and secondary anal plates. Clasper oblong, with about 17 primary teeth; a triangular process on the inner side above.

Phallic organs (Figure 4.30): Penis broad and oblong in ventral aspect, oval in lateral aspect; apodeme large. Anterior gonapophyses oblong, the outer apex pointed, the inner tip with about 7 sensilla. Lateral process of hypandrium protruded. P.I. = 1.0.

Drosophila crassifemur, from Hawaii.

External genital apparatus (Figure 2.31): Similar to the form from Molokai, but with the following differences. Under margin of genital arch with about 5 bristles. Clasper with about 11 primary teeth; triangular process of clasper rather longer than on the Molokai specimens.

Phallic organs (Figure 4.31): Penis flask-shaped in lateral aspect. Outer apex of anterior gonapophyses roundish. P.I. = 0.5.

Drosophila crassifemur, from Kauai.*

External genital apparatus (Figure 2.32): Differing from the form from Molokai as follows: under margin of genital arch with about 3 bristles; clasper with about 10 primary teeth in a concave row; the triangular process of the clasper very long.

Phallic organs (Figure 4.32): Penis cocoon-shaped, with a tubelike process at the medio-ventral portion. Tip of anterior gonapophyses rounded and with about 7 sensilla along the apical margin. Lateral process of hypandrium slender and pointed at tip. P.I. = 1.0.

Drosophila species X, from Maui. *Conchoptera*

External genital apparatus (Figure 2.38): Genital arch broad, with 3 bristles at the middle; heel pointed. Anal plate oval, the rear angle pointed, separated into a primary and a secondary anal plate. Clasper banana-shaped, with 11-12 stout primary teeth on the posterior margin.

* Editor's note: this is being described as a new species by Hardy (this Bulletin).

