XI. The Relationships of the Endemic Hawaiian Drosophilidae[1]

LYNN H. THROCKMORTON[2]

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INTRODUCTION

During the summer of 1963 and that of 1964 I had the opportunity to study the anatomy of many individuals from Drosophilid species endemic to Hawaii. This remarkable fauna was first commented on by Perkins (1913), and more recently its importance for evolutionary studies was emphasized by Zimmerman (1948, 1958). However, the major taxonomic treatment of these species has been through the work of Hardy (1965), and it is largely through his efforts that evolutionary studies of this group are now practical. At present over 400 species of endemic Drosophilids are known from Hawaii, and this group constitutes one of biology's most challenging examples of explosive evolutionary radiation on islands. It is now being studied by a group of investigators using approaches ranging from the cytological and genetic through the taxonomic to the ecologic and behavioral. The objectives of the work reported herein have been several:

[2] Department of Zoology, The University of Chicago, Chicago, Illinois.

1) to determine the relationships of the Hawaiian Drosophilids within the phylogeny of the genus *Drosophila*, 2) to determine the number and sources of the introductions from which the Hawaiian Drosophilid fauna is derived, and 3) to investigate the paths of evolution of this group within the Hawaiian archipelago, insofar as this can be done with the presently existing materials.

The first of these objectives was, in one sense, readily accomplished. The general phylogenetic position of the Hawaiian Drosophilids is clear and reasonably unequivocal. However, an unanticipated complication became apparent during the analysis of relationships. The two major groups of endemic Drosophilids, "Hawaiian Drosophila" and *Scaptomyza*, appear to be each other's nearest relatives. It is therefore necessary to examine the possibility that the genus *Scaptomyza* originated in Hawaii, radiated there, and also escaped to the mainland where it again achieved a major radiation. Determining the number and sources of introductions was also relatively simple, although the number of introductions must remain uncertain if the place of origin of *Scaptomyza* is doubtful. Determining the paths of evolution within Hawaii is not easy, but considerable information can be brought to bear on this question. This information is sufficient to provide evidence of an evolutionary situation of fascinating complexity. It is not yet adequate to resolve any issues. Conclusions, problems and possibilities relative to these three major questions will be discussed below.

MATERIALS AND METHODS

By far the great majority of the specimens used in this study have been collected in the wild at various localities in Hawaii. Most of them were collected by me, but many valuable specimens were contributed by other persons. I am much indebted to Drs. Frances Clayton, Marshall Wheeler, Hampton Carson, William Heed, Elmo Hardy and Harrison Stalker for such material. The species used are listed in the Appendix, together with their identification numbers and collection localities. The identification numbers relate the specimens to my notes on their dissection. The classification followed is that of Hardy (1965). As a general indication of broad groupings, informal designations have been given also. Thus, Hawaiian species fall into two major clusters, and these are indicated in the Appendix and in the figure legends as Drosophiloid and Scaptoid. This usage greatly facilitates reference, since each of these clusters includes several genera, subgenera and other groups of such general over-all similarity that they are best treated together as a unit. Also, certain species are classified as *Drosophila* on the basis of diagnostic features, even though in general conformation and morphology they are *Scaptomyza*. These three species (*D. crassifemur, D. nasalis* and *D. parva*) are treated here as Scaptoids, and the justification for this will become apparent as the different characteristics are discussed. The justification for disposing of the other genera as either Drosophiloid or Scaptoid should also become evident as the descriptions proceed.

Some of the taxonomic structure within the above named groups is indicated by the formal classification. In other cases, particularly for species classified as *Drosophila*, further subdivision is desirable. In part owing to the complex evolu-

tionary patterns in Hawaii, the taxonomy of species groups has not yet been accomplished. As an expedient, descriptive vernacular names have been given to the more conspicuous groups. Thus we have the "picture wings" (with heavily patterned wings), the "modified mouthparts" (with special adaptations of the mouthparts of the male for grasping the posterior abdomen of the female during courtship), the "bristle tarsi," the "spoon tarsi," and the "split tarsi" (denoting various tarsal ornaments in the male), and the "white tip scutellum" flies. These last are a very distinct group of slender, rather low-bodied *Drosophila* that show several Scaptoid characteristics. The group designations are very loose and informal at the present time, but they do have a certain validity. When, in the future, these forms have been arranged in species groups, the species groups will be, for the most part, subdivisions of the larger and less homogeneous groups designated informally now.

Generally, results from specimens of only one locality are reported, although in a number of instances the same species has been seen from several localities. In a few cases results from two localities have been given, since in those instances the differences seem either to reflect a considerable degree of polymorphism or to indicate the existence of species not detectable from external anatomy alone. The number of specimens dissected for each species has varied greatly, being determined mostly by the availability of material. In some cases only one individual could be found. During the summer of 1963 I avoided dissecting from species so meagerly represented in the collections, hoping to save these as possibly unique types. At that time it seemed unlikely that species abundant in collections would be undescribed. This turned out not to be the case. Also, it very soon became evident that single specimens would need to be dissected, since insufficient material would be available otherwise. Hence, during the summer of 1964 procedures were changed. Notes were taken on abdominal color and markings when unique specimens were used. Then the abdomens were removed and dissected. The remainder of the specimen, generally quite undamaged, was pinned for permanent reference. The genitalia of each such specimen was cleared in phenol and preserved in glycerin in a small vial pinned with the specimen. Aside from these modifications, and except where otherwise noted, methods have been those reported earlier (Throckmorton, 1962).

When possible, observations were made on characteristics of the eggs and of the pupae. Eggs were often laid in the vials used for holding each species of fly prior to dissection. In many instance the eggs were found in the vagina, or mature eggs were present in the ovaries. However, it was impossible to obtain eggs from all species included in this study. Pupae were even more difficult to obtain. I am particularly indebted to Frances Clayton and Marshall Wheeler for giving me many pupae from their cultures of endemic species.

Species identifications were made by Dr. D. Elmo Hardy from the pinned specimens. I am grateful to him for undertaking this very considerable task. The value of authoritative determinations for a study such as this can hardly be overemphasized. With one or two exceptions, only named species are treated in this report. Surprisingly, fully 20 percent of the species in my collection of dissected flies are unnamed at the present time. Fortunately, there is a great deal
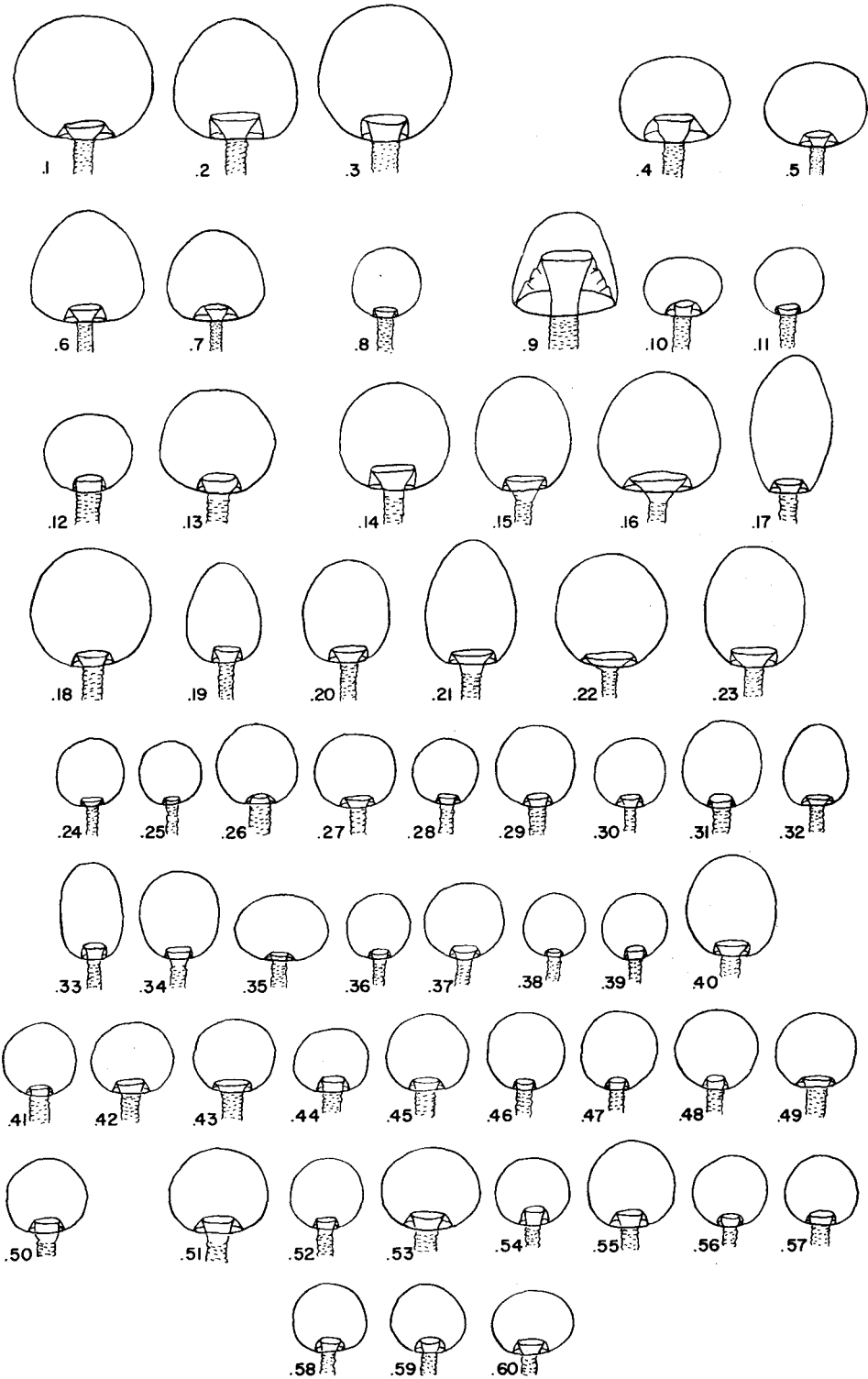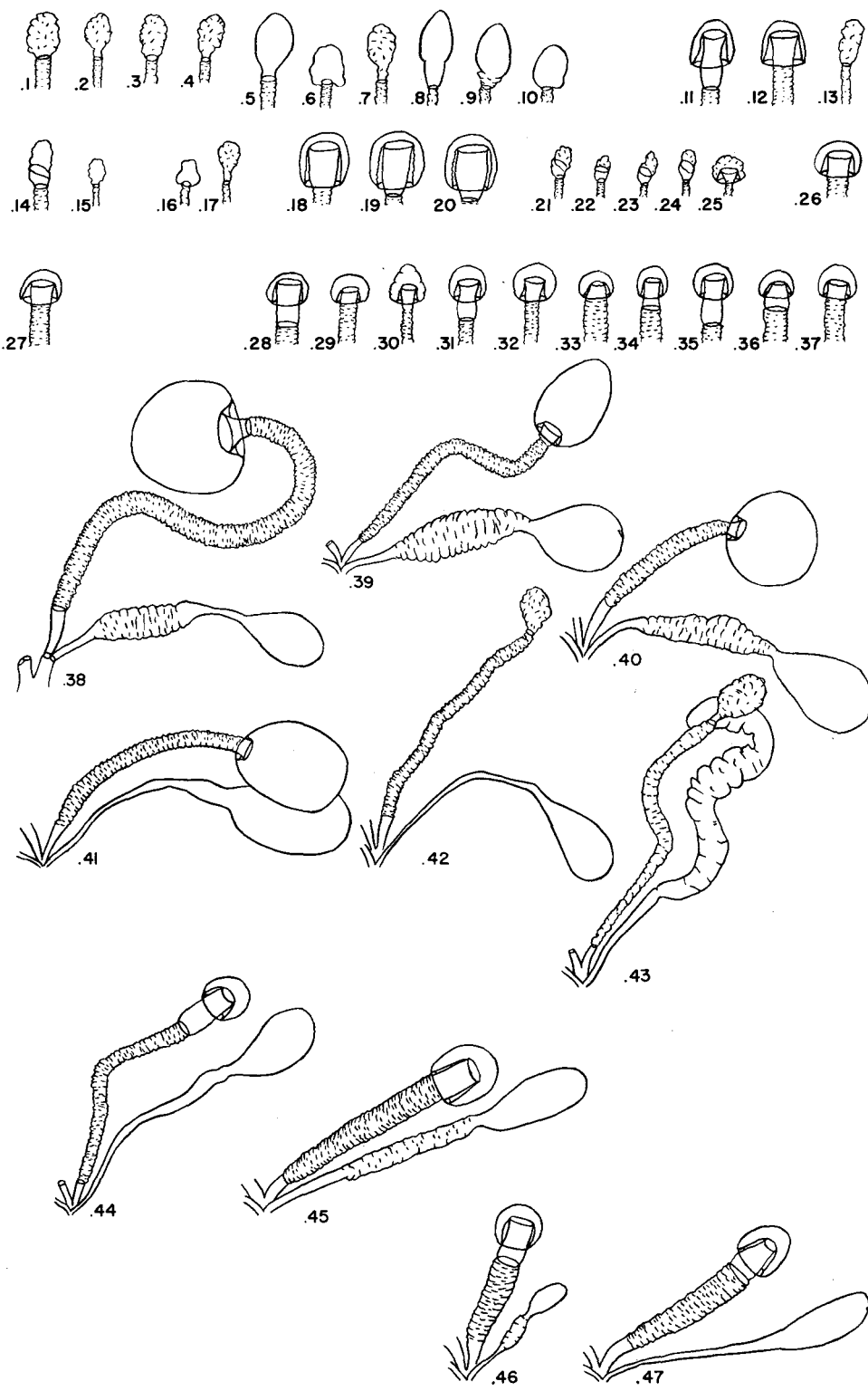
of uniformity of many of the characters of these species, and omitting unnamed ones from consideration now does not materially affect conclusions to be drawn concerning the endemic Hawaiian Drosophilids.

THE CHARACTERISTICS

Spermathecae—There are essentially three types of spermathecae found in species from Hawaii. All three are found in the Drosophiloid species and two of them are found also in the Scaptoids (see Appendix for the arrangement of species by groups). The spermathecae are shown in Figures 1 and 2. The most common type is nearly spherical with an unusually short introvert. Previously, this type of spermathecae has been seen only from *D. populi*, a species collected from cottonwood trees near Anchorage, Alaska (Wheeler and Throckmorton, 1960). In Hawaii this type has so far been seen only from the Drosophiloids. It is always

FIG. 1. Spermathecae

DROSOPHILOIDS
  Genus: IDIOMYIA
    .1 obscuripes
    .2 perkinsi
    .3 picta
  Genus: ANTOPOCERUS
    .4 aduncus
    .5 diamphidiopodus
    .6 longiseta
    .7 orthopterus
  Genus: NUDIDROSOPHILA
    .8 aenicta
  Genus: DROSOPHILA
    Miscellaneous
      .9 anomalipes
      .10 caccabata
      .11 hirtitibia
      .12 imparisetae
      .13 truncipenna
    Picture wings
      .14 adiastola
      .15 crucigera
      .16 engyochracea
      .17 fasciculisetae
      .18 grimshawi
      .19 musaphilia
      .20 picticornis
      .21 pilimana
      .22 punalua
      .23 villosipedis
    Modified mouthparts
      .24 aquila
      .25 araiotrichia
      .26 asketostoma
      .27 comatifemora
      .28 conjectura

    .29 dissita
    .30 eurypeza
    .31 flavibasis
    .32 freycinetiae
    .33 hirticoxa
    .34 involuta
    .35 ischnotrix
    .36 kauluai
    .37 mimica
    .38 mycetophila
    .39 residua
    .40 scolostoma
    Bristle tarsi
      .41 apodasta
      .42 basimacula
      .43 expansa
      .44 perissopoda
      .45 (T.) petalopeza
      .46 prodita
      .47 redunca
      .48 seclusa
      .49 torula
      .50 trichaetosa
    Spoon tarsi
      .51 conformis
      .52 contorta
      .53 disticha
      .54 incognita
      .55 neutralis
      .56 polliciforma
      .57 sordidapex
    Split tarsi
      .58 ancyla
      .59 fundita
      .60 pectinitarsus

pigmented, either dark brown or black, and the spermathecal envelope is thick and uniformly distributed over the capsule. At its opening into the spermatheca the spermathecal duct may flare widely (Figure 1.16) or not (Figure 1.10). This character of the spermathecal duct shows no indication of phylogenetic pattern, although the flared type is more common in the more derivative Hawaiian groups (*Idiomyia*, etc.).