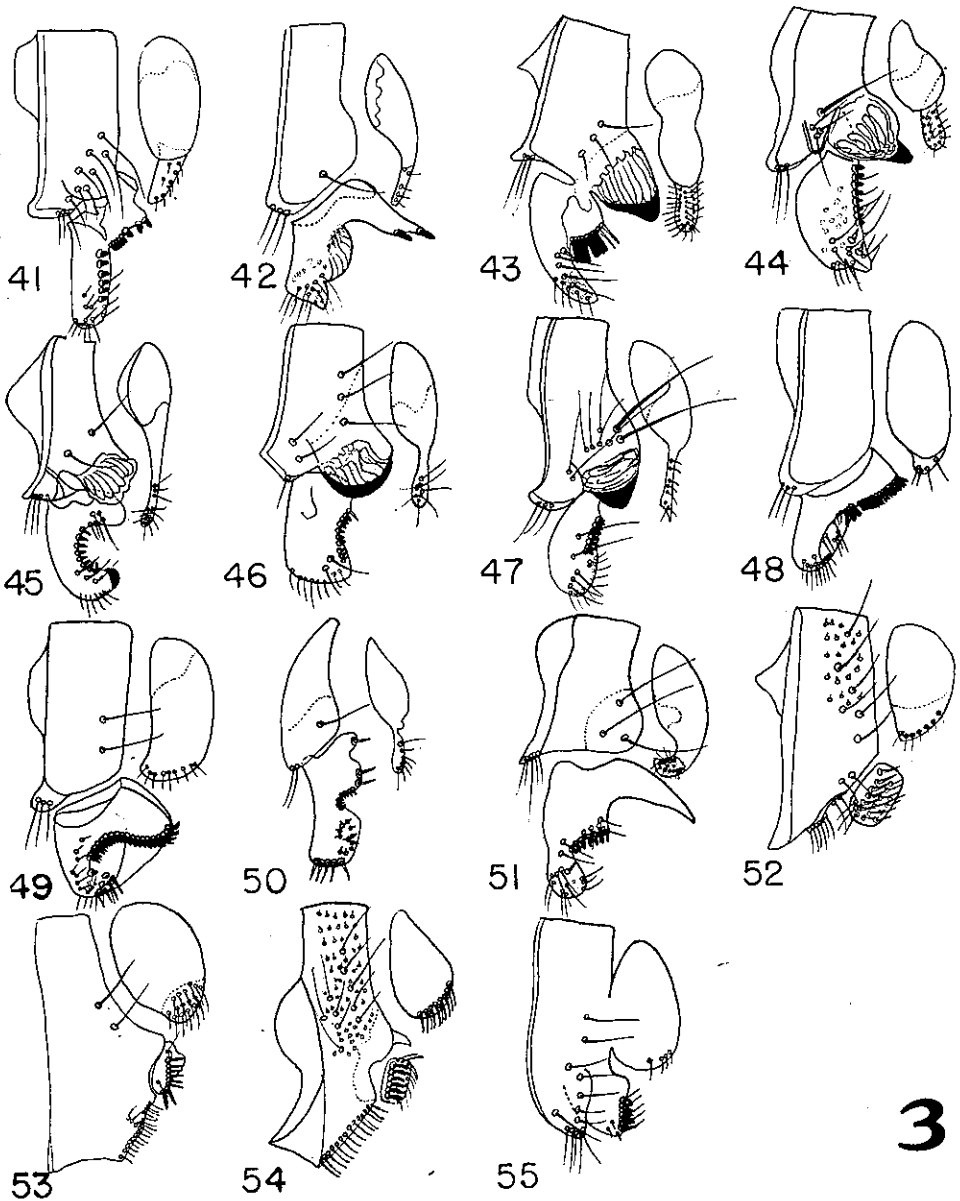


FIG. 3. Male external genital apparatus of 15 species of Hawaiian Drosophilidae (see Table 1).

Phallic organs (Figure 4.38): Penis slender, the apodeme long. Anterior gonapophyses small, with 3 sensilla at tip. P.I. = 0.8.

Drosophila ochracea Grimshaw.

External genital apparatus (Figure 3.55): Genital arch broad, the heel not prominent, the toe pointed downward. Anal plate oval, fused to genital arch. Clasper with about 7 primary teeth.

Phallic organs (Figure 4.55): Penis small, oval, pointed dorsad subapically.

Anterior gonapophyses small, with a sensillum. Hypandrium semicircular; with paramedian spines and a median notch. P.I. = 3.0.

Dettopsomyia nigrovittata Malloch.

External genital apparatus (Figure 2.34): Under margin of genital arch with 5 spines, middle portion with a bristle; heel and toe only slightly evident, forming a large rounded expansion covering half of clasper. Clasper oblong, with about 10 primary teeth, about 4 secondary teeth, and 2 large, strong bristles which are inserted on the lower tip. Anal plate oblong, fused with the arch; the under margin with numerous short bristles.

Phallic organs (Figure 4.34): Penis large and cylindrical, curved dorsad apically as seen in lateral view. Anterior gonapophyses fused with hypandrium, cylindrical, bearing numerous hairy sensilla. Hypandrium triangular, with a median notch but lacking paramedian spines. P.I. = 3.0.

Titanochaeta contestata Hardy.

External genital apparatus (Figure 2.35): Genital arch rectangular, with about 4 bristles just above the clasper, the heel pointed downward, the toe absent. Anal plate separated from arch, separated into two parts: the upper part oblong, the lower part finger-like in shape and with about 6 bristles.

Phallic organs (Figure 4.35): Penis banana-shaped. Anterior gonapophyses small, crescent-shaped, with 3 apical sensilla. Lateral processes of hypandrium V-shaped. P.I. = 1.5.

Scaptomyza (Exalloscaphomyza) mauiensis (Grimshaw).