The second type of spermatheca is subspherical to quadrate in outline, and the introvert extends inward half to three-quarters of the diameter of the capsule. Only one Drosophiloid species (*D. anomalipes*, Figure 1.9) has this type of spermatheca. It is far more common among the Scaptoids (Figure 2) and is, indeed, the typical *Scaptomyza* spermatheca. Its color varies from dark brown to pale yellow. The spermathecal envelope is heavy apically but in many species it is thinner toward the base of the capsule. The third major type of spermatheca is prominent among the *Scaptomyza*, and it is also characteristic of the "white tip scutellum" forms. The spermatheca in this case lacks an introvert, and there is no evidence that this represents a regressed or degenerate form. This is, substantially, the primitive spermatheca of the Drosophilid stem (see Throckmorton, 1962). Generally the capsule of this spermatheca is very weakly sclerotized and not pig-

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FIG. 2. Spermathecae (Numbers refer to specimens listed in the Appendix)

DROSOPHILOIDS
  Genus: DROSOPHILA
    White tip scutellum
     .1 cilifemorata
     .2 fungicola
     .3 haleakalae
     .4 iki
     .5 melanoloma
     .6 melanosoma
     .7 nigra
     .8 bipolita
     .9 canipolita
     .10 demipolita
SCAPTOIDS
  Genus: DROSOPHILA
    .11 crassifemur
    .12 nasalis
    .13 parva
  Genus: TITANOCHAETA
    .14 contestata
    .15 #8
  Genus: SCAPTOMYZA
    Subgenus: *Alloscaptomyza*
     .16 longisetosa
     .17 stramineifrons
    Subgenus: *Bunostoma*
     .18 anomala
     .19 palmae
     .20 xanthopleura
    Subgenus: *Exalloscaptomyza*
     .21 mauiensis

.22 #165 (Hawaii)
.23 #166 (Oahu)
.24 #168 (Kauai)
.25 #167 (Molokai)
Subgenus: *Parascaptomyza*
  .26 pallida
Subgenus: *Tantalia*
  .27 varipicta
Subgenus: *Trogloscaptomyza*
  .28 argentifrons
  .29 articulata
  .30 connata
  .31 hackmani
  .32 inaequalis
  .33 intricata
  .34 latitergum
  .35 levata
  .36 retusa
  .37 rostrata
Representatives of spermathecae and parovaria
  .38 *Antopocerus longiseta*
  .39 *Drosophila musaphilia* (picture wing)
  .40 *D. imparisetae* (misc.)
  .41 *D. hirtitibia* (misc.)
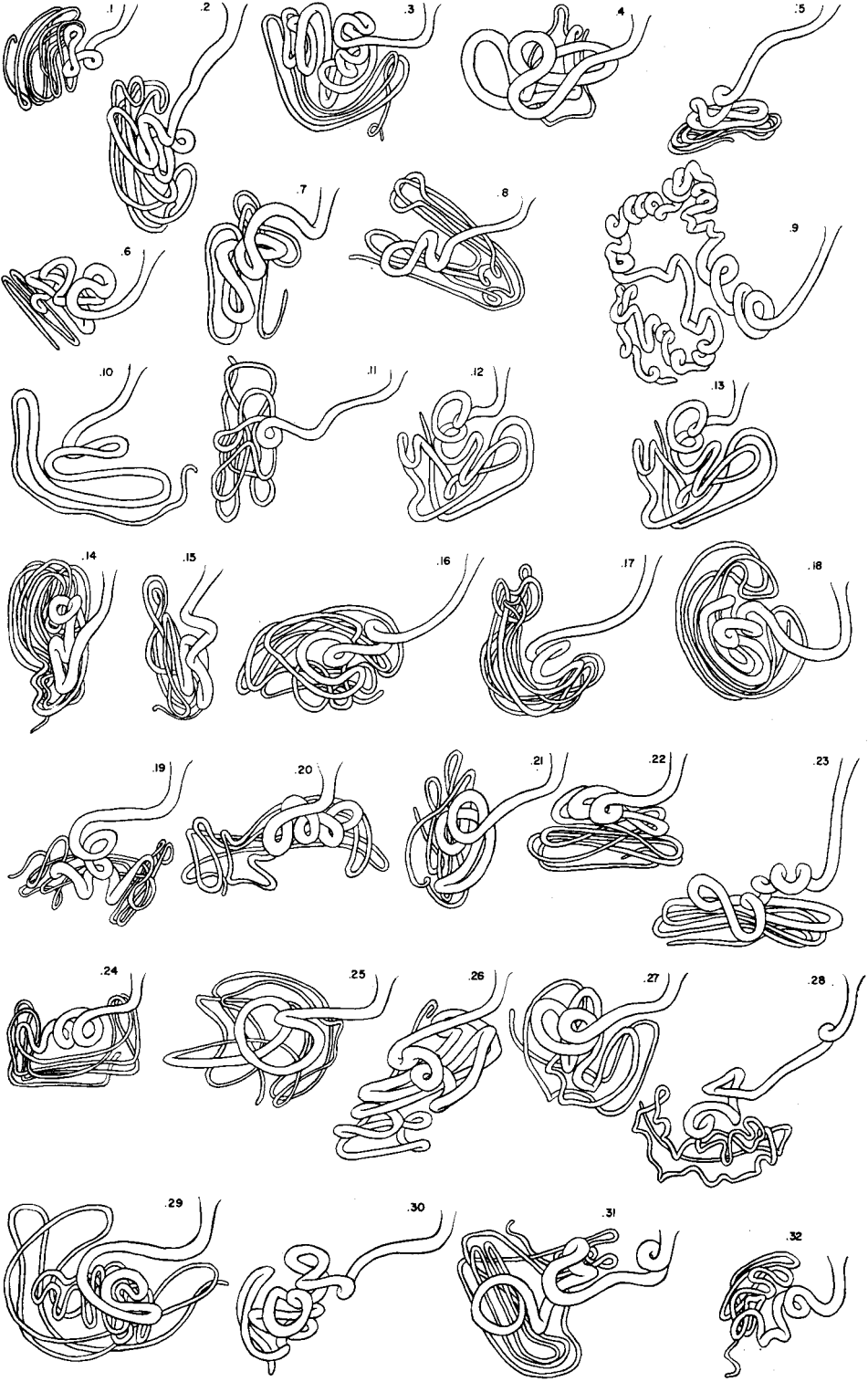 .42 *D. fungicola* (white tip scutellum)
  .43 *D. nigra* (white tip scutellum)
  .44 *D. crassifemur* (Scaptoid)
  .45 *D. nasalis* (Scaptoid)
  .46 *Scaptomyza argentifrons*
  .47 *S. retusa*

mented. In appearance there is very little to distinguish these spermathecae from parovaria. Spermathecae of this type are shown in Figures 2.1 to 2.10.

The spermathecae shown in Figures 2.14 and 2.21 to 2.25 are not of this last type although they may superficially resemble it. They represent regressions from a fully introverted type. The introvert remains as a well sclerotized structure, but the capsule itself is only a shrivelled remnant and hardly sclerotized at all. The form shown in Figure 2.25 is probably near the type these were derived from. It is very weakly sclerotized and collapses readily in phenol, where most specimens evert and give the appearance of those shown in Figures 2.21 to 2.24. However, it is just possible to determine in untreated specimens that the form shown in Figure 2.25 is normal in the living individual.

Some of the spermathecae of Scaptoid species have another character not shared with the Drosophiloids. Generally the spermathecal duct is regularly annulate from the base of the capsule to a point above where it enters the vagina (Figures 2.38–.43, etc.) In several of the Scaptoids the annulae do not start immediately below the capsule. Instead there is a continuation of the smooth surface of the spermathecal duct from within the introvert. This may extend a distance almost approximating the diameter of the capsule before the annulations start (Figures 2.11, .28, .35, etc.). Both *D. crassifemur* and *D. nasalis* have the *Scaptomyza* spermatheca, and *D. crassifemur* (Figure 2.11) also has this smooth apical portion of the spermathecal duct.

Parovaria—Some general features of the spermathecae and parovaria are shown in Figures 2.38 to 2.47. The structures are shown as they appear under low magnifications of the compound microscope after clearing in phenol. As a rule the ducts of parovaria are undifferentiated. This is true for all of the new world species of *Drosophila* that I have examined and, to my knowledge, no differentiation of this structure is reported elsewhere. However, many of the Hawai-

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FIG. 3. Ventral receptacles

DROSOPHILOIDS
  Genus: IDIOMYIA
    .1 obscuripes
    .2 perkinsi
    .3 picta
  Genus: ANTOPOCERUS
    .4 aduncus
    .5 diamphidiopodus
    .6 longiseta
    .7 orthopterus
  Genus: NUDIDROSOPHILA
    .8 aenicta
  Genus: DROSOPHILA
    Miscellaneous
      .9 anomalipes
      .10 caccabata
      .11 hirtitibia
      .12 imparisetae
      .13 truncipenna
    Picture wings

    .14 adiastola
    .15 crucigera
    .16 engyochracea
    .17 fasciculisetae
    .18 grimshawi
    .19 musaphilia
    .20 picticornis
    .21 pilimana
    .22 punalua
    .23 villosipedis
  Modified mouthparts
    .24 aquila
    .25 araiotrichia
    .26 asketostoma
    .27 comatifemora
    .28 conjectura
    .29 dissita
    .30 eurypeza
    .31 flavibasis
    .32 freycinetiae

ian species have this duct expanded and sclerotized as shown, for example, in Figure 2.38. The more usual condition for *Drosophila* and its related genera is shown in Figure 2.41. As for so many of the characteristics of the Hawaiian species, this character is distributed in a rather random fashion. At least some species from all the major groups (which includes all of the informal groupings) of Drosophiloids have it, although its expression among the "white tip scutellum" flies (Figure 2.43) is somewhat atypical. It is doubtful that this differentiation is present in any of the Scaptoids, but some slight development of this region is seen in some species (Figures 2.45 and .46).

Ventral receptacles—The ventral receptacles are shown in Figures 3 to 6. In all Hawaiian species the distal end of the ventral receptacle is completely free of the vagina. Generally there is a straight basal section, then a series of coils, and then a much-folded section. In some species (Figure 3.10) the short coiled section is absent. In others (Figures 5.15, .26, etc.) the coiled section is much expanded and forms a major part of the organ. In one species (*D. anomalipes,* Figure 3.9) the ventral receptacle lacks the folded section entirely. It has the coiled ventral receptacle that characterizes flies from the subgenus *Drosophila* from elsewhere in the world. The typical ventral receptacle of the Hawaiian species (Figure 3.3, etc.) may be considered as intermediate between the folded type seen in *Pholadoris, Sophophora* and *Dorsilopha* and the coiled type seen in the subgenus *Drosophila.* As inspection of Figures 3 to 6 will show, the ventral receptacles from Drosophiloid and Scaptoid species are substantially alike. The major types, and the ranges of variation within them, are approximately the same in both groups. Some of the species of "white tip scutellum" flies have ventral receptacles with exceptionally long straight sections basally (*e.g.,* Figure 5.8), and no Scaptoid species has a true coiled ventral receptacle, although some approximate this (Figures 5.15, .26). Otherwise the species are very much alike for this character. The figures show the ventral receptacle as seen with the compound microscope after clearing in phenol.

The ovipositor—As a genus, *Drosophila* does not show conspicuous versatility in its ovipositors. Eggs are generally inserted just under the surface of the food

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FIG. 4. Ventral receptacles

DROSOPHILOIDS
  Modified mouthparts (cont.)
    .1 hirticoxa
    .2 involuta
    .3 ischnotrix
    .4 kauluai
    .5 mimica
    .6 mycetophila
    .7 residua
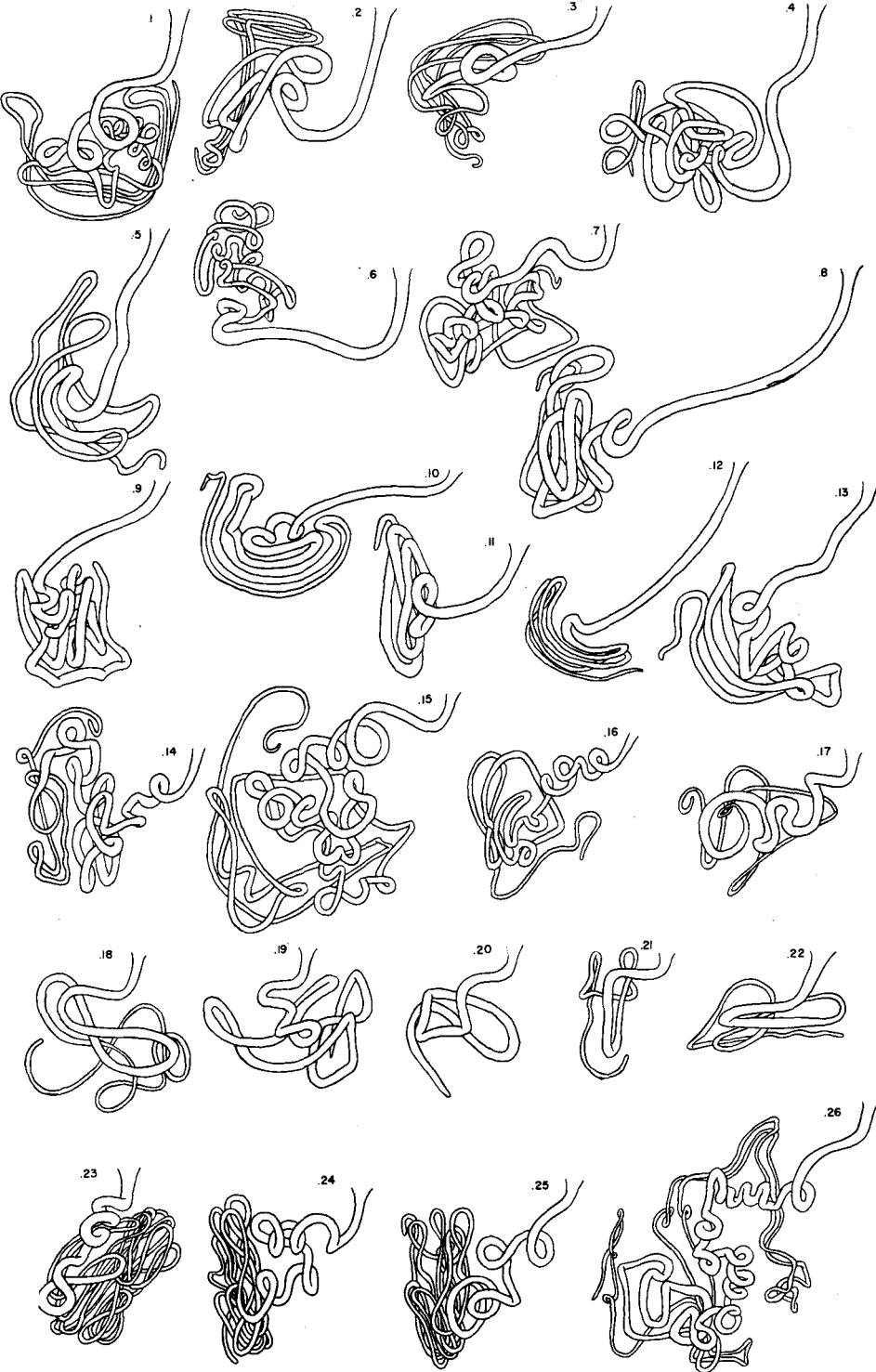   .8 scolostoma
  Bristle tarsi
    .9 apodasta
    .10 basimacula
    .11 expansa
    .12 perissopoda

    .13 (T.) petalopeza
    .14 prodita
    .15 redunca
    .16 seclusa
    .17 torula
    .18 trichaetosa
  Spoon tarsi
    .19 conformis
    .20 contorta
    .21 disticha
    .22 incognita
    .23 neutralis
    .24 polliciforma
    .25 sordidapex

and the ovipositor required for this is not very elaborate. Many of the Hawaiian Drosophilids have departed from this fashion. They may have unusually long and almost tubular ovipositors, or the ovipositors may be of the more standard type but still long, and heavily sclerotized with stout, peg-like teeth. The development of the ovipositor is associated with some internal modifications that often give to the Drosophiloid female a truncated, or blunt and heavy bodied aspect in lateral view. Figure 7.1 shows in lateral view the internal reproductive organs of the female. The most conspicuous feature is the pronounced development of the vagina and its associated muscles. For clarity the muscles have been omitted from the figure. As seen in figure 7.1 the vagina is very long. It folds anteriorly before turning ventrally to enter the ovipositor. In many species, particularly those having a long membranous ovipositor (figure 7.8), the inner sheath of the vagina moves freely within the muscular coat and has its wall supported by very tough, spiral cords. In the figure this inner sheath is shown pulled out somewhat. In consequence of this great development, the vagina itself is displaced from its usual position more or less parallel with the rectum. The muscles of the system arise from the inner surface of the last abdominal tergite. On each side one mass extends to the anterior part of the vagina and attaches to it in the region of the spermathecae and ventral receptacle. These muscles exert a force back and down, so the dorsal surface of the vagina is held closely in contact with the ventral surface of the rectum, and in many cases the nominal dorsal surface of the vagina is directed more posteriorly than dorsally. In consequence both the spermathecae and parovaria are forced to bend laterally around the anterior end of the vagina and the oviduct. The folded vagina also displaces the ventral receptacle, and it curves laterally (to the left) and dorsally. Generally the distal folded section of the ventral receptacle is attached by tracheae to the left spermatheca. A second set of muscles leads from the last abdominal tergite to the base of the ovipositor. In the relaxed state the ovipositor rests with its tip high (as in Figure 7). If this

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Fig. 5. Ventral receptacles (numbers refer to specimens listed in the Appendix)

DROSOPHILOIDS
  Split tarsi
    .1 ancyla
    .2 fundita
    .3 pectinitarsus
  White tip scutellum
    .4 cilifemorata
    .5 fungicola
    .6 haleakalae
    .7 iki
    .8 melanoloma
    .9 melanosoma
    .10 nigra
    .11 bipolita
    .12 canipolita
    .13 demipolita
SCAPTOIDS
  Genus: DROSOPHILA

    .14 crassifemur
    .15 nasalis
    .16 parva
  Genus: TITANOCHAETA
    .17 contestata
    .18 #8
  Genus: SCAPTOMYZA
    Subgenus: *Alloscaptomyza*
    .19 longisetosa
    .20 stramineifrons
    Subgenus: *Bunostoma*
    .21 anomala
    .22 palmae
    .23 xanthopleura
    Subgenus: *Exalloscaptomyza*
    .24 forms from Kauai, Oahu, and Hawaii
    .25 form from Molokai
    .26 mauiensis

FIG. 6. Ventral receptacles

SCAPTOIDS
  Genus: SCAPTOMYZA
    Subgenus: *Parascaptomyza*
      .1 pallida
    Subgenus: *Tantalia*
      .2 varipicta
    Subgenus: *Trogloscaptomyza*
      .3 argentifrons
      .4 articulata

.5 connata
.6 hackmani
.7 inaequalis
.8 intricata
.9 latitergum
.10 levata
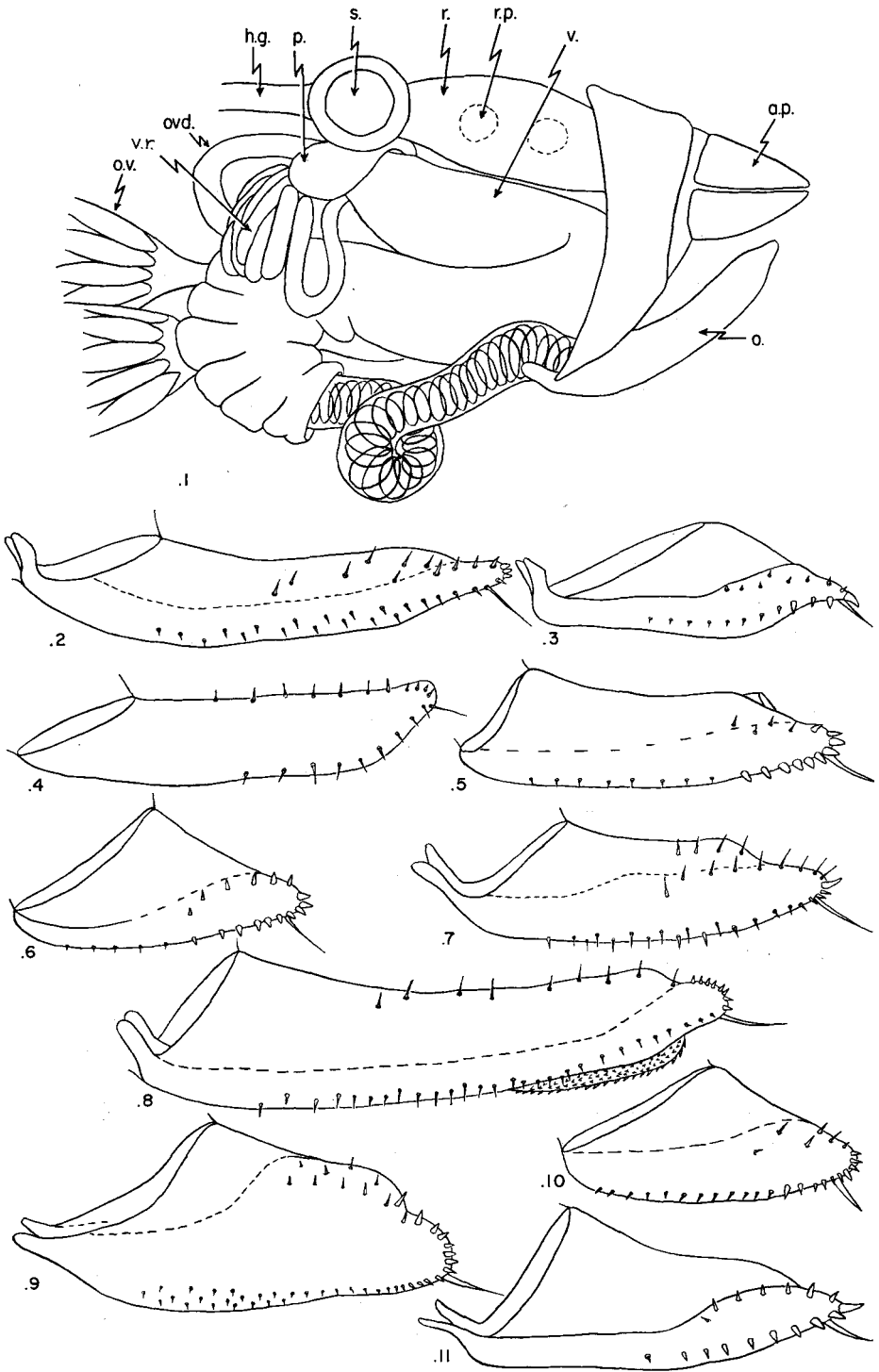.11 retusa
.12 rostrata

second set of muscles contracts the tip of the ovipositor is lowered. In many species (*e.g.*, Figure 8.2) the proximal section of the ovipositor is modified and has a special extension for the attachment of these muscles.