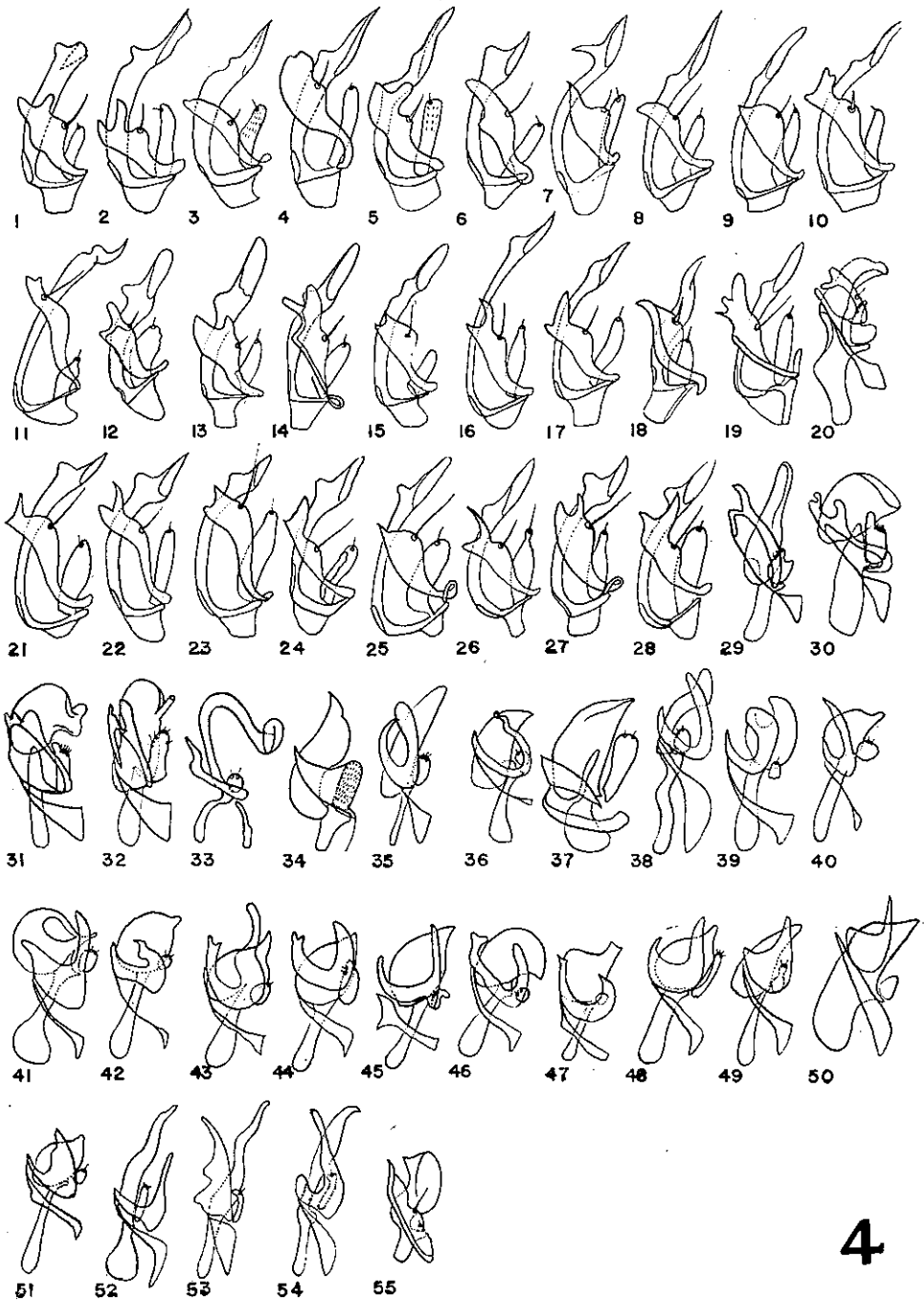
External genital apparatus (Figure 2.33): Genital arch narrow and long. Clasper absent. Lower portion of genital arch rounded, with about 15 bristles and 6 stout bristles on the posterior margin of the middle and lower portion. Anal plate oval, composed of two parts, the secondary anal plate with about 4 bristles on the under margin.

Phallic organs (Figure 4.33): Penis long and slender, curved ventrally at middle, apically bilobed and elliptically flattened in ventral aspect and rectangularly curved dorsad. Anterior gonapophyses small, rounded, with 2 apical sensilla. Hypandrium U-shaped. Posterior gonapophyses stout and pointed at tip. P.I. = 3.0.

Scaptomyza (Tantalia) albovittata (Malloch).

External genital apparatus (Figure 2.36): Genital arch with a strongly convex posterior margin and with two groups of bristles: 4 on the lower middle portion, and 3 on the heel; heel pointed downward, the toe absent. Anal plate oblong, separated, lower portion with a finger-like shape and with 4 bristles at the tip. Clasper large, W-shaped, with 4 primary teeth, 1 secondary tooth on the upper portion; middle part without teeth; lower portion with about 20 sensillum-like bristles.

Phallic organs (Figure 4.36): Penis massive, hammer-shaped. Anterior gonapophyses small, with a sensillum at tip. Lateral process of hypandrium V-shaped. P.I. = 1.0.



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FIG. 4. Male phallic organs (in lateral aspect) of 55 species of Hawaiian *Drosophilidae* (see Table 1).

Scaptomyza species 5, from Hawaii.

External genital apparatus (Figure 2.37): Genital arch broad, the lower portion with about 4 bristles. Anal plate separated, oval, with 4 bristles at the tip. Clasper broad, with about 5 primary teeth occupying the upper half of the posterior margin.

Phallic organs (Figure 4.37): Penis massive, hammer-shaped; base of the apodeme broad in lateral aspect. Anterior gonapophyses rather large, with 2 apical sensilla. P.I. = 1.5.

Scaptomyza species 6, from Maui.

External genital apparatus (Figure 2.39): Posterior margin of genital arch convex at middle, with 8–10 spine-like bristles on the middle portion; heel and toe present. Anal plate large, crescent-shaped, with about 40 tiny bristles on the under margin. Clasper slender, with about 6 scattered primary teeth, and with 3 bristles on the upper anterior portion.

Phallic organs (Figure 4.39): Penis rounded, apically concave, with a large apodeme. Anterior gonapophyses small, triangular, with a sensillum at the tip. P.I. = 0.7.

Scaptomyza (Trogloscaptomyza) species 7, from Maui.

External genital apparatus (Figure 2.40): Genital arch simple, the lower portion with about 7 bristles; heel conical, the toe high and rounded; arch with about 15 sensilla on upper portion. Anal plate oblong, broad below, and with about 6 bristles on the under margin. Clasper crescent-shaped, with about 8 primary teeth on the upper posterior margin, and 2–3 spines on the lower portion.

Phallic organs (Figure 4.40): Penis, in ventral aspect, resembling an isosceles triangle, the tip pointed. Anterior gonapophyses square, with 2 sensilla at the inner tip. Apodeme of penis rather long. Hypandrium U-shaped. P.I. = 0.7.

Scaptomyza (Trogloscaptomyza) species 8, from Maui.

External genital apparatus (Figure 3.41): Genital arch broad, both the anterior and posterior margins straight; heel swollen, with about 8 bristles; toe pointed, with about 3 bristles. Primary teeth of clasper in two sets: about 8 in the upper set and about 6 in the lower set. Anal plate oblong, composed of two parts, the lower one with about 8 tiny bristles.

Phallic organs (Figure 4.41): Penis flask-shaped, the tip pointed. Apodeme of penis massive, rather long. Anterior gonapophyses small, triangular, with 2 apical sensilla. Hypandrium V-shaped, the lateral process U-shaped in ventral aspect. P.I. = 0.5.

Scaptomyza (Trogloscaptomyza) species 9, from Kauai.

External genital apparatus (Figure 3.42): Genital arch broad below, with a bristle on the under margin; toe rounded, the heel rectangular and with 3 bristles. Anal plate crescent-shaped, with about 5 tiny bristles on the finger-like tip. Clasper swollen at middle, the upper portion projecting horn-like, and with 2 teeth at the tip; with marginal bristles on the lower portion.

Phallic organs (Figure 4.42): Like *Scaptomyza* species 8, with the following differences. Hypandrium semicircular; lateral process of hypandrium rather small, apically sinuate. P.I. = 0.6.

Scaptomyza (Trogloscaptomyza) species 10, from Maui.

External genital apparatus (Figure 3.43): Genital arch broad, the toe projecting like a membranous sac and with 3 bristles just above it; tip sclerotized; heel pointed, with 3 bristles. Anal plates guitar-shaped; secondary anal plate with numerous tiny bristles.

Phallic organs (Figure 4.43): Like *Scaptomyza* species 8, but with these differences. Anterior gonapophyses with a sensillum. Hypandrium bow-shaped; lateral process of hypandrium V-shaped, rather long. P.I. = 1.0.

Scaptomyza (Trogloscaptomyza) species 11, from Maui.

External genital apparatus (Figure 3.44): Genital arch broad, the toe projecting like a cone, its tip sclerotized, and with 4 bristles just above it; heel rounded, with 3 bristles.