Not all of the Hawaiian Drosophilids show internal differentiation and the development of the ovipositor. This is seen to a greater or lesser degree in all Drosophiloids except the "white tip scutellum" species. It is not seen in the Scaptoids that I have examined to date. Among the Drosophiloids that do show development there is considerable variation. Those species that would be considered most primitive on other grounds also have this system less conspicuously developed. It is apparent that the evolution of this suite of characters has been directly correlated with adaptation to a variety of food niches and the exploitation of oviposition sites not generally accessible to *Drosophila*.

Figures 7 and 8 show some examples of ovipositors of Hawaiian species. They are shown as they appear after clearing in phenol. Figures 7.6 or 7.10 show ovipositors that must be very near the primitive type from which all other Hawaiian types were derived. Only the left half, or the left valve, of the ovipositor is shown in the figure. In most cases the ovipositor consists of a pair of sclerotized valves joined together antero-ventrally by a narrow sclerotized bridge. Dorsally the valves are connected by membrane, and the posterior extent of this membrane varies from species to species. In many of the Hawaiian Drosophiloids this membranous connection extends almost to the tip of the ovipositor. Among the Scaptoids the connection may be virtually absent and the valves almost unattached to each other. Ventrally there is also a membranous connection that generally does not extend as far posteriorly as does the dorsal connection. This is a continuation of the inner lining of the vagina and its inner surface is covered with short, recurved spines. As the ovipositor is extended and an egg deposited this lining everts and in some species may form a tube-like extension almost as long as the ovipositor. The spines would then serve to hold this tube in position while eggs are laid. Not infrequently, at least in laboratory cultures, eggs may be laid in clusters of up to half a dozen or so, and the ovipositor is probably kept in position and not re-inserted for each egg. Figure 7.8 shows a part of this ventral lining. The terminus of the dorsal connection is shown in Figure 7.5.

Not all ovipositors are distinctly composed of two valves. Sclerotization in many is reduced so that the ovipositor is entirely membranous. If one wished, an almost complete graded series of ovipositors could be arranged. At one extreme would be those with distinct, heavily sclerotized valves. In Figures 7 and 8 these are indicated by a solid line separating the upper and lower halves of the ovipositor (Figures 7.3, .11; Figures 8.1–.3, etc.). In other cases the ventral margin of a valve may be sclerotized but the region of sclerotization may grade almost imperceptibly into the membranous dorsal part. These have been indicated by dashed lines separating the dorsal and ventral halves (Figures 7.2, .5, etc.). Then there are those that are almost completely membranous (Figure 7.4; Figure 8.8, etc.). These are tube-like and quite flexible. With a dissecting needle they can be turned inside out very readily. Most of the types in which the degree of sclerotization grades from a "strong" ventral margin to a weak dorsal margin exhibit this type of flexibility. Obviously, such ovipositors could not be used to insert eggs into a very firm substrate. They seem more suited to pushing eggs into crevices or into soft, porous materials.

Among the Drosophiloids three major trends in ovipositor development may be detected. One is toward the elongate, membranous type of ovipositor just men-

tioned. These are found primarily among *Idiomyia, Nudidrosophila* and the "picture wings." Incipient development in this direction is seen primarily among flies with modified mouthparts. A second line of development is toward a very strongly sclerotized ovipositor of very characteristic shape. This type is shown in Figure 7.3. It is found in some flies with modified mouthparts (Figure 7.11) but it is most characteristic of flies in the genus *Antopocerus*, and among the flies with tarsal ornaments in the male, particularly within the "bristle tarsi" group. Very often species in a group may have one or the other of two basic types of ovipositors. These two general types are shown in Figure 8 (Figures 8.4 and .5). Many times, two species will be collected at a given locality and be almost indistinguishable for most of their characters. However, one will have the type of ovipositor shown in Figure 8.4, the other that shown in Figure 8.5. Presumably these reflect some niche separation between the two species. Precisely what each type of ovipositor is adapted for remains uncertain.

The third trend in ovipositor development is seen among the flies with the white tip scutellum. Some of these (Figure 8.7) have the type usual for the Hawaiian Drosophiloids, and others show evidence of the trend toward elongate, membranous ovipositors (Figures 8.6 and 8.8). Many, however, show a trend toward reduction. This trend is evidenced both in the reduction of sclerotization and in the reduction of size and loss of bristles (Figures 8.10 and .11). Some, of course, have their own peculiarities (Figure 8.9) and evidence independent divergence.

The trend toward reduction of ovipositors is most pronounced among the Scaptoids. Here there are many peculiar forms, but a more or less graded series could be arranged for some species. Some *Scaptomyza* (Figure 8.22) have the usual ovipositor with a pair of sclerotized valves and with a dorsal and a ventral range of bristles. Others have reduced sclerotization, the shape of the valve is changed, and the arrangement of bristles is less typical (Figures 8.14, .15, .22 and .24). The extreme reduction is seen in such forms as that shown in figure 8.25, where the valve is reduced to a small sclerotized plate and the bristles are almost all lost. Species of *Scaptomyza* from the subgenus *Exalloscaptomyza* have the most divergent types. Here the two valves seem to have fused together ventrally to form a single median structure. Some of these are shown in Figures 8.16 to 8.21. In each case both ventral and lateral views are shown. The most divergent type, found in the species of *Exalloscaptomyza* from the island of Molokai (Figures 8.20, .21), is Y-shaped, attached only basally, and is freely movable in a vertical plane.

Figures 8.12 and 8.13 show the ovipositors of *D. crassifemur* and *D. nasalis*. They are obviously distinct from the usual Drosophiloid type. *D. crassifemur*

FIG. 7.1. Internal genital system of the female shown in lateral view. The species figured is *Drosophila hirtitibia*. a.p.—anal plate; h.g.—hind gut; o.—ovipositor; ov.—ovary; ovd.—oviduct; p.—paragonium; r.—rectum; r.p.—rectal papilla; s.—spermatheca; v.—vagina; v.r.—ventral receptacle. The remainder of the drawings are of the left side of DROSOPHILOID ovipositors. .2) *Idiomyia perkinsi*, .3) *Antopocerus orthopterus*, .4) *Nudidrosophila aenicta*, .5) *Drosophila caccabata*, .6) *D. imparisetae*, .7) *D. fasciculisetae* (picture wing), .8) *D. engyochracea* (picture wing), .9) *D. asketostoma* (modified mouthparts), .10) *D. comatifemora* (modified mouthparts), .11) *D. dissita* (modified mouthparts).
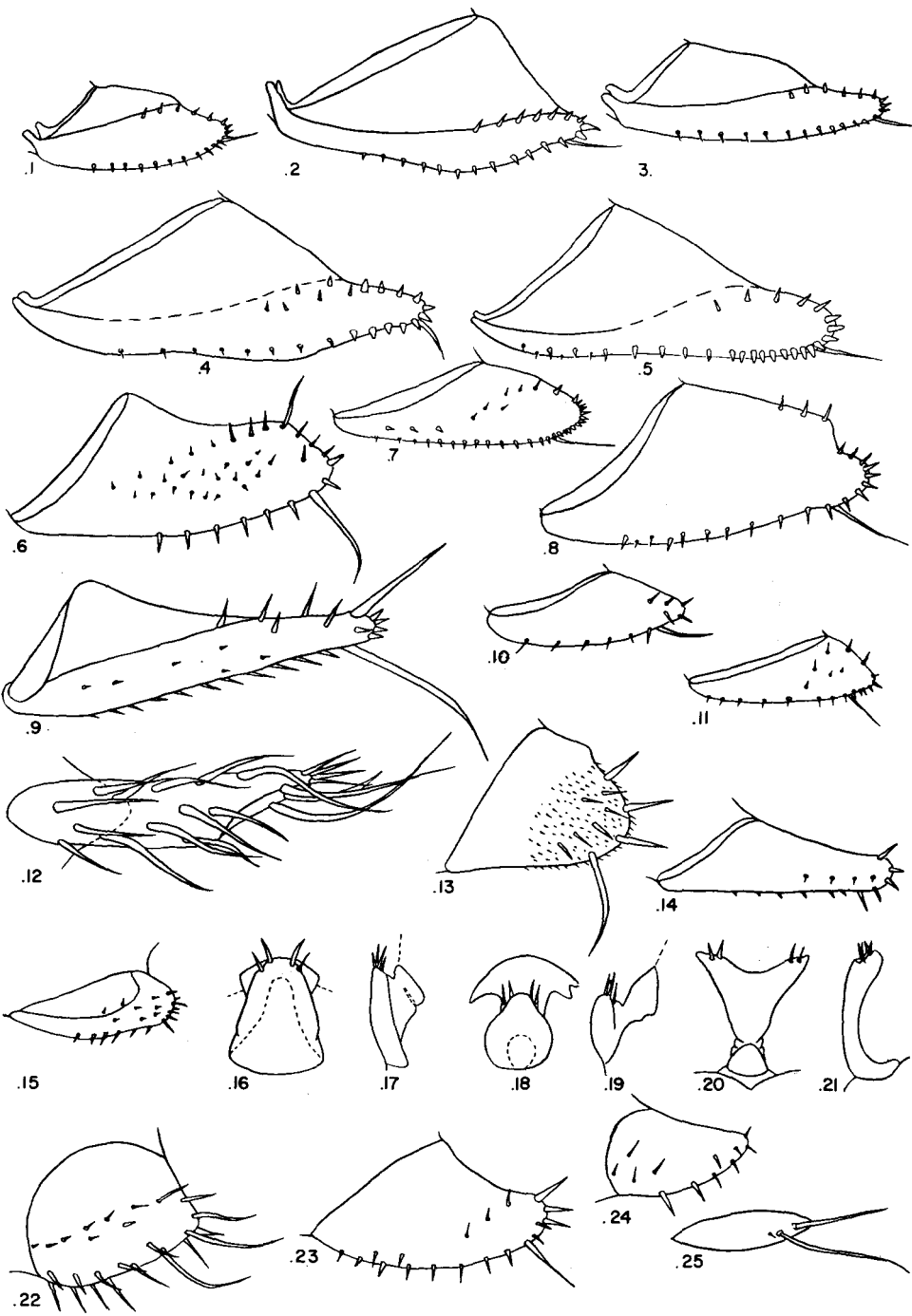
has an ovipositor with two valves (Figure 8.12). These are each slender and elongate and attached only basally. Each is covered with much elongated bristles, among which the typical dorsal and ventral ranges of bristles can be homologized without too much difficulty. *D. nasalis* has an ovipositor that is much more Scaptoid in conformation. Sclerotization is much reduced and the valve is more or less fleshy. In addition to the few remaining bristles, the apical part of each valve is covered with many short hairs (Figure 8.13).

Eggs—Figures 9 and 10 show eggs of Hawaiian species. There is an unusual variety of types. In order to represent the important features most clearly, each egg is shown in lateral and in ventral view. The egg filaments have been omitted from the ventral view (to the left in each figure).

Among the Scaptoids the number of egg filaments varies from zero to four. Among the Drosophiloids the number varies from two to four. The character of the filaments is quite different between these two major groups. Among the Scaptoids the filaments are short and heavy. In many cases they are more like small lobes than like filaments (*e.g.*, Figure 10.25). In some cases the posterior filaments are simply anterior extensions of a pair of heavy white ridges that extend along the ventral surface of the egg (Figures 10.19, .23, .27). Among the Drosophiloid species there are two major types of eggs. One is seen among the "white tip scutellum" species, the other among the remainder of the Hawaiian Drosophiloids. "White tip scutellum" flies have eggs with either two or four very short filaments (Figures 10.1–.8). These filaments are slender, as is typical for *Drosophila* filaments. In those having only two filaments (Figures 10.6–.8) these are very fine, very short, and set close together near the ventral margin of the opercular area. The remainder of the Drosophiloids have eggs with four long filaments. Some of these (Figure 9.5) appear to be identical to the type seen from non-Hawaiian species of the subgenus *Drosophila*. Others are quite different. Generally the anterior and posterior filaments differ in length, with the posterior filaments being the longer. In many instances the posterior filaments are very much longer than the anterior (Figure 9.2, .6, .7, .13). In other cases both the anterior and posterior filaments are very long (*e.g.*, Figure 9.9). Species having the long, membranous ovipositor lay the eggs with the exceptionally long filaments.

Two distinct patterns of egg chorion can generally be distinguished. In one, typical for most *Drosophila*, the surface is finely and uniformly sculptured. In the other there are distinct longitudinal striations. These two patterns are shown in the figures by stippling for sculpturing, by lines for striae. In some cases the

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FIG. 8. Ovipositors

DROSOPHILOID: bristle tarsi: .1) *Drosophila apodasta*, .2) *D. basimacula*, .3) *D. torula*; spoon tarsi: .4) *D. conformis*, .5) *D. incognita*; white tip scutellum: .6) *D. fungicola*, .7) *D. iki*, .8) *D. melanoloma*, .9) *D. nigra*, .10) *D. canipolita*, .11) *D. demipolita*.
SCAPTOID: .12) *Drosophila crassifemur*, .13) *D. nasalis*, .14) *Titanochaeta contestata*, .15) *Titanochaeta* sp. #8, *Scaptomyza* (*Exalloscaptomyza*) species, .16) from Hawaii (ventral), .17) from Hawaii (lateral), .18) from Oahu (ventral), .19) from Oahu (lateral), .20) from Molokai (ventral), .21) from Molokai (lateral), .22) *S.* (*Trogloscaptomyza*) *latitergum*, .23) *S.* (*T.*) *retusa*, .24) *S.* (*T.*) *rostrata*, .25) *Scaptomyza* species.
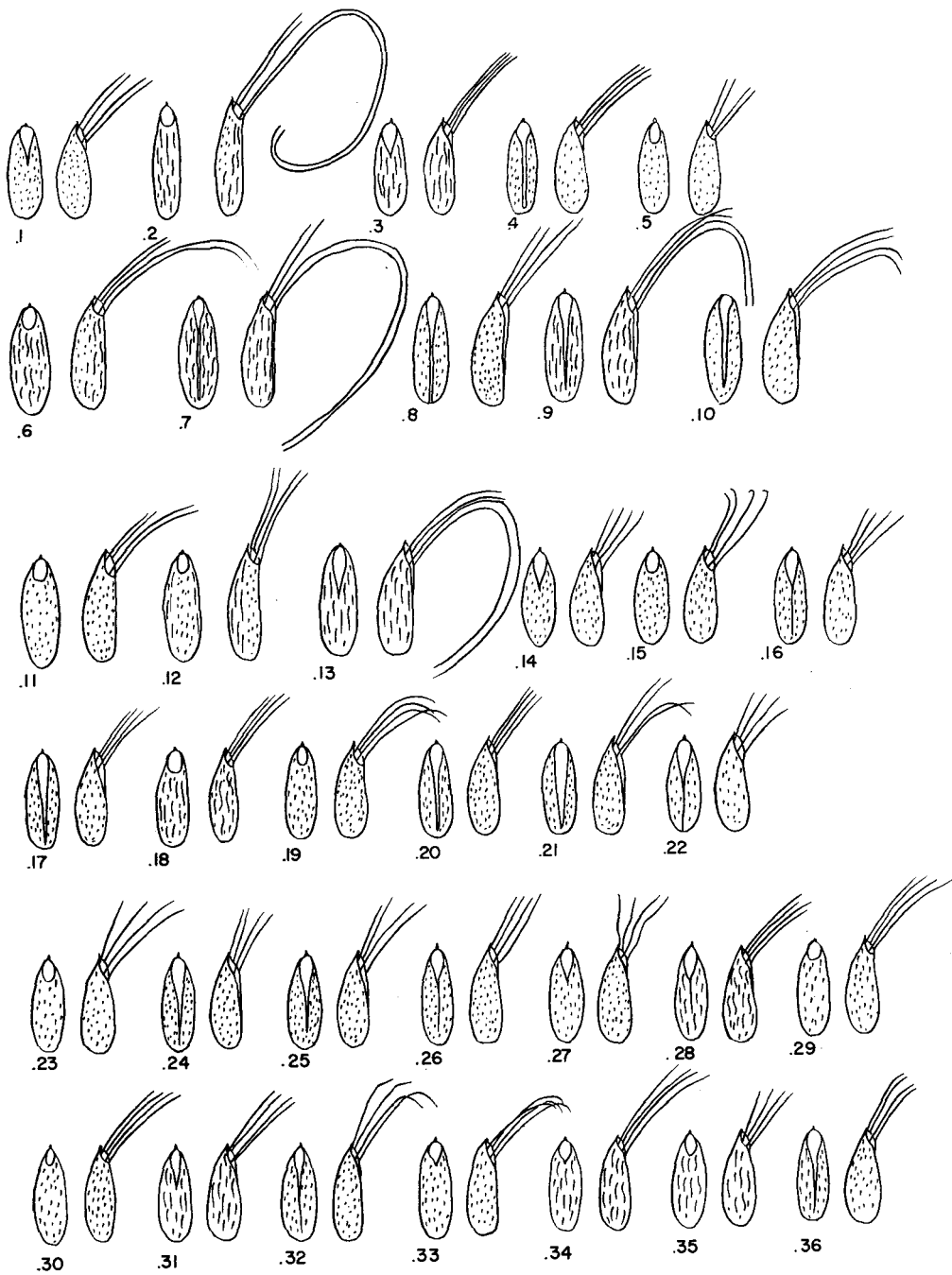
two patterns are mixed, *i.e.*, eggs show both striae and sculpturing. In some the striae are ventral, the sculpturing dorsal (Figures 9.2, .6), in some the reverse (Figure 9.12) and in others both are intermingled (Figure 9.18). Both Drosophiloid and Scaptoid eggs show these features. In some cases the chorion is almost completely devoid of character. It seems that eggs retained for some time in the vagina tend to loose the features of the chorion mentioned above. For example, the species of *Exalloscaptomyza* lay very large eggs (Figure 10.17) and, occasionally, larvae. Apparently the female can retain the egg for a rather long period until she finds a suitable oviposition site. During this period the egg may hatch and the larva be retained in the vagina. If newly collected females are dissected there is usually an egg or a larva in the vagina, one nearly mature egg in one ovary, and no egg at all in the other ovary. Females taken from culture generally have no egg in the vagina, suggesting that they lay the egg as soon as it is mature when a suitable oviposition site is available. Eggs taken from culture are very weakly sculptured. Those found in the vagina rarely show any evidence of sculpturing. The same seems to be true of *D. nasalis* (Figure 10.10), although I have dissected only a few of these females. At least some species of *Titanochaeta* also follow this pattern. The egg of one undescribed form from this genus is shown in Figure 10.12. When a female from another species, *T. contestata*, was dissected she was found with a larva in the vagina. *Titanochaeta* are parasitic on spider egg cases, but the ovipositor of this species (Figure 8.14) is not well suited for inserting an egg into a spider egg case. The larva in the vagina of the female was perfectly healthy and vigorous. Its mouth hooks were developed to form a single median stylet that was very long and sharp. When freed from the vagina

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Fig. 9. Characteristics of eggs. For each form a ventral (left) and lateral (right) view is shown. The egg filaments have been omitted from the ventral view.

DROSOPHILOID

  Genus: ANTOPOCERUS
    .1   diamphidiopodus
  Genus: DROSOPHILA
    Miscellaneous
    .2   anomalipes
    .3   imparisetae
    .4   truncipenna
    Picture wings
    .5   adiastola
    .6   crucigera
    .7   engyochracea
    .8   fasciculisetae
    .9   grimshawi
    .10 picticornis
    .11 pilimana
    .12 punalua
    .13 villosipedis
    Modified mouthparts
    .14 aquila
    .15 asketostoma
    .16 comatifemora
    .17 conjectura

    .18 eurypeza
    .19 freycinetiae
    .20 hirticoxa
    .21 infuscata
    .22 involuta
    .23 ischnotrix
    .24 mimica
    .25 mycetophila
    .26 residua
    Bristle tarsi
    .27 basimacula
    .28 expansa
    .29 perissopoda
    .30 (T.) petalopeza
    .31 torula
    Spoon tarsi
    .32 disticha
    .33 neutralis
    .34 sordidapex
    Split tarsi
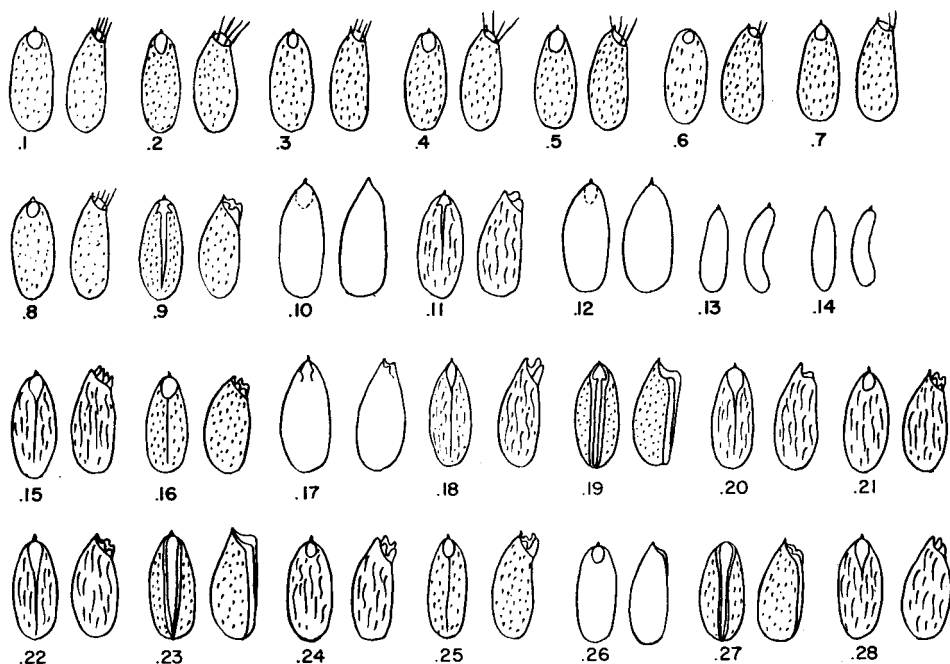   .35 ancyla
    .36 pectinitarsus

FIG. 10. Characteristics of eggs. For each form a ventral (left) and lateral (right) view is shown. The egg filaments have been omitted from the ventral view.

DROSOPHILOID
  Genus: DROSOPHILA
    White tip scutellum
      .1 fungicola
      .2 haleakalae
      .3 melanoloma
      .4 melanosoma
      .5 nigra
      .6 bipolita
      .7 canipolita
      .8 demipolita
SCAPTOID
  Genus: DROSOPHILA
    .9 crassifemur
    .10 nasalis
    .11 parva
  Genus: TITANOCHAETA
    .12 #8
  Genus: SCAPTOMYZA
    Subgenus: *Alloscaptomyza*
      .13 longiseta

    .14 stramineifrons
  Subgenus: *Bunostoma*
    .15 anomala
    .16 palmae
  Subgenus: *Exalloscaptomyza*
    .17 forms from all islands
  Subgenus: *Parascaptomyza*
    .18 pallida
  Subgenus: *Tantalia*
    .19 varipicta
  Subgenus: *Trogloscaptomyza*
    .20 argentifrons
    .21 articulata
    .22 connata
    .23 hackmani
    .24 inaequalis
    .25 intricata
    .26 latitergum
    .27 levata
    .28 rostrata

the larva exhibited a behavior pattern in which it extruded the stylet, held it in an extended position, and then pulled, as if it were attempting to tear its way through a fabric. Whether or not this behavior was adapted to gaining entrance into a spider egg case is, of course, not known. At any rate, some *Titanochaeta*, some *Scaptomyza*, and *D. nasalis* all seem to share the ability to lay few and large

eggs which may on occasion hatch in the vagina without adverse effect on either the female or the larva.

Two species from the subgenus *Alloscaptomyza* (Figures 10.13, .14) both lay very small eggs. When females of these species were dissected the vagina was found to be very large and packed with eggs. It occupied almost the entire abdomen and the ovaries were degenerating and almost non-existent. Apparently these species are adapted to do just the reverse of what *Exalloscaptomyza* and *Titanochaeta* do. They lay many small eggs and hold them all until a proper site is found, then lay them *en masse*. These eggs gave no indication of hatching in the vagina.

There is one other important feature of the eggs of Hawaiian species. In many forms the thinly sculptured opercular area extends down the ventral surface of the egg almost to the posterior end. In some cases (Scaptoid) this area is bounded by lateral ridges (Figures 10.19, .23, .27). In others (Drosophiloid) these ridges are lacking (Figures 9.4, .7, .9, etc.). I will refer to this ventral area as a *cleft*. Sometimes the edges of this cleft are fused to form a single midventral ridge, which I will refer to as a *suture*. These features are found in various combinations. Some eggs lack both cleft and suture (Figure 9.2), which is the usual state for non-Hawaiian *Drosophila*. Some have only a cleft, and this may be either long (Figure 9.4) or short (Figure 9.33). Some have only a suture (Figure 10.16). Many have a short cleft plus a suture (Figures 9.26; 10.15. etc.). Eggs having the cleft bounded by lateral ridges are found in species elsewhere in the world. One of these is *D. populi*. Others are in a pair of related genera, *Leucophenga* and *Amiota*. To my knowledge, eggs having the simple cleft, the suture, or the cleft and suture are found only in the genus *Scaptomyza* and in the Hawaiian Drosophiloids.

The paragonia and vasa deferentia—Figures 11, 12 and 13 show the internal reproductive tract of the male. Testes are not included in the figures. The paragonia of the Drosophiloids show a considerable range of types. They also tend to be somewhat variable within species and often are not bilaterally symmetrical (*e.g.*, Figure 11.38). The number of folds in the paragonia varies from somewhat more than one (Figure 11.9) to about five (Figure 11.38). In this respect these species resemble flies from the *"virilis-repleta section"* of the subgenus *Drosophila* or some species of *Pholadoris*. One of the most characteristic features of the paragonia of Hawaiian Drosophiloids is the low first arch (Figures 11 and 12). This is in marked contrast to the condition in the Scaptoids, where the first arch is generally high (Figures 13.7–.34). A few Drosophiloid species have a rather high first arch (Figures 11.31, 12.25, .26), but it is never as high as that seen characteristically in the Scaptoids. However, several of the Scaptoids do have the typical Drosophiloid paragonia (Figures 13.9, .33).

At the present time very little association is seen between type of paragonia and species groups. One of the more characteristic types (Figures 11.1, .10, .23, .27, etc.) tends to be found among *Idiomyia, Nudidrosophila* and "modified mouthparts." Another (Figure 12.10) tends to be found most frequently among flies with tarsal ornaments in the male. It is possible that more regular groupings will be apparent when the species group taxonomy has been worked out. Until then, the major importance of the characters of the paragonia lie in the evidence
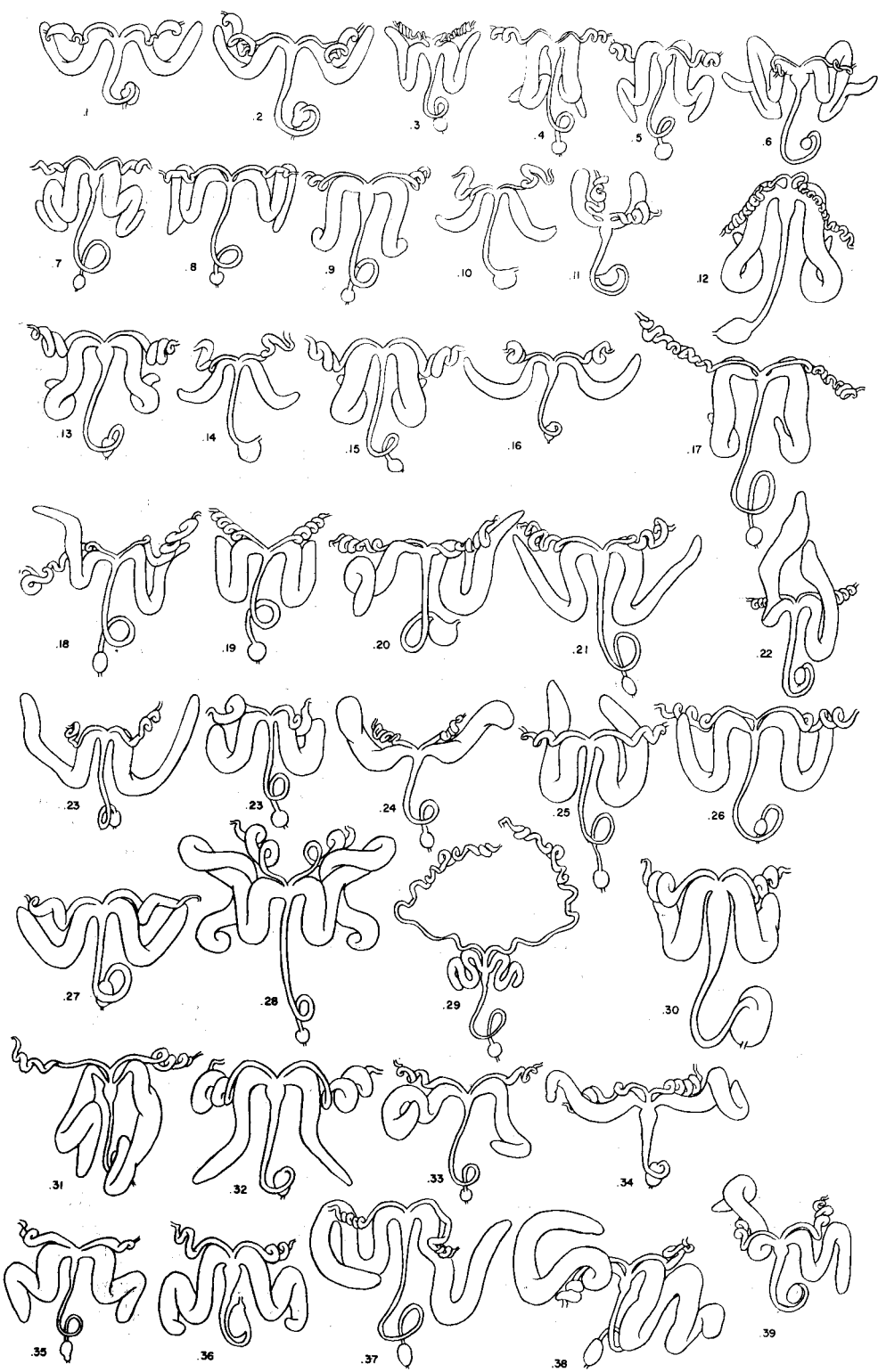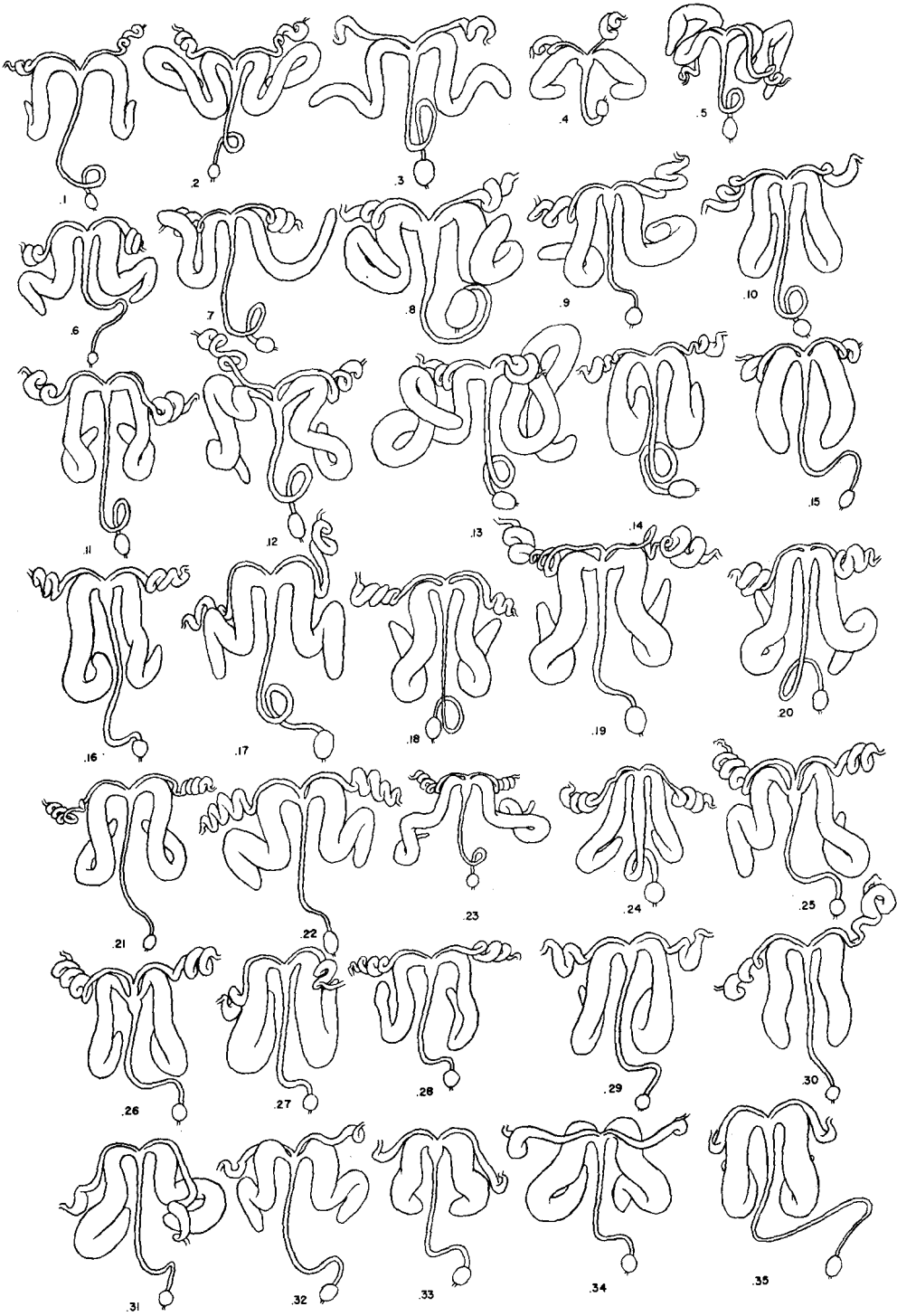
they provide for the origin of the Hawaiian Drosophilids and in the evidence they provide for differentiating the Drosophiloids from the Scaptoids in Hawaii. It may be noted that the "white tip scutellum" flies, whose eggs and spermathecae are Scaptoid, have paragonia that are fully Drosophiloid.

It is probable that the paragonia also provide species characters. In Figures 12 and 13 I have included some possible examples of this. In Figures 12.1 and 12.2 are shown the male genital tracts from flies from two localities on Oahu. The first is from Pupukea, the second from Mt. Tantalus, and both are identified by Hardy as *D. ischnotrix*. Figures 12.25 and 12.26 show the characteristics of *D. sordid-apex*, one from Kulani Road and one from Kilauea on the island of Hawaii. Figures 12.32 and 12.33 show the characteristics of *D. fungicola* from Kipuka Puaulu and the Paauilo Experiment Station on the island of Hawaii. In this last case the individuals also differ in testis color between these two localities. In Figures 13.2 and 13.3 are shown the characteristics of *D. melanosoma* from Kumuwela Ridge and Halemanu Valley in Kokee State Park on the island of Kauai. In the case of *D. fungicola*, I have dissected flies from the listed localities both in 1963 and 1964. The characteristics shown are true for the two localities in both seasons. While it seems probable that differences of the type noted here are species differences, it is also possible that they represent simple polymorphisms or local racial differences. This can only be determined by laboratory breeding tests and until these can be made it seems best to leave the question of species status open.