Phallic organs (Figure 4.44): Similar to *Scaptomyza* species 9, with the following differences. Anterior gonapophyses oblong, with 2 sensilla at inner apical portion. Lateral process of hypandrium large, V-shaped. P.I. = 1.0.

Scaptomyza (Trogloscaptomyza) species 12, from Kauai.

External genital apparatus (Figure 3.45): Genital arch broad below, the toe projecting like a membranous sac; heel pointed, with 3 bristles; arch with 2 bristles at middle. Clasper crescent-shaped, with about 8 primary teeth; the upper and lower tips rounded, the lower one with a knob-like process. Anal plate long, flask-shaped, with about 12 bristles on the lower portion.

Phallic organs (Figure 4.45): Like *Scaptomyza* species 11, but with the following differences. Anterior gonapophyses comma-shaped, with 2 sensilla on the anterior surface. P.I. = 1.0.

Scaptomyza (Trogloscaptomyza) species 13, from Maui.

External genital apparatus (Figure 3.46): Genital arch broad, with 3 bristles on the posterior margin and 2 bristles just above the heel; heel square, bearing a bristle; toe projecting as a broad sac, the posterior margin sclerotized. Clasper rectangular, with about 9 primary teeth. Anal plate bottle-shaped, narrow below, with 7-8 tiny bristles.

Phallic organs (Figure 4.46): Similar to *Scaptomyza* species 12, with the following differences. Penis small; anterior gonapophyses small and circular. P.I. = 1.0.

Scaptomyza (Trogloscaptomyza) photophilia Hardy.

External genital apparatus (Figure 3.47): Genital arch broad below, the toe projecting cone-like, the tip sclerotized; arch with about 8 bristles including 2 stout ones just above the toe; heel very prominent, with 3 bristles. Clasper oval, with about 7 primary teeth. Anal plate oblong with a bar-shaped secondary anal plate below bearing about 8 tiny bristles.

Phallic organs (Figure 4.47): Penis cap-shaped, pointed at the apex. Anterior gonapophyses small, without a sensillum. P.I. = 1.0.

Scaptomyza (Trogloscaptomyza) species 14, from Maui.

External genital apparatus (Figure 3.48): Genital arch broad, the heel rounded and bearing 3 bristles. Clasper large, wide, and short, the primary teeth forming two groups: upper group with about 18 teeth, the lower one with 3. Anal plate

oval, pointed at the tip, and with about 4 short bristles.

Phallic organs (Figure 4.48): Like *Scaptomyza* species 11, with the following differences. Anterior gonapophyses slender, with about 4 apical sensilla. P.I. = 0.8.

Scaptomyza (Trogloscaptomyza) longipecten Hackman.

External genital apparatus (Figure 3.49): Similar to *Scaptomyza* species 14, with these differences. Genital arch with 2 bristles on the posterior portion. Clasper large, crescent-shaped, with a clasper lobe on the inner side; about 25 primary teeth. Anal plate with about 8 bristles along the under margin.

Phallic organs (Figure 4.49): Anterior gonapophyses flask-shaped, with 2 sensilla at tip. Lateral process of hypandrium broad, V-shaped. P.I. = 1.0.

Scaptomyza (Trogloscaptomyza) cryptoloba Hardy.

External genital apparatus (Figure 3.50): Genital arch broad below, the lower portion with a bristle; heel almost rectangular, with 2 bristles; toe broad and rounded. Anal plate bottle-shaped, the lower portion with about 7 tiny bristles. Clasper large, W-shaped, the upper tip with a spine, the middle one with 2 spines and about 7 sensilla, the lower one with several sensilla; the under margin with about 5 marginal bristles.

Phallic organs (Figure 4.50): Penis and apodeme massive, oblong, pointed at the tip. Hypandrium circular; lateral process rather high. Anterior gonapophyses trapezoidal in ventral aspect, without sensilla. P.I. = 1.0.

Scaptomyza (Trogloscaptomyza) latitergum Hardy.

External genital apparatus (Figure 3.51): Genital arch broad and short, with 3 bristles on the lower posterior part; heel pointed, with about 5 bristles; toe rounded. Clasper large, the upper portion projecting like a horn, the middle portion concave and bearing about 7 primary teeth, and the lower part rounded and with a tooth. Anal plate comma-shaped, the tip curved anteriorly and with numerous short bristles.