The vasa deferentia tend to follow the curvature of the first arch of the paragonia in both the Drosophiloids and the Scaptoids. The association is generally

FIG. 11. Paragonia and vasa deferentia

DROSOPHILOIDS
Genus: IDIOMYIA
   .1 obscuripes
   .2 perkinsi
   .3 picta
Genus: ANTOPOCERUS
   .4 aduncus
   .5 diamphidiopodus
   .6 longiseta
   .7 orthopterus
   .8 tanythrix
   .9 villosus
Genus: NUDIDROSOPHILA
   .10 aenicta
   .11 lepidobregma
Genus: ATELEDROSOPHILA
   .16 preapicula
Genus: DROSOPHILA
  Miscellaneous
   .12 anomalipes
   .13 caccabata
   .14 hirtitibia
   .15 imparisetae
   .17 quasianomalipes

Picture wings
   .18 adiastola
   .19 crucigera
   .20 engyochracea
   .21 fasciculisetae
   .22 picticornis
   .23 pilimana
   .24 punalua
   .25 villosipedis
Modified mouthparts
   .26 aquila
   .27 araiotrichia
   .28 asketostoma
   .29 chaetopeza
   .30 comatifemora
   .31 conjectura
   .32 dissita
   .33 eurypeza
   .34 flavibasis
   .35 freycinetiae
   .36 furvifacies
   .37 hirticoxa
   .38 infuscata
   .39 involuta

rather loose, but it is strong in some of the Scaptoids. In this respect the Hawaiian Drosophilids are intermediate between the condition characteristic of the more primitive *Pholadoris, Sophophora, Chymomyza* and *Dorsilopha* and the more derivitive *Drosophila, Phloridosa, Dettopsomyia, Zaprionus* and *Mycodrosophila*.

Among the Drosophiloids three general types of vasa are seen. One is an extreme coiled and folded type (Figures 11.3, .12, .17, .29, etc.) that is found particularly among *Idiomyia,* "picture wings" and flies with modified mouthparts. Elsewhere (Throckmorton, 1962) I commented on the coiling of the vas deferens among species of *Drosophila* and concluded (following Stern, 1940) that the coiling of the vas represented countercoils produced as a result of the coiling of the testis. This conclusion still holds for the flies dealt with there, but this interpretation can be only partly correct for the species just mentioned. Here the number of coils in the vas is often higher than the number of coils in the testis, and there are several *reversals* of coiling direction along the vas (*e.g.*, Figure 11.17). While other explanations are possible, it is probable that there is some intrinsic determination of form for these vasa. Hence, these species show a characteristic that may be peculiar to this group of flies. In any case, this characteristic seems to link two odd species (*D. anomalipes* and *D. quasianomalipes*) with the "picture wings," *Idiomyia,* and flies with modified mouthparts. This is of some importance, since the female of *D. anomalipes* (I have not seen the female of *quasianomalipes*) is the only Drosophiloid to have a true coiled ventral receptacle. She also has a type of spermatheca that is different from other Drosophiloid types, although it is seen among the Scaptoids. This might suggest the independent origin of *anomalipes* and its relatives, a question that will be discussed later. However, both with respect to characters of the paragonia and to characters of the vasa, *anomalipes* is an ordinary Hawaiian Drosophiloid.

FIG. 12. Paragonia and vasa deferentia

DROSOPHILOIDS
  Genus: DROSOPHILA
    Modified mouthparts (cont.)
      .1 ischnotrix (Pupukea, Oahu)
      .2 ischnotrix (Mt. Tantalus, Oahu)
      .3 kauluai
      .4 mimica
      .5 mycetophila
      .6 pychnochaetae
      .7 residua
      .8 scolostoma
    Bristle tarsi
      .9 apodasta
     .10 basimacula
     .11 expansa
     .12 perissopoda
     .13 (T.) petalopeza
     .14 prodita
     .15 redunca
     .16 seclusa
     .17 torula
     .18 trichaetosa

Spoon tarsi
     .19 conformis
     .20 contorta
     .21 disticha
     .22 incognita
     .23 neutralis
     .24 policiformis
     .25 sordidapex (Kulani Road, Hawaii)
     .26 sordidapex (Kilauea, Hawaii)
Split tarsi
     .27 ancyla
     .28 clavata
     .29 fundita
     .30 pectinitarsis
White tip scutellum
     .31 cilifemorata
     .32 fungicola (Kipuka Puaulu, Hawaii)
     .33 fungicola (Paauilo Expt. Sta.,
         Hawaii)
     .34 haleakalae
     .35 iki
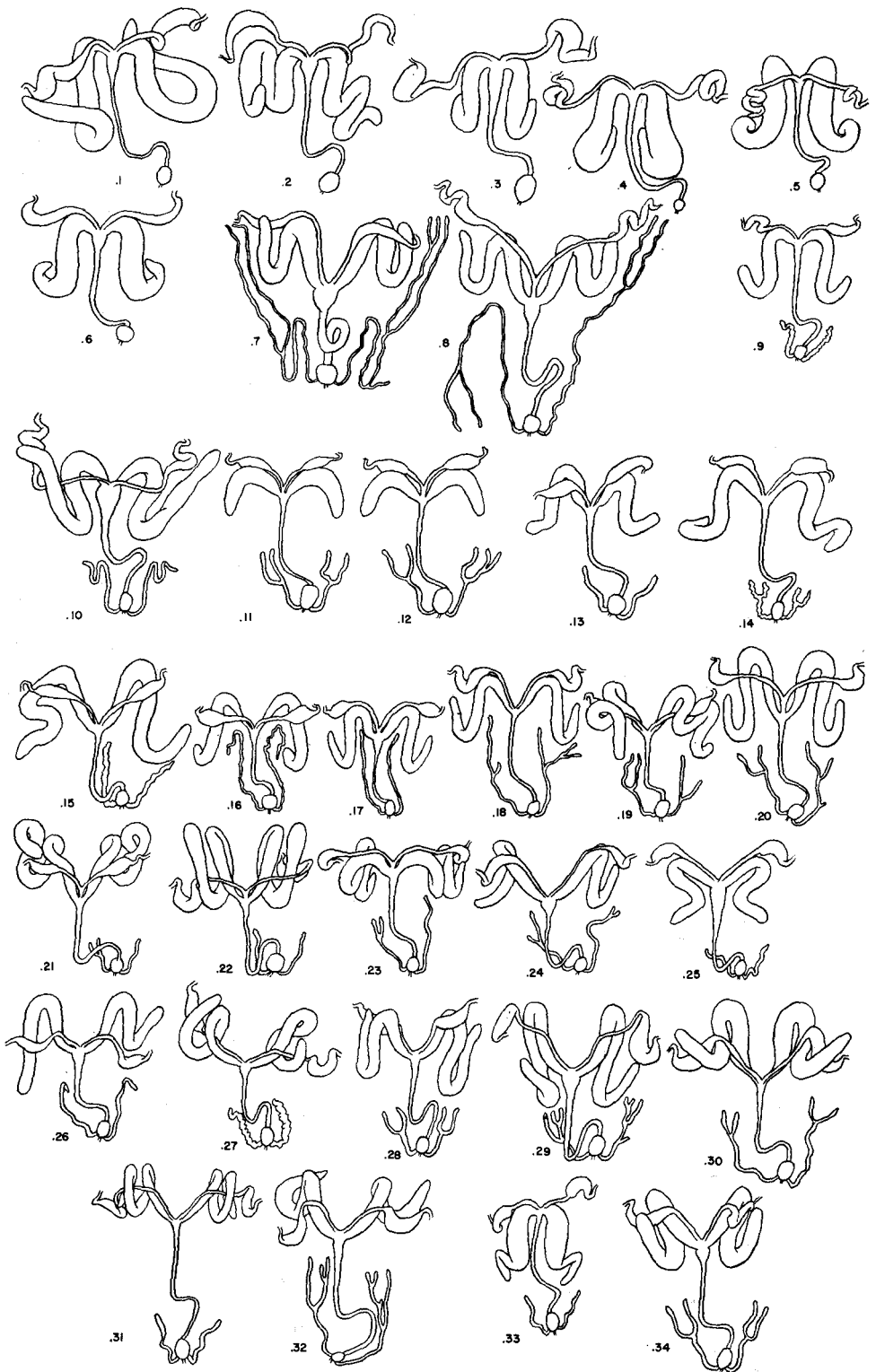
The second type of vasa is the one that is most common, both in Hawaii and elsewhere. The distal end of the vas is moderately enlarged and generally coiled about three times. In this type, the number of coils in the vas follows the number of coils in the testis and is always less than the number of coils in the testis. This type is shown in Figures 11.4, .5, .6, etc.

In the third type the distal section of the vas is generally strongly enlarged, somewhat sausage-shaped and very little coiled. This is seen, for example, among some species of *Idiomyia* (Figure 11.1) but it is most pronounced among the "white tip scutellum" flies. Here the vas is almost completely uncoiled (Figures 12.31–.35, 13.1–.6). This is, essentially, a Scaptoid characteristic (Figures 13.7–.34). Among the Scaptoids the differentiated section of the vas is completely uncoiled, plump, and nearly barrel-shaped at its most extreme development (Figure 13.14).

As a general rule the pigmentation of the vas deferens falls into two general types. In the Drosophiloid type the pigmentation extends from the testis to the base of the vas. Among the Scaptoids the pigmentation extends only over the differentiated section. The base is completely unpigmented. An intermediate condition is found in the "white tip scutellum" species. In these the pigmentation generally extends about midway between the differentiated section and the base. In *D. crassifemur* (Figure 13.7), which is otherwise fully Scaptoid, pigmentation of the vas extends almost to its base. In *D. nasalis* and *D. parva* pigmentation is of the Scaptoid type.

The ejaculatory bulb—Figures 11, 12 and 13 include some of the character-

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Fɪɢ. 13. Paragonia and vasa deferentia

DROSOPHILOIDS
  Genus: DROSOPHILA
    White tip scutellum (cont.)
      .1 melanoloma
      .2 melanosoma (Kumuwela Ridge, Kauai)
      .3 melanosoma (Halemanu Valley, Kauai)
      .4 nanella
      .5 canipolita
      .6 demipolita
SCAPTOIDS
  Genus: DROSOPHILA
    .7 crassifemur
    .8 nasalis
    .9 parva
  Genus: TITANOCHAETA
    .10 contestata
  Genus: SCAPTOMYZA
    Subgenus: *Alloscaptomyza*
      .11 longisetosa
      .12 stramineifrons
    Subgenus: *Bunostoma*
      .13 anomala
      .14 palmae

      .15 xanthopleura
    Subgenus: *Exalloscaptomyza*
      .16 from Hawaii
      .17 from Maui
      .18 from Molokai
      .19 from Oahu
      .20 from Kauai
    Subgenus: *Parascaptomyza*
      .21 pallida
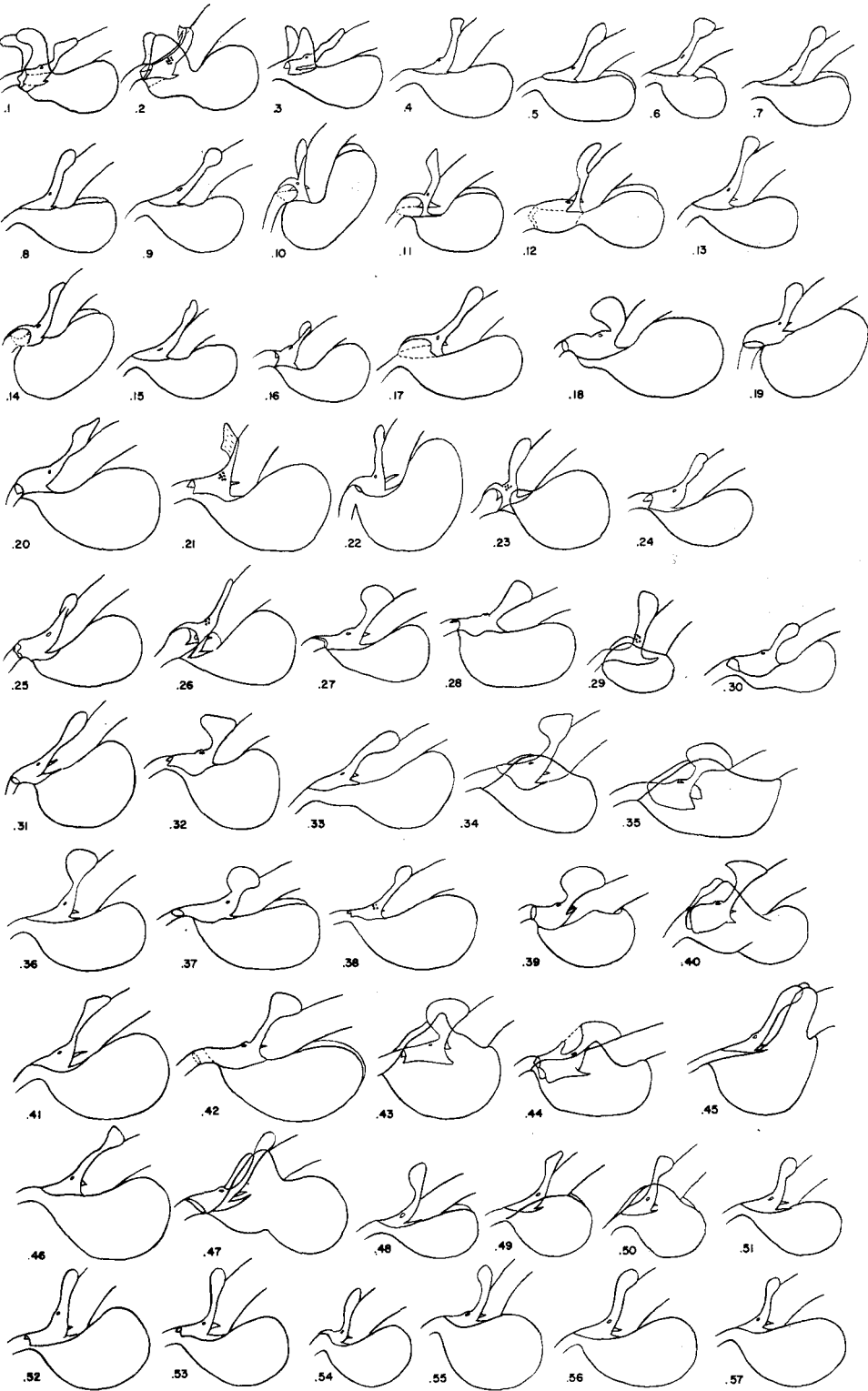   Subgenus: *Rosenwaldia*
      .22 abrupta
    Subgenus: *Tantalia*
      .23 varipicta
    Subgenus: *Trogloscaptomyza*
      .24 argentifrons
      .25 articulata
      .26 connata
      .27 hackmani
      .28 inaequalis
      .29 intricata
      .30 latitergum
      .31 levata
      .32 retusa
      .33 rostrata
      .34 silvicola

istics of the ejaculatory bulbs. Here the gross details are shown and the general conformation of the long caecae can be seen. The Drosophiloids and Scaptoids are sharply different with respect to ejaculatory caecae. These are conspicuous in Scaptoids and either absent or inconspicuous in Drosophiloids. Generally the caecae of Hawaiian Drosophiloids are not apparent until after clearing the ejaculatory bulb in phenol. In Figure 13 the Scaptoid caecae are shown extended. *In situ* they make up a tangled mass occupying the posterior part of the abdomen.

More complete details of the ejaculatory bulb and ejaculatory apodeme are shown in Figures 14 and 15. These diagrams show the bulb after clearing in phenol. Only the bases of the Scaptoid caecae are shown in Figure 15. In the figures, anterior is toward the right, ventral toward the top.

In most Drosophiloid species the ejaculatory bulb is a simple sac-like structure. In general shape the type shown in Figure 14.4 is very near the primitive for the genus *Drosophila*, and this has not been much modified among the Hawaiian forms. Among the Drosophiloids there is only slight development of ejaculatory caecae. Short caecae are found in some *Idiomyia* (Figures 14.1–.3), in some

FIG. 14. Ejaculatory bulb and ejaculatory apodeme

DROSOPHILOID
  Genus: IDIOMYIA
    .1 obscuripes
    .2 perkinsi
    .3 picta
  Genus: ANTOPOCERUS
    .4 aduncus
    .5 diamphidiopodus
    .6 longiseta
    .7 orthopterus
    .8 tanythrix
    .9 villosus
  Genus: NUDIDROSOPHILA
    .10 aenicta
    .11 lepidobregma
  Genus: ATELEDROSOPHILA
    .16 preapicula
  Genus: DROSOPHILA
    Miscellanous
      .12 anomalipes
      .13 caccabata
      .14 hirtitibia
      .15 imparisetae
      .17 quasianomalipes
    Picture wings
      .18 adiastola
      .19 crucigera
      .20 engyochracea
      .21 fasciculisetae
      .22 grimshawi
      .23 picticornis
      .24 pilimana
      .25 punalua
      .26 villosipedis

Modified mouth parts
  .27 aquila
  .28 araiotrichia
  .29 asketostoma
  .30 chaetopeza
  .31 comatifemora
  .32 conjectura
  .33 dissita
  .34 eurypeza
  .35 flavibasis
  .36 freycinetiae
  .37 furvifacies
  .38 hirticoxa
  .39 infuscata
  .40 involuta
  .41 ischnotrix
  .42 kauluai
  .43 mimica
  .44 mycetophila
  .45 pychnochaetae
  .46 residua
  .47 scolostoma
Bristle tarsi
  .48 apodasta
  .49 basimacula
  .50 expansa
  .51 perissopoda
  .52 (T.) petalopeza
  .53 prodita
  .55 seculsa
  .54 redunca
  .56 torula
  .57 trichaetosa

"picture wings" (Figures 14.23, .26) and in some flies with modified mouthparts (Figures 14.40, .43, .45, .47). In the latter cases it is problematical whether the structures involved are "lateral lobes" or caecae. Since these probably represent variations of the same thing, the distinction is not critical. Lateral lobes are seen mostly among flies with modified mouthparts (Figures 14.29, .34, .39, .44), although some are also seen in the "bristle tarsi" group (Figures 14.49, .50). So far only one species of the "white tip scutellum" flies (Figure 15.12) has been found with the lateral lobes. Among the Drosophiloids the major development of caecae and lateral lobes is thus seen among *Idiomyia*, "picture wings" and "modified mouthparts."