Phallic organs (Figure 4.51): Penis cap-shaped, broad in ventral aspect. Anterior gonapophyses oblong, with an apical sensillum. P.I. = 0.6.

Scaptomyza (Bunostoma) anomala Hardy.

External genital apparatus (Figure 3.52): Genital arch broad, with about 6 bristles and many sensilla near posterior margin; heel conical, the toe high; under margin of arch with about 10 bristles. Clasper rather small, rectangular, bearing about 17 bristles arranged in 3 rows. Anal plate oval, separated, with about 8 tiny bristles on under margin.

Phallic organs (Figure 4.52): Penis slender, sinuate and pointed at the tip; base of apodeme broad. Lateral process of hypandrium high. Anterior gonapophyses rod-shaped, with 2 sensilla on top. P.I. = 2.0.

Scaptomyza (Bunostoma) cnecosoma Hardy.

External genital apparatus (Figure 3.53): Genital arch broad below, with 2 bristles on the posterior margin; undermargin nearly straight, with numerous fine bristles along it; heel obtuse, the toe high. Clasper small, folded at about the

inner half, with about 8 primary teeth. Anal plate oval, the tip rounded and bearing numerous short bristles.

Phallic organs (Figure 4.53): Similar to *Scaptomyza anomala*, but with these differences. Lateral process of hypandrium as long as penis. Anterior gonapophyses slender, with an apical sensillum. P.I. = 3.0.

Scaptomyza (Bunostoma) palmae Hardy.

External genital apparatus (Figure 3.54): Both anterior and posterior margins of genital arch convex at middle, and with about 10 bristles on the middle portion; toe rounded and bearing a finger-like process; under margin concave and with numerous fine bristles; heel nearly rectangular. Clasper small, oblong, with 6 primary teeth. Anal plate oblong, broad below, the under margin with 10 bristles.

Phallic organs (Figure 4.54): Like *Scaptomyza cnecosoma* with the following differences. Anterior gonapophyses crescent-shaped; tip of the penis swollen in ventral aspect. P.I. = 2.5.

DISCUSSION

Figure 5 represents an abbreviated phylogeny of the Hawaiian Drosophilidae, based on the structure of the phallic organs. The representatives chosen as examples of the three major branches within the Hawaiian fauna indicate the more typical types.

In most respects, species from the genus *Scaptomyza*, subgenus *Exalloscaptomyza*, show primitive characters. The species of the endemic fauna present a great variety of modifications of the penis form as can be seen in Figure 4.

The vertical rod is a process which projects ventrally from the junction of the penis and its apodeme; it is absent or, if present, minute, in *Exalloscaptomyza*, *Bunostoma*, *Titanochaeta*, *Tantalia*, and *Trogloscaptomyza*. The "phallosomal index" (P.I.) which was proposed by Okada (1953) for the ratio in length between the penis and its apodema, tends to become larger in the more peripherally located groups. It is about 1.0 or less in *Exalloscaptomyza*, *Titanochaeta*, *Tantalia*, *Trogloscaptomyza*, *D. species X*, *D. nasalis* and *D. crassifemur*; it is about 2.0 in *Bunostoma* and *D. parva*, and it is more than 4.0 in *D. fungicola* and all other members of the endemic Hawaiian Drosophilidae which have been examined.

Figure 6 represents an abbreviated phylogeny of the Hawaiian Drosophilidae based on the structures of the external genital apparatus. The Hawaiian species present 11 basic genitalial types, as can be seen from Figures 1 to 3. In most respects, species from the subgenus *Exalloscaptomyza* illustrate the primitive characteristics, as they did with the penis forms.

The general features of the external male genitalia of the Drosophilidae show a gradual complication from genus to genus. Some of the features of the various genera and subgenera of Hawaiian Drosophilidae are as follows:

Exalloscaptomyza:—Lacks the primary clasper and the primary tooth on the genital arch; anal plate with a secondary anal plate.

Bunostoma:—Clasper present and bearing primary teeth; secondary anal plate present.

Titanochaeta:—Secondary anal plate elongated downward.

Tantalia:—Clasper rather more complicated than in *Titanochaeta*.

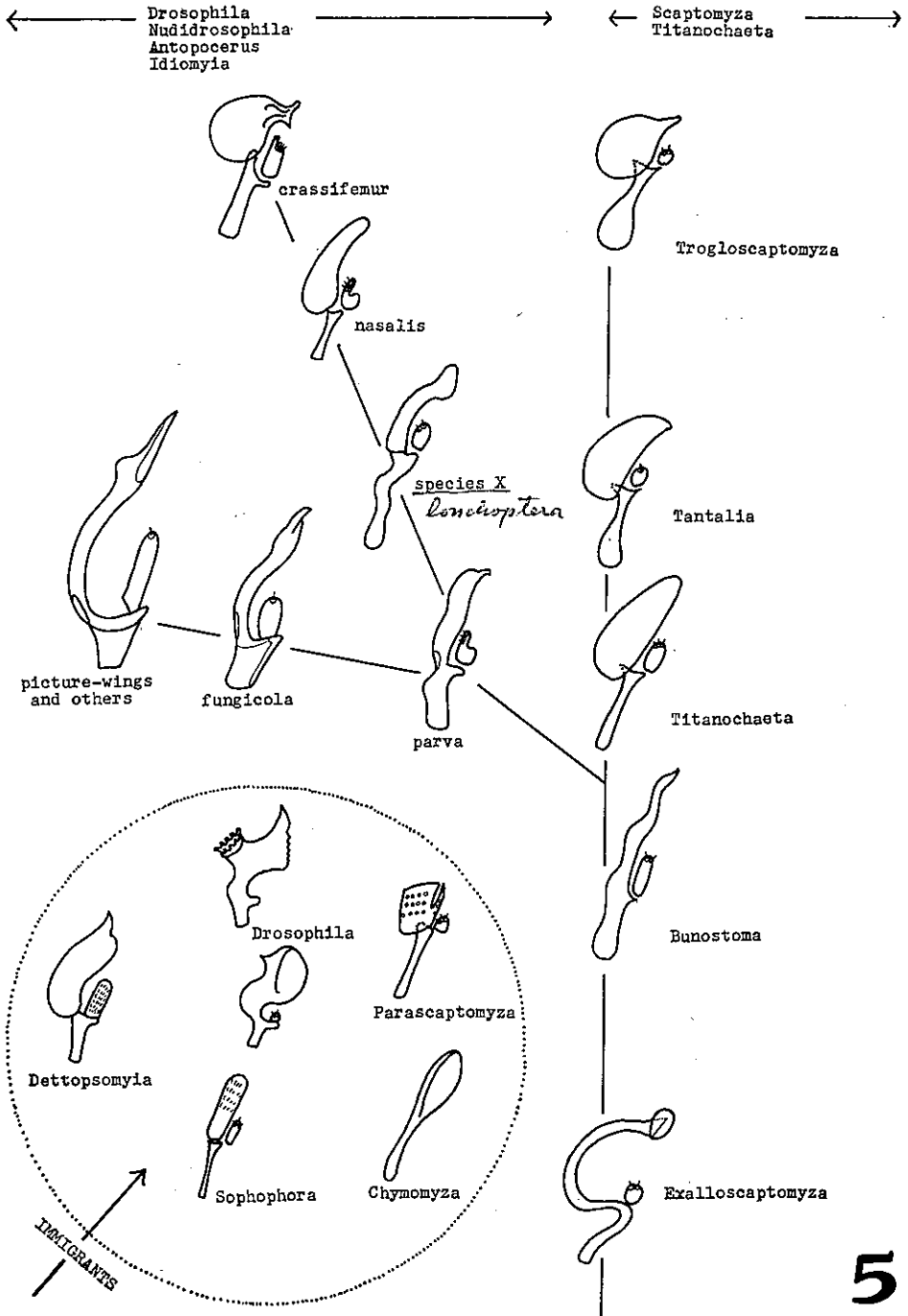


FIG. 5. Pictorial phylogeny of the Hawaiian Drosophilidae, based on the structure of the phallic organs.