There has been an unusual amount of diversification of the apodeme among Hawaiian Drosophilids and in many species the apodeme is very large and conspicuous. Among the "picture wings," *Nudidrosophila*, and *Idiomyia* there has
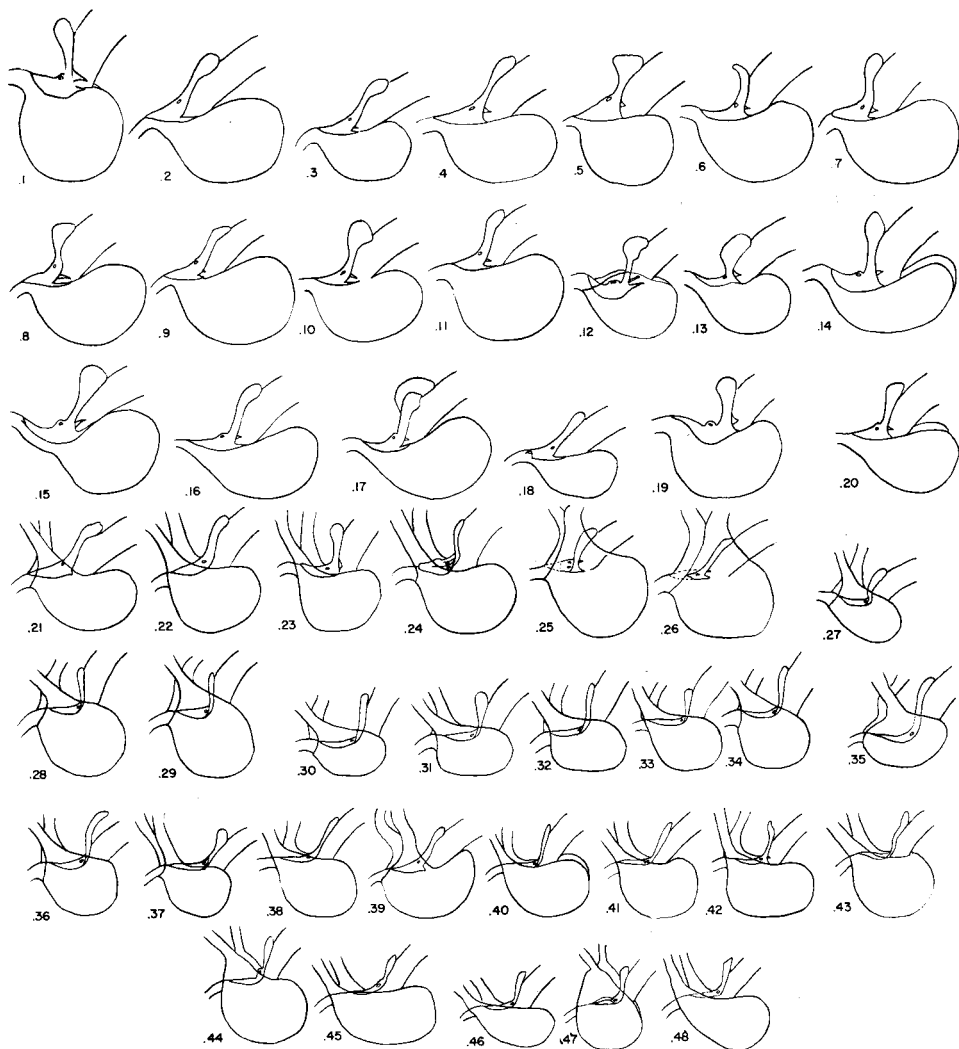
been a trend toward the sclerotization of the posterior ejaculatory duct (toward the left in the figures). The basic apodeme, from which that of the Hawaiian species is almost certainly derived, is similar to the one shown in Figure 14.46. The plate is spade-like and roughly triangular in outline. Among some of the Hawaiian Drosophiloids there has been an increase in the sclerotization lateral to the plate so that the sides of the posterior ejaculatory duct are more or less solidly enclosed (Figures 14.3, .21, .40, etc.). In others the sclerotization continues and completely surrounds the posterior duct, but this additional area is not pigmented (indicated by dashed lines in Figures 14.2, .10, .11, .12, .14, .17, etc.). In still others the duct is heavily sclerotized and pigmented (Figures 14.1, .18, .19, etc.). Again, these trends are most conspicuous in *Idiomyia*, *Nudidrosophila*, "picture wings" and the flies with modified mouthparts. *D. anomalipes* and *D. quasianomalipes* also fall into this group. An additional, and apparently independent, trend is also seen among the species with modified mouthparts. In many of these flies the ejaculatory bulb is very wide (not figured), sometimes almost twice as broad as long. The plate of the ejaculatory apodeme is also very broad in these cases. Generally, an apodeme that surrounds the posterior ejaculatory

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Fig. 15. Ejaculatory bulb and ejaculatory apodeme

DROSOPHILOID
  Genus: DROSOPHILA
    Spoon tarsi
      .1 conformis
      .2 contorta
      .3 disticha
      .4 incognita
      .5 neutralis
      .6 polliciforma
      .7 sordidapex
    Split tarsi
      .8 ancyla
      .9 clavata
      .10 fundita
      .11 pectinitarsus
    White tip scutellum
      .12 cilifemorata
      .13 fungicola
      .14 haleakalae
      .15 iki
      .16 melanoloma
      .17 melanosoma
      .18 nanella
      .19 canipolita
      .20 demipolita
SCAPTOID
  Genus: DROSOPHILA
    .21 crassifemur
    .22 nasalis
    .23 parva
  Genus: TITANOCHAETA
    .24 contestata

Genus: SCAPTOMYZA
  Subgenus: *Alloscaptomyza*
    .25 longisetosa
    .26 stramineifrons
  Subgenus: *Bunostoma*
    .27 anomala
    .28 palmae
    .29 xanthopluera
  Subgenus: *Exalloscaptomyza*
    .30 from Hawaii
    .31 from Maui
    .32 from Molokai
    .33 from Oahu
    .34 from Kauai
  Subgenus: *Parascaptomyza*
    .35 pallida
  Subgenus: *Rosenwaldia*
    .36 abrupta
  Subgenus: *Tantalia*
    .37 varipicta
  Subgenus: *Trogloscaptomyza*
    .38 argentifrons
    .39 articulata
    .40 connata
    .41 hackmani
    .42 inaequalis
    .43 intricata
    .44 latitergum
    .45 levata
    .46 retusa
    .47 rostrata
    .48 silvicola

duct is narrow (Figure 14.47), and one that is very wide does not surround the duct (Figure 14.28). Some, however, do both (Figures 14.37, .42).

In many of these species the ejaculatory apodeme has a slightly different shape that seems to be peculiar to Hawaiian Drosophilids. The difference is difficult to describe but it can be seen by comparing the apodeme in Figure 14.46 with that in Figure 14.7. That seen in Figure 14.7 is the Hawaiian type. Elements of this shape can be seen even in some of the more derivative types (*e.g.*, Figures 14.1, .14, etc.). This type of apodeme is found most conspicuously among species of *Antopocerus* (Figures 14.4–.9) and among those species whose males have tarsal ornaments (Figures 14.48–.57, 15.1–.11). In this latter group the apodeme may occasionally be of the standard type (Figure 15.4, etc.). Among the "white tip scutellum" species the apodeme is also generally of one of these two types, with the additional feature that it is often flexed, sometimes strongly so (*e.g.*, Figure 15.19). In some of these species also the anterior (toward the right) flanges of the plate may encircle the *anterior* ejaculatory duct and form a completely sclerotized ring around it (not shown, but present in some undescribed species).

Among the Scaptoids there is considerably less variation in ejaculatory bulbs and ejaculatory apodemes. All bulbs have caecae, and sometimes these are branched (Figure 13). The apodeme is rarely of the standard type (Figure 15.21). More generally it is of the kind very typical of *Scaptomyza*. In this the plate is very much flattened so that it almost disappears in lateral view. The anterior flanges or angles of the plate are much reduced (Figure 15.23) or rounded off completely (Figure 15.24, etc.). The handle is almost always simple. At most it may have a small blade (Figure 15.31), which is quite in contrast to the elaborate developments (*e.g.*, Figure 14.44) of some Drosophiloids.

The testes—Table 1 lists the number of testis coils and testis color among Hawaiian species. The range in number of coils is restricted relative to that found among species of *Drosophila* from elsewhere in the world. In an earlier sample (Throckmorton, 1962) of 195 species, approximately 36 per cent had more than six coils in the testes. Here (Table 1) only 2 per cent of the Drosophiloids and 4 per cent of the Scaptoids have such high numbers. The range in number of testis coils reaches from zero (elliptical testes) to more than twenty among non-Hawaiian species. It reaches from approximately one to nine coils among the Hawaiian Drosophilids. Thus far no species have been found in Hawaii having elliptical testes, although some species among the "white tip scutellum" flies have less than one coil. These are not listed in Table 1, since the species are undescribed.

The righthand columns in Table 1 indicate the distribution of testis colors among the Hawaiian forms. A preponderance (about 70 per cent) of the Drosophiloids have testes that are basically yellow. About 60 per cent of the Scaptoids have testes that are basically orange. There is a great deal of variation in intensity of color, but no attempt has been made to indicate this in the table. Development of pigment is greatly influenced by age, and since most individuals were collected from the wild, age was unknown.

Abdominal sternites in the male—As discussed by Wheeler (1960) and Throckmorton (1962) presence or absence of the first and sixth abdominal sternites in the male may provide evidence of evolutionary position. In general the

TABLE 1

Number of testis coils and testis color among the Hawaiian Drosophilids

Group	Number of coils			Testis color			
	1–3	3–6	6–9	yellow	yellow-brown	yellow-orange	orange
Drosophiloid							
Idiomyia	.	3	.	2	.	1	.
Antopocerus	6	.	.	6	.	.	.
Nudidrosophila	.	2	.	2	.	.	.
Miscellaneous	5	.	1	3	1	1	1
picture wings	2	7	.	6	2	.	1
modified mouthparts	5	15	1	11	1	4	5
bristle tarsi	.	10	.	7	1	2	.
spoon tarsi	.	8	.	7	.	1	.
forked tarsi	.	4	.	3	.	1	.
white tip scutellum	9	.	.	3	.	6	.
Scaptoid							
Titanochaeta	1	.	.	1	.	.	.
Alloscaptomyza	2	.	.	.	.	1	1
Bunostoma	2	1	.	.	.	.	3
Exalloscaptomyza	.	4	1	.	.	.	5
Parascaptomyza	1	.	.	1	.	.	.
Rosenwaldia	.	1	.	.	.	.	1
Tantalia	.	1	.	1	.	.	.
Trogloscaptomyza	2	9	.	7	.	.	4
Total Drosophiloid	27	49	2	50	5	16	7
Total Scaptoid	8	16	1	10	.	1	14

males of Sophophoran species have the sixth sternite present as a polished and generally unbristled plate. Among species of the subgenus *Pholadoris* and *Chymomyza*, the sixth sternite may be unreduced and fully bristled or it may be partly reduced and present only as a pair of bristled plates. With the exception of *D. testacea*, species from the subgenus *Drosophila* are not known to possess the sixth sternite.

The first sternite is generally not present in Sophophorans (except *D. populi* and very faint remnants in some species of the saltans group). It is present in some species of *Chymomyza* and *Pholadoris* and absent in others. It is generally absent in species of the subgenus *Drosophila* and in the other genera and subgenera closely related to it (*Zaprionus, Mycodrosophila, Dettopsomyia, Phloridosa*).

Among the Hawaiian Drosophilids I have seen the sixth sternite present and unreduced in *Idiomyia picta*, *D. adiastola* and *D. villosipedis*. The last two are both "picture wings." It is present but reduced in *D. picticornis* (present as paired plates), in *D. furvifacies* (a normal sclerite thinly sclerotized in the midline) and in *D. mimica* (only remnants seen). It is present as paired patches in the male of *D. nasalis* collected from Paliku in Haleakala Crater on the island of Maui. It was not seen in *D. nasalis* males collected from Molokai. It is very faintly evident in males of a species of *Exalloscaptomyza* collected at Kamuela on the island
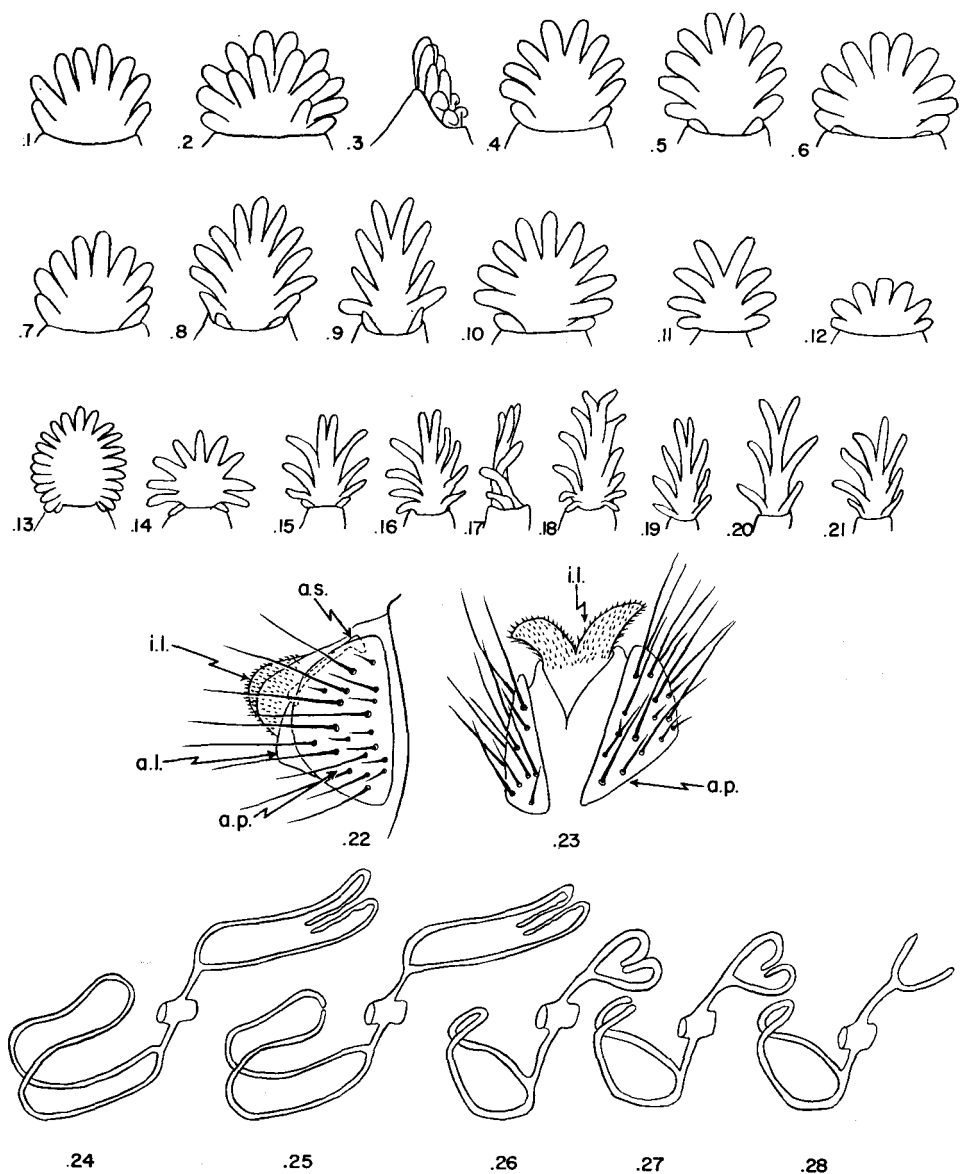
FIG. 16. Anterior pupal spiracles, intra-anal lobes and Malpighian tubules.
DROSOPHILOID spiracles: .1) *Drosophila crucigera*, .2) *D. adiastola* (face view), .3) *D adiastola* (side view), .4) *D. grimshawi*, .5) *D. pilimana*, .6) *D. punalua*, .7) *D. villosipedis*, .8) *D. eurypeza*, .9) *D. ischnotrix*, .10) *D. mimica*, .11) *D. mycetophila*, .12) *D. melanosoma*.
SCAPTOID spiracles: .13) *D. crassifemur* (Paliku), .14) *D. crassifemur* (Kauai), .15) *D. parva*, .16) *Scaptomyza palmae* (face view), .17) *S. palmae* (side view), .18) *S. mauiensis*, .19) *S. pallida*, .20) *S. varipicta*, .21) *S. argentifrons*.
Intra-anal lobes: .22 lateral view, .23 ventral view; a.l.—anal lining; a.p.—anal plate; a.s.—anal sclerite (dashed line); i.l.—intra-anal lobe.
Malpighian tubules: .24—.28. See text.

of Hawaii. The area of the sixth sternite is sclerotized but not bristled in *D. anomalipes* and *D. engyochracea*. The sixth sternite is thus seen among the Drosophiloids from *Idiomyia*, the "picture wings," and the "modified mouthparts." It is also seen in *D. anomalipes* and *D. quasianomalipes*. From the Scaptoids it is seen in *D. nasalis* and in *Exalloscaptomyza*.

The first sternite is present in *Idiomyia obscuripes*, *I. picta* and *I. perkinsi*. It is also seen in *S. (Bunostoma) palmae* from Kamuela, Hawaii, and in a species of *Exalloscaptomyza* from Molokai.

Intra-anal lobes in the male—Figures 16.22 and 16.23 show a peculiar structure that is present in many of the Hawaiian Drosophiloids. This takes several forms and I have made no attempt to note all of them. The figure shows the most extreme development of the characteristic that I have seen. In these cases there exists a pair of lobes covered with a fine dense pile and lying between the anal plates in the male. These lobes can be completely withdrawn between the anal plates or they can be extruded as shown in the figures. The lobes are not present in the female. Associated with the lobes is a special sclerite that lies in the median line between the lobes when they are present (shown by dashed line in Figure 16.22). It is anchored in the dorsal membrane just posterior to the genital arch and it apparently serves as a support for muscles that act to retract the lobes when they are not in use. This sclerite is seen in many males that do not show evidence of the lobes themselves. Drosophiloid males may thus fall in one of three categories: without anal sclerite or intra-anal lobes, with anal sclerite but without intra-anal lobes, and with both anal sclerite and intra-anal lobes. This is probably also an evolutionary sequence from primitive to derivative, with presence of intra-anal lobes being most derivative. These lobes are most highly developed among "picture wings," but at least some species from all major groups of Drosophiloids except the "white tip scutellum" flies show at least the anal sclerite.

Spieth (this Bulletin) has described courtship behavior from many species of Drosophiloid males. Two behavior patterns seem relevant in the present context. In one case the male during courtship elevates and bends the abdomen so that the anal region is pointed toward the female. At the same time, probably through abdominal pressure, the lining of the anal passage may be extruded as a distinct cylinder of tissue and a drop of liquid hangs on its end. Presumably this has some function as a sexual stimulant. I have dissected males of some of the species with this behavior pattern and found the anal sclerite present, but not the intra-anal lobes. Apparently the sclerite functions in the withdrawal of the extruded anal lining after this phase of courtship is complete. Since I have never made a detailed micro-examination of the anal lining in these species, it is possible that some less conspicuous form of the intra-anal lobes was present in these flies also. In other instances the male may be seen touching the tip of its abdomen to the substrate or dragging it along the substrate. In the species which show this type of activity, the male does have the intra-anal lobes. Spieth suggests that the male may be laying an odor trail or laying down scent to act as an aggregation point. The anal lobes, with their dense covering of very short hairs, may be especially adapted for this purpose, although it is quite possible that they also function in the production of a sexual stimulus during courtship. To date, observations on these peculiar structures of the male Drosophiloid are too fragmentary to warrant

further discussion. A systematic study of the structural modifications, correlated with a detailed study of behavior, would undoubtedly be rewarding.

Pupal spiracles—The major features of the anterior pupal spiracles of the Hawaiian Drosophilids are shown in Figure 16. They are of a very simple type, but I have not seen this form elsewhere. The branches are short and cylindrical. Generally they stand erect. In this respect they resemble the branches of pupal spiracles from species in the subgenus *Drosophila*. In many respects these spiracles resemble those of species in the virilis group and they are perhaps as close to them as to any other. However, even here the similarities are not striking. Most of the figures show a face view of the spiracle (a latero-ventral view). Figure 16.3 shows a side view of the spiracle of *D. adiastola,* and Figure 16.17 shows a side view of the spiracle of *S. (Bunostoma) palmae.* As inspection of Figure 16 will indicate, these spiracles are very much alike. Although the more typical Drosophiloids spiracle (Figure 16.6) is quite distinct from the typical Scaptoid spiracles (Figure 16.21) the two types intergrade so smoothly that it is impossible, in Hawaii, to be certain of the genus from which a given spiracle comes. One of the characteristic features of the Scaptoid spiracle is that the antibasal branches tend to be elongated and fused basally. This feature is also seen in several of the Drosophiloid spiracles (*e.g.,* Figure 16.9). Conversely, spiracles that are very similar to the Drosophiloid type are seen in Scaptoids (compare Figures 16.11 and .14). One of the Scaptoids, *D. crassifemur,* has rather variable spiracles. Figure 16.14 shows one extreme of the type found from flies collected at Paliku, Maui. Several pupae were examined from this culture and the number of branches varied from twenty-two (shown) to seventeen. Another culture from flies collected at Kokee State Park, Kauai,* showed spiracles with from fifteen to eleven branches. This latter type is shown in Figure 16.14. It is probable that additional cultures from the two localities might have produced pupae that overlapped completely in their characteristic number of branches. Whether or not these intergrade completely, there is a distinct gradation between these two populations from fully Drosophiloid spiracles (Figure 16.13) toward the Scaptoid type.

I am not certain that I have seen pupae from *Titanochaeta.* I am indebted to Mrs. Meredith Carson for bringing to my attention some puparia she found partially embedded in a spider egg case. The egg case was small and there were only three puparia. Two were partially within the egg case and the third was almost completely on its surface. These puparia were all alike and had spiracles very similar to the type shown in Figure 16.12. That is, the spiracles were fully Drosophiloid.†

Malpighian tubules—Malpighian tubules from Hawaiian species are shown in Figures 16.24 to 16.28. All Drosophiloid species have the type shown in Figure 16.24. This is the type usual for species in the subgenus *Drosophila*. The stalks are short and the posterior tubules have their tips fused, the lumen continuous. The Malpighian tubules of the Scaptoids are variable. About half of these species have the type shown in Figure 16.24, and about half have the type shown in

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* Editor's note: The form from Kauai is a different species; see Hardy, this Bulletin.

† During the summer of 1965 I saw pupae from Mrs. Carson's recent collection. *Titanochaeta* had emerged from them in the laboratory. The spiracles were as shown in Figure 16.12.

Figure 16.25 (posterior tips apposed). Several species show both types. Thus, *S. hackmani* from Molokai has the posterior tips fused, that from Hawaii has the tips apposed. *S. palmae* from Mt. Tantalus, Oahu, has the tips apposed, that from Hawaii has the tips fused. Since these came from different collecting localities it is possible that cryptic species are being dealt with instead of geographical strains. These may also represent polymorphisms, and there are at least two cases where this is probably the case. Species of *Scaptomyza* from the subgenus *Exalloscaptomyza* are quite variable in this respect. Flies collected from a single locality at Kokee State Park, Kauai, had both types of Malpighian tubule. Some had the posterior tips apposed. Some had the posterior tips fused. The strain of *D. crassifemur* collected from Molokai also showed this type of variation. It is probable that more species would be found to show this type of variation if this character were investigated more fully, particularly in wild-caught individuals. Several Scaptoid species have more sharply modified Malpighian tubules. In specimens of *Exalloscaptomyza* collected from Oahu, Molokai, and Maui, the stalk of the posterior tubule was about 2X the usual length and both the anterior and posterior tubules were very short (Figure 16.26). This type of Malpighian tubule was also found in the two species from the subgenus *Alloscaptomyza* (*S. longiseta* and *S. stramineifrons*). Two species, *S. inaequalis* and *S. articulata*, had this same type of tubule, except that the posterior tubules were apposed (Figure 16.27). In one species, *S. varipicta*, the posterior tubules were fused and the anterior tubules were much shortened (Figure 16.28). Of the two species from the genus *Titanochaeta*, one had the posterior tubules fused, the other had them apposed. Thus, for this character also, *Titanochaeta* is Scaptoid.

DISCUSSION

The interrelationships of the Drosophiloids—For all their diversity in external features (Hardy, 1965), the Drosophiloids are a remarkably compact and cohesive group of species. The sharpest division within this group, between the "white tips" and the other Drosophiloids, is not presently recognized by the formal taxonomy, mainly because the characteristics that distinguish these are not among those characters customarily used to differentiate groups of Diptera. Conversely, several groups, otherwise undistinguished, are set off formally as genera because of novelty in conventional characters. This tends to give a misleading impression of divergence. Thus the genera, *Idiomyia, Antopocerus*, and *Nudidrosophila* are based on far more trivial and less extensive complexes of characters than would be a division between the "white tip scutellum" species and the other Drosophiloids. I am not intending here to quarrel with the formal taxonomy of these species as it stands today. It is simply necessary to remind the reader that taxa of equivalent rank are not necessarily of the same biological or evolutionary significance, and this is particularly true of many of the Hawaiian genera and subgenera. Thus, for most of the earlier descriptions in this paper, it has been possible to treat Hawaiian species in two groups, Drosophiloid and Scaptoid, regardless of their formal classification. It should have been evident in these descriptions that, for the characteristics covered herein, group designations are of little consequence. Most of these characteristics are characteristics of

Hawaiian Drosophiloids, not of any particular group of Drosophiloids. Even some of the most distinctive features (some ovipositors, some egg characteristics, some ejaculatory bulbs, etc.) are not confined to single groups or even characteristic of any presently recognized group. While this situation is symptomatic of the type of evolution occurring among Hawaiian species (see later), and is of interest for that reason, it makes the analysis of Drosophiloid relationships *inter se* very difficult. Oftentimes speculation must be based on only a few characters and hence, for the present, phylogenetic relationships are quite tentative. The method of phylogenetic analysis follows that of Throckmorton (1962, 1965).

As indicated above, the major cleavage among the Hawaiian Drosophiloids is that between the "white tip scutellum" species and the other forms. The "white tips" have a very characteristic external *"gestalt,"* and they can be recognized and separated in the field without the aid of magnification. At least three subgroups can be discerned within this group. One includes such extreme forms as *nigra*, and another is the *"polita* complex" (in this study, *bipolita, canipolita* and *demipolita*). A third group is made up of such species as *fungicola* or *melanoloma*. These last forms occupy a more or less central position within the "white tips" but do not constitute a phylogenetic unit as such. They are the forms that are nearest in general morphology to the other Drosophiloids. *D. fungicola* and *imparisetae*, for example, have a superficial resemblance in wing pattern, and in several other features (the light tip of the scutellum, for example) *imparisetae* diverges toward the "white tips" in its characteristics. I have grouped *imparisetae* with the "miscellaneous" species in the Appendix and in the figures. It is certainly not a "white tip," but it represents a rather nondescript cluster of species that have retained the more general *Drosophila* characters rather than diverging in the peculiar ways of other Hawaiian forms. On the basis of external characters, it seems reasonable to infer an origin of the "white tips" from Hawaiian species not too different from *imparisetae* and its relatives.

On the basis of internal characters also, there can be little question that the "white tips" are descended from the same ancestor as the other Hawaiian species. Even a cursory inspection of Figures 1 through 16 will show the extent to which these species share basic Hawaiian characteristics with other forms. There are only two major characters, the egg and the spermatheca, that have states restricted to these species. Other characters are either the standard Hawaiian types or obvious modifications of them. The fundamental unity of the Hawaiian character complexes can best be appreciated if they are contrasted with like complexes from other groups within the genus. Such data have been presented elsewhere (Throckmorton, 1962) and the reader is referred to that paper for more detailed information on the characters of continental forms.

Three of the major characters are of particular importance in giving evidence of the distinctness and unity of the Hawaiian Drosophiloids. These are the ventral receptacle, the paragonia and the pupal spiracle. A summary of these and other characters is given in Figure 17. The ventral receptacles are of a type rarely seen elsewhere in the genus, and one of their most critical features is not particularly evident in the figures. This concerns the relationship of the ventral recep-

tacle to the vagina and its disposition among the other internal organs. The ventral receptacles of Hawaiian Drosophiloids are of three major types (Figure 17.6–.8), with the two types shown in Figure 17.6 and 17.7 predominating. The type shown in Figure 17.6 appears, in the figure, to be very similar to types seen, for example, among Sophophorans. It differs, however, in that it is completely free of the vagina rather than being reflexed against its surface and partially embedded in it. This sets the Hawaiian ventral receptacle apart from all others of its general conformation. For this character the "white tip scutellum" flies are quite like other Hawaiian species and are, indeed, often more extreme (*e.g.*, Figure 5.8). As inspection of Figures 3 through 6 will show, there are likewise no other characters of the ventral receptacles that serve to set the "white tip scutellum" flies apart from other Drosophiloids. Without reference to the figure legends, it is impossible to determine, in the figures, the point of transition from ventral receptacles of other Drosophiloids to ventral receptacles of the "white tip scutellum" species. When the basic similarities seen in Figures 3 through 6 of this paper are contrasted with the wide variety of types seen elsewhere in the genus (Figures 34–40 in Throckmorton, 1962) it is difficult to avoid the conclusion that, for this character, Hawaiian Drosophiloids are a compact group, and the "white tip scutellum" species are full members of this group.

The paragonia (Figures 17.35–.39) are likewise of a distinct Hawaiian type, even though they show considerable variety among themselves. Inspection of Figures 3 through 14 in Throckmorton (1962) amply enforces this conclusion. One of the most characteristic features of the Drosophiloid paragonium is its low first arch. In general, this sets these forms apart from most other species in the genus. Here, as for the ventral receptacles, the "white tip scutellum" species have characteristics that are of the basic Hawaiian type. Also, they share with the other Drosophiloids certain specific types of paragonia that are unique to Hawaii (*e.g.*, Figures 12.10 and 12.35). Thus, the characteristics of the paragonia indicate that the "white tip scutellum" species are full Hawaiian Drosophiloids.

So far as my experience extends, the anterior pupal spiracles of Hawaiian Drosophiloids are unique. On the basis of pupal characters, it is impossible to separate "white tip scutellum" species from other Drosophiloids. Hence, this character also enforces the conclusion that the Hawaiian Drosophiloids, including the "white tip scutellum" species, are a compact and cohesive group. The reader is referred to Figures 42 through 45 of my earlier paper (1962) and to Figure 16 in this one for a comparison of the spiracle types.

For most of the remaining characteristics, character states in Hawaiian forms are seen to diverge from states seen elsewhere in the genus, and at least some Hawaiian species show character states common elsewhere in the world. The egg filaments (Figures 17.12–.16) are good examples of this. The four-filament type seen in Figure 17.14 is the type common to most species in the subgenus *Drosophila*. The "white tip scutellum" species diverge from this type and have either four or two short filaments. The other Drosophiloids diverge from this type toward eggs with four very long filaments. For this character, therefore, we have evidence for two distinct lineages in Hawaii, one showing a reduction in size and number of filaments, the other an increase in length of the filaments. Bearing in
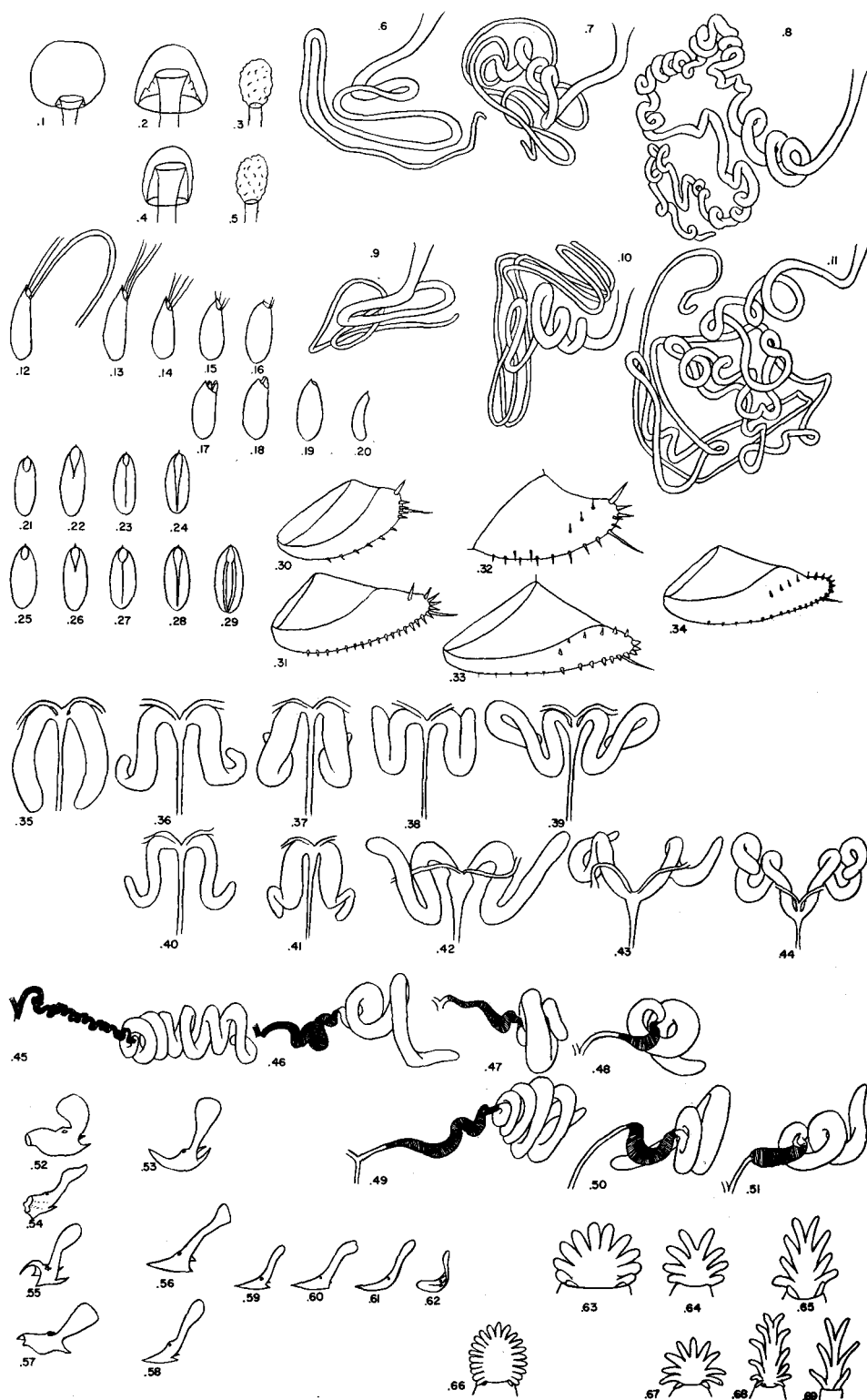
mind the evidence from the paragonia, ventral receptacles and pupal spiracles, these lineages seem more probably to represent divergence within Hawaii than lineages separately introduced to Hawaii.

Evidence from the ovipositors almost directly parallels that from the eggs. As discussed earlier, there are two major trends in ovipositor development among Hawaiian forms. One is toward a reduction of the ovipositor, the other toward either a strongly sclerotized type or a membranous, tubular type. One type of ovipositor (Figures 7.10 and 8.7) is common to both the "white tip scutellum"

FIG. 17. Summary of the data

Drosophiloid spermathecae
  .1 *D. truncipenna*
  .2 *D. anomalipes*
  .3 *D. cilifemorata*
Scaptoid spermathecae
  .4 *S. varipicta*
  .5 *S. stramineifrons*
Drosophiloid ventral receptacles
  .6 *D. caccabata*
  .7 *D. truncipenna*
  .8 *D. anomalipes*
Scaptoid ventral receptacles
  .9 *S. palmae*
  .10 *S. hackmani*
  .11 *D. nasalis*
Drosophiloid egg filaments
  .12 *D. engyochracea*
  .13 *D. punalua*
  .14 *D. adiastola*
  .15 *D. nigra*
  .16 *D. bipolita*
Scaptoid egg filaments
  .17 *S. inaequalis*
  .18 *S. pallida*
  .19 *S. latitergum*
  .20 *S. stramineifrons*
Drosophiloid ventral surface of egg
  .21 *D. ancyla*
  .22 *D. villosipedis*
  .23 *D. disticha*
  .24 *D. infuscata*
Scaptoid ventral surface of egg
  .25 *S. intricata*
  .26 *S. rostrata*
  .27 *S. argentifrons*
  .28 *S. connata*
  .29 *S. hackmani*
Drosophiloid ovipositors
  .30 *D. pseudoobscura*
  .31 *D. pattersoni*
  .32 *S. retusa*
  .33 *D. imparisetae*
  .34 *D. immigrans*

Drosophiloid paragonia
  .35 *D. redunca*
  .36 *D. demipolita*
  .37 *D. imparisetae*
  .38 *D. crucigera*
  .39 *D. ischnotrix*
Scaptoid paragonia
  .40 *D. parva*
  .41 *S. rostrata*
  .42 *T. contestata*
  .43 *S. retusa*
  .44 *S. pallida*
Drosophiloid vasa diferentia
  .45 *D. anomalipes*
  .46 *D. hirtitibia*
  .47 *D. fungicola*
  .48 *D. demipolita*
Scaptoid vasa diferentia
  .49 *D. nasalis*
  .50 *S. retusa*
  .51 *S. anomala*
Drosophiloid ejaculatory apodeme
  .52 *D. adiastola*
  .53 *D. iki*
  .54 *I. obscuripes*
  .55 *D. picticornis*
  .56 *D. residua*
  .57 *D. araiotrichia*
  .58 *A. orthopterus*
Scaptoid ejaculatory apodeme
  .59 *S. articulata*
  .60 *D. crassifemur*
  .61 *D. nasalis*
  .62 *S. palmae*
Drosophiloid spiracles
  .63 *D. punalua*
  .64 *D. mycetophila*
  .65 *D. ischnotrix*
Scaptoid spiracles
  .66 *D. crassifemur* (Paliku)
  .67 *D. crassifemur* (Kauai)
  .68 *S. mauiensis*
  .69 *S. varipicta*

species and the other Drosophiloids. This type is probably also the "primitive" type for Hawaiian forms. Both the "white tip scutellum" species and the other Drosophiloids diverge from this, and hence evidence from the ovipositors is consistent with the development of these two lineages in Hawaii.