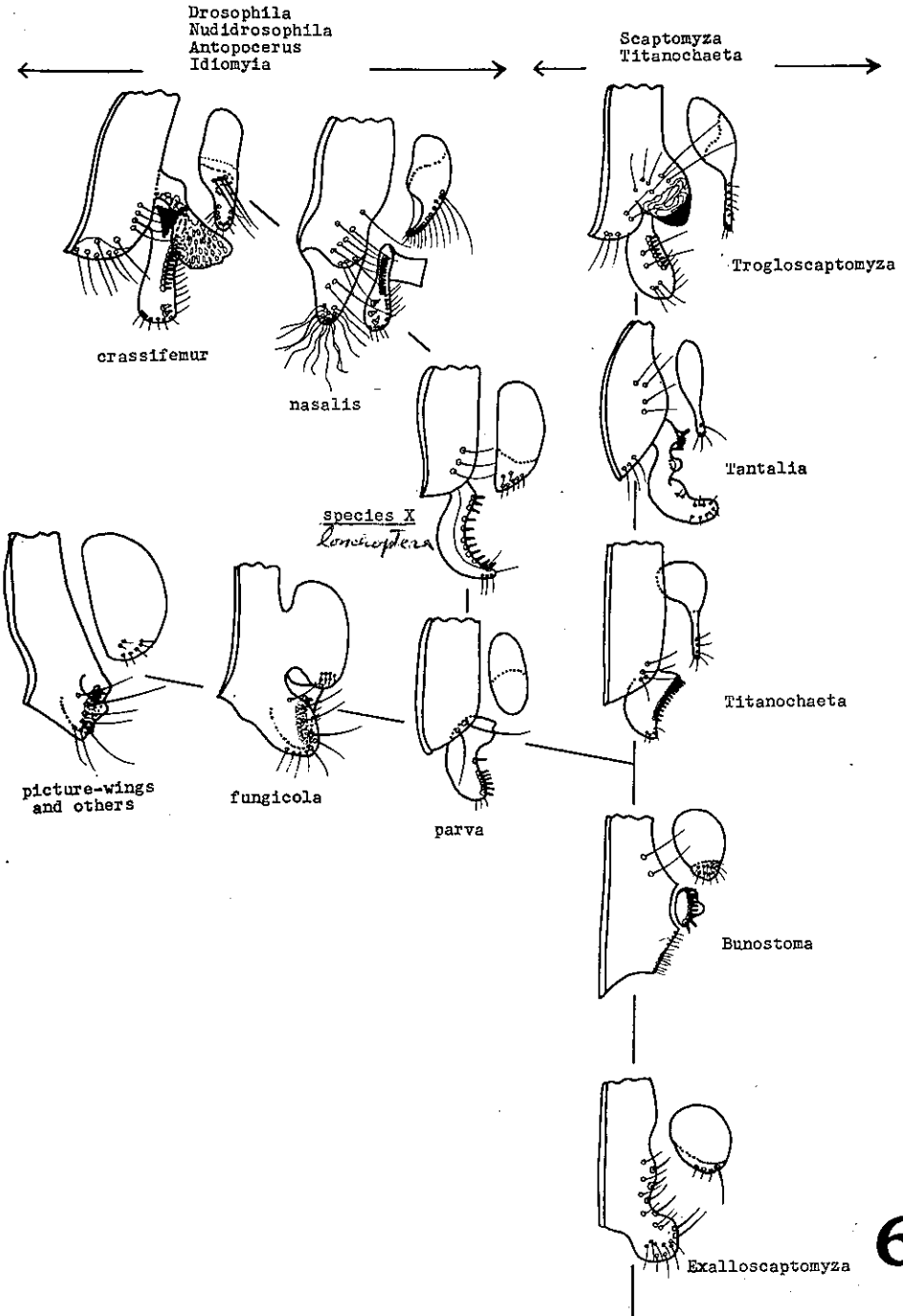


FIG. 6. Pictorial phylogeny of the Hawaiian Drosophilidae, based on the structures of the external genital apparatus.

Trogloscaptomysa:—Top of genital arch projecting as a conical modification.

Drosophila parva:—External genital apparatus rather simple; anal plate with differentiated secondary anal plate.

Drosophila species X:—Clasper slender; anal plate with secondary anal plate.

Drosophila nasalis:—External genital apparatus rather complicated.

Drosophila crassifemur:—Genital arch with a semi-membranous process extending from posterior margin.

Drosophila fungicola:—Anal plate fused with genital arch; lower portion of genital arch well developed.

Drosophila species, including the "picture-wings":—Anal plate separated from the genital arch.

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