The spermathecae show the "white tip scutellum" forms to be sharply distinct from the other Drosophiloids. The major types are shown in Figures 17.1 to .3. All of these types are seen in species from elsewhere in the world, although neither that shown in Figure 17.1 nor that in 17.3 is very common except in Hawaii. These cannot be used as evidence for the uniqueness of the Hawaiian species or as evidence for the origin of the two major Hawaiian lineages. However, they do indicate the uniformity of the lineages within themselves. The uniformity of spermathecal type among the "other Drosophiloids" is phenomenal (Figure 1). Continental groups of comparable external diversity show far greater variation of the spermathecae than do the Hawaiian forms (see Figures 27–32 of Throckmorton, 1962).

The vasa of the Hawaiian forms show divergence from a relatively common character state. The important types are shown in Figures 17.45 to .48. The general type, and the type seen elsewhere in the genus, is that shown in Figure 17.46. The "white tip scutellum" species diverge from this toward the type seen in Figure 17.48. The other Drosophiloids generally retain the common type but in some groups the extreme forms seen in Figure 17.45 exists. Here, as for the egg filaments and ovipositors, the "white tip scutellum" species and the other Drosophiloids appear to have diverged from a common type. The same is also true for characteristics of the ejaculatory bulb. The "white tip scutellum" species have retained the simple bulb, and the ejaculatory apodeme has diverged from the basic type (Figure 17.56) on an independent line of its own (Figure 17.53). Here the trend has been toward the sclerotization of the base of the *anterior* ejaculatory duct by extension of the anterior corners or flanges of the apodeme plate. Among the other Drosophiloids there has been a development of bulbs with lateral lobes, or caecae, or peculiar shapes (Figures 14.2, .12, .40, .47, etc.). There has also been a development of some rather bizarre ejaculatory apodemes (Figures 17.52, .54, .55, .57) based primarily on the sclerotization of the *posterior* ejaculatory duct.

In summary, there is ample evidence for two major lineages among the Hawaiian Drosophiloids. For all character states but those of the spermathecae, these two lineages either intergrade (diverge from a common type) or they share the same (unique or nearly unique) character states. Evidence from external anatomy indicates much the same thing. Thus, for the Drosophiloids, derivation from a single ancestral type is strongly indicated. There is no reason to assume that these forms were derived from more than one introduced species, and presumably they were derived from a single individual.

Figure 18 shows the tentative phylogeny for the Hawaiian forms. Our present discussion is concerned with the relationships within the left branch of the phylogeny shown to the left in this figure (the Drosophiloid branch of the Hawaiian Drosophilids). The evidence discussed to this point establishes the dichotomy between the "white tip scutellum" forms and the other Drosophilids. There remains the problem of the relationships among these other species. This can-

not be resolved with any certainty, but some general trends are apparent. As indicated earlier, the *groups* named in Figure 18 are groups based on external characters. While the groups themselves are probably amenable to further sub-division, they represent for the most part reasonably good phyletic lineages. The major exception to this is the "picture wings" where probably two major lineages are involved. On the basis of our present meager evidence, the phylogenetic positions of these two lineages of "picture wings" seem to be so nearly the same that I have not attempted to differentiate them further.

External anatomy indicates three major complexes of species among the "other Drosophiloids." These are the species with tarsal ornaments in the male, the species with modified mouthparts in the male, and the species with neither modified mouthparts nor tarsal ornaments. As might be expected, the latter category is rather heterogeneous. In Figure 18 all of the species with modified mouthparts are lumped together to the top left. While there is much diversity among them, there is no concrete evidence that they are not each other's nearest relatives, and there is considerable evidence that they are. Characteristics of the ejaculatory bulb in particular tend to suggest that these species are a coherent group in spite of considerable external variation in form. The species with tarsal ornaments in the male (*Trichotobregma*, bristle tarsi, spoon tarsi, forked tarsi) are likewise treated as a unit. Most of their characteristics, external as well as internal, show a mosaic pattern of distribution. While no character is exclusive to them, the characters that they do have are distributed in such a seemingly random fashion among them that no rational division of these species can be made at the present time. It is probable that more detailed studies of these forms will detect group boundaries among them. It is unlikely, however, that further studies will show them to have closer relatives than each other, but this remains for the future to determine.

The other five groups (*Nudidrosophila, Ateledrosophila, Idiomyia, Antopocerus* and picture wings) fall into the negative category of not having modified mouthparts and not having tarsal ornaments. Of these five groups, four show relationships to the species with modified mouthparts; the other (*Antopocerus*) seems to share most of its characteristics with species having tarsal ornaments in the male. The evidence for this division can be stated briefly. At least some species of *Nudidrosophila, Ateledrosophila, Idiomyia* and the picture wings share characteristics of the ovipositor, ejaculatory bulb, ejaculatory apodeme, egg filaments, paragonia and vasa with species having modified mouthparts (see earlier descriptions of the characters). Species having tarsal ornaments in the male share characteristics of the ovipositor, ejaculatory bulb and ejaculatory apodeme with *Antopocerus*. In other respects *Antopocerus* is neutral. It is placed in the phylogeny of Figure 18 in an equivocal position at a branch point, although the weight of evidence favors placing it with forms having tarsal ornaments. The other groups (*Idiomyia*, etc.) are shown as more closely related to species with modified mouthparts, and no detailed relationships can be discerned among them.

Many of the "miscellaneous" species are omitted from this phylogeny. They could be placed almost anywhere on the basis of present evidence. One group, represented by *imparisetae*, probably is closely related to the forms from which the "white tip scutellum" species arose. Another group, represented by *anomal-*

ipes, shares characteristics with *Idiomyia, Nudidrosophila*, etc. This last form deserves some further comment. It is the one in which the female has a true coiled ventral receptacle. The spermathecae are also of a type unique for Hawaiian Drosophiloids (but not for Hawaiian Drosophilidae). Were it not for the *anomalipes* female there would be only two instead of three types of ventral receptacles and spermathecae seen among the Drosophiloids (Figures 17.1–.3; .6–.8). It is peculiar that a form aberrant for one character should also be aberrant for another. This is particularly true when all of the other characters of the species are fully of the Hawaiian type, and many, indeed, are of highly derivative types. The derivative characters (of the ejaculatory bulb, ejaculatory apodeme, ovipositor, egg filaments, paragonia and vasa) virtually preclude an independent origin (from a separate introduction) for *anomalipes* (see the characteristics of this species in Figures 1 to 16). In addition, most Hawaiian Drosophiloids have a distinctive "*gestalt*" that is recognizable by persons experienced with these species. To my eye, in external morphology *anomalipes* is an ordinary Hawaiian Drosophiloid, and M. R. Wheeler (personal communication) concurs with me in this judgment. Hence, the great majority of the characteristics of *anomalipes* seem to be of Hawaiian origin, and this species cannot be interpreted as a member of a separate lineage independently introduced into Hawaii. The problem this species raises is not that of the origin of the species itself. Rather it is the question of the mechanism of origin of a few "continental" character states that seem to have appeared suddenly in a lineage where they are not expressed in related species. It is possible, however, that the present sample is inadequate and that the characteristics of the spermathecae and of the ventral receptacle are more widespread among Hawaiian species than available evidence suggests. The present sample of 81 Drosophiloids includes less than a third of the known species. It is quite possible that, as this sample is enlarged, more of the "aberrant" forms will be encountered.

The phylogenetic position of the Drosophiloids—There are two major phyletic lineages in the genus *Drosophila*. One of these includes the genus *Chymomyza* and the subgenus *Sophophora*. The other includes the subgenera *Dorsilopha*, *Phloridosa* and *Drosophila*. This latter also includes the genera *Scaptomyza*, *Zaprionus*, *Mycodrosophila* and *Dettopsomyia*. The subgenus *Pholadoris* seems to have been derived earlier in time than were the others and hence is considered the most primitive subgenus (see Throckmorton, 1962, 1965). The characteristics of the Hawaiian Drosophiloids indicate that they were derived from near the base of the major branch leading to the subgenus *Drosophila*. The evidence from the various characters can be summarized as follows. The spermathecae give no evidence of phylogenetic position within the genus. The ventral receptacles indicate an intermediate position between forms having a folded ventral receptacle that is strongly appressed to the vagina and forms having a coiled ventral receptacle that is completely free of the vagina. In the Hawaiian forms the ventral receptacle is completely free of the vagina, coiled basally and folded distally. The folded, appressed condition is characteristic of *Pholadoris, Chymomyza* and *Sophophora*. The free and coiled condition is characteristic of the subgenus *Drosophila*, of *Phloridosa*, and *Dettopsomyia*. The intermediate position between these groups is on the major branch leading to the subgenus *Drosophila*.

The egg filaments likewise indicate a position between two major groups. Generally there are four egg filaments in Drosophiloid eggs but in some groups there are two. The four-filament condition is characteristic of species in the subgenus *Drosophila*, although there are many exceptions and a considerable number of species have two filaments, three filaments, or one filament. The two-filament condition is characteristic of *Sophophora*. Again, the phylogenetic position that reconciles these variables is on the major branch leading to the subgenus *Drosophila*.

The characteristics of the ovipositor are not very useful for determining phylogenetic position, but I have indicated some characteristic forms in Figure 17. The basic Hawaiian type, Figure 17.33, is more nearly that of species of the subgenus *Drosophila* (Figure 17.34) than of other major groups (Figures 17.30 and .31).

The paragonia are, in themselves, not strongly indicative of phylogenetic position, except that they indicate that several phylogenetic positions are improbable. They are almost certainly not Sophophoran and not from members of the quinaria section of the subgenus *Drosophila*. In the relatively large number of folds present in some forms they resemble species in either the *virilis-repleta* section of the subgenus *Drosophila* or possibly species in the subgenus *Pholadoris*. When characteristics of the vasa are considered, the possibilities are narrowed considerably. To date, no species other than those related to the subgenus *Drosophila* are known to have vasa associated with the paragonia. Almost all of the Drosophiloids do have vasa associated with the paragonia, although the association is not so strong as that seen from most species in the subgenus *Drosophila*. Thus, the characteristics of the paragonia and the vasa combine to indicate a position on the branch leading to the subgenus *Drosophila*.

Neither the color nor the coiling of the testis can give any indication of phylogenetic position since these are variable throughout the genus. The generally simple nature of the ejaculatory bulb precludes a highly derivative position in the genus, but it does not, of itself, give positive indication of phylogenetic position. The ejaculatory apodeme likewise is of a simple, general type, excepting the special Hawaiian types that are irrelevant in this context. The evidence from these structures is consistent with a position on the branch leading to the subgenus *Drosophila*.

The characters of the anterior pupal spiracles exclude the Hawaiian forms from large portions of the genus. They do not resemble the highly derivative types found in the subgenus *Drosophila*, and they are neither Sophophoran nor representative of *Pholadoris*. The spiracle is simple, but it differs from other simple spiracles (*e.g.*, those of *Pholadoris*) in having heavy, erect branches instead of slender, recurved branches. It could be considered a simple derivative of the *Pholadoris* type, or the converse. This type of spiracle may actually be more primitive than the types seen in *Pholadoris*. Hence, the spiracles suggest an origin of the Hawaiian forms from a lineage prior to the development of complex derivative types. This is consistent with a position toward the base of the branch leading to the subgenus *Drosophila*, but, of course, it does not require that they be placed there.

The Malpighian tubules of the Drosophiloids are of the type found generally

in species of the subgenus *Drosophila*. The tips of the posterior tubules are fused, the lumen continuous. This condition, however, is also found in species of the subgenus *Pholadoris*, in *Chymomyza*, etc. It is consistent with a position on the branch leading to the subgenus *Drosophila*.

The abdominal sternites of the male indicate a fairly early derivation within the genus. Most of the species lack the first sternite, but it is present in some forms. When the first sternite is present, its characters are those of species in the subgenus *Pholadoris*. It is not the wide, polished plate of the Sophophorans. Again, this suggests a position on the branch leading to the subgenus *Drosophila*, but quite close to the base and perhaps rather close to *Pholadoris*.

In summary, characteristics of the egg filaments, ventral receptacles, and vasa strongly indicate a position on the branch leading to the subgenus *Drosophila*. All other characteristics are consistent with this interpretation. The characteristics of the anterior pupal spiracles and of the abdominal sternites in the male suggest a fairly early separation from this branch. The position indicated to the upper right in Figure 18 is therefore a best approximation for the phylogenetic relationships of these species.

The origin of the Drosophiloids—It is fairly easy to suggest where the Drosophiloids did *not* come from. They show no close relationships to any of the major new world groups of species that are known to me. Assuming that these are a reasonably representative cross-section of the new-world *Drosophila*, North, South and Central America can be excluded as probable sources for the Hawaiian Drosophiloids. There is little if any positive evidence for the origin of the Hawaiian forms from the islands of the south Pacific, but the *Drosophila* from this part of the world are not well enough known to allow firm conclusions to be drawn. Recently (Wheeler and Takada, 1964) a number of species have been described from Micronesia and the groups present in Micronesia seem not to be good candidates for the ancestors of the Hawaiian species. Four subgenera, *Drosophila*, *Hirtodrosophila*, *Sophophora* and *Scaptodrosophila*, are present in the area from which Wheeler and Takada's material was drawn, and none of these is known to possess characters that would relate it closely with Hawaiian forms. It is desirable, however, that more material be collected from these areas, and particularly the higher altitudes in the high islands. It will also be necessary to obtain information on the internal anatomy of these species before final conclusions are reached. For the present, origin of the Hawaiian fauna from the islands of the south Pacific seems doubtful, but it is not absolutely precluded.

Having more or less excluded the north, east, south and southwest, few directions remain from which the Hawaiian forms might have come. The east coast of Asia, and particularly Japan, seems a reasonable possibility, and there is some positive evidence to suggest a derivation of the Hawaiian Drosophiloid fauna from the Japanese Drosophilid fauna. Okada (1956), in his study of the Japanese Drosophilids, included figures of the internal anatomy of many species. Among these species are some that appear to have characteristics similar to those seen among Hawaiian forms. In particular, the ventral receptacle, and perhaps the paragonia, of some Japanese species suggest affinities with the Hawaiian forms. This possibility is currently being investigated jointly by Dr. Okada of Tokyo Metropolitan University, Dr. Takada of Kushiro Women's College, Dr. Wheeler

of the University of Texas, and myself. The results of this study will be published later.

The origin and relationships of the Scaptoids—For discussion, the Scaptoids can be divided into three groups: *Titanochaeta, Scaptomyza* and the three species of *Drosophila* that are true Scaptoids. The species of the genus *Scaptomyza* are, for most of the characters treated here, rather uniform. When they are not uniform, the variation is generally of such a nature that little information of phylogenetic value (for relationship *inter se*) is provided. Of the subgenera available for this study (see Appendix), *Tantalia* and *Alloscaptomyza* are the most derivative, at least for some internal characters, or characters of the eggs. The remainder of the subgenera do not differ among themselves in any way that would suggest phylogenetic sequence. There is very little more that can be said about *Scaptomyza*, except that one need not postulate more than a single introduction to account for it, if, indeed, it is not better interpreted as originating in Hawaii. *Titanochaeta* is so much a Scaptoid that its origin from the basic *Scaptomyza* line is almost certain and no additional introduction is required to account for it.

Each of the three *Drosophila* species departs from the more usual *Scaptomyza* pattern in some way. *D. parva*, for example, has paragonia that are fully Drosophiloid. Otherwise, all of its characteristics are completely Scaptoid. *D. nasalis* is fully Scaptoid, except that coiling of the vasa and the distribution of the pigment along the vasa are both Drosophiloid. Also, the ejaculatory apodeme of *nasalis* is intermediate in shape between the unmodified *Drosophila* type and that typical of *Scaptomyza* (Figure 17.61). *D. crassifemur* is almost completely Scaptoid, except that the pigmentation of the vasa containues almost to the base (Drosophiloid), and the ejaculatory apodeme is of the conventional *Drosophila* type (Figure 17.60). Also, the anterior pupal spiracle of one strain of *crassifemur* is completely Drosophiloid (Figure 17.66), although there is some variation within the species toward the *Scaptomyza* type (Figure 17.67). Only a few species of the genus *Titanochaeta* were available for this study, but these species were fully Scaptoid in all of their characters. (If the pupae mentioned in the earlier descriptions were actually pupae of *Titanochaeta*, then the pupal spiracles of these species are Drosophiloid). Hence, the Scaptoids presently not classified as *Scaptomyza* tend to vary in the direction of *Drosophila*, and, for several characters (pigmentation of the vasa, pupal spiracles and paragonia), specifically in the direction of Hawaiian Drosophiloids. Since three of these species are sufficiently equivocal in their external diagnostic features to have been classified as *Drosophila*, we must investigate the possibility that the Scaptoids (*Titanochaeta* and *Scaptomyza*) originated in Hawaii from the same ancestor as did the Drosophiloids, and that species such as *crassifemur, nasalis* and *parva* reflect some characteristics of early transitional populations.

The phylogenetic position of *Scaptomyza* has been discussed earlier elsewhere (Throckmorton, 1962). At that time only a few species were available, but the position indicated then is the same as that indicated by the larger sample from Hawaii. This position (see Figure 53 of Throckmorton, 1962) is toward the base of the major phyletic branch leading to the subgenus *Drosophila*, which is substantially the position indicated for the Hawaiian Drosophiloids. The evidence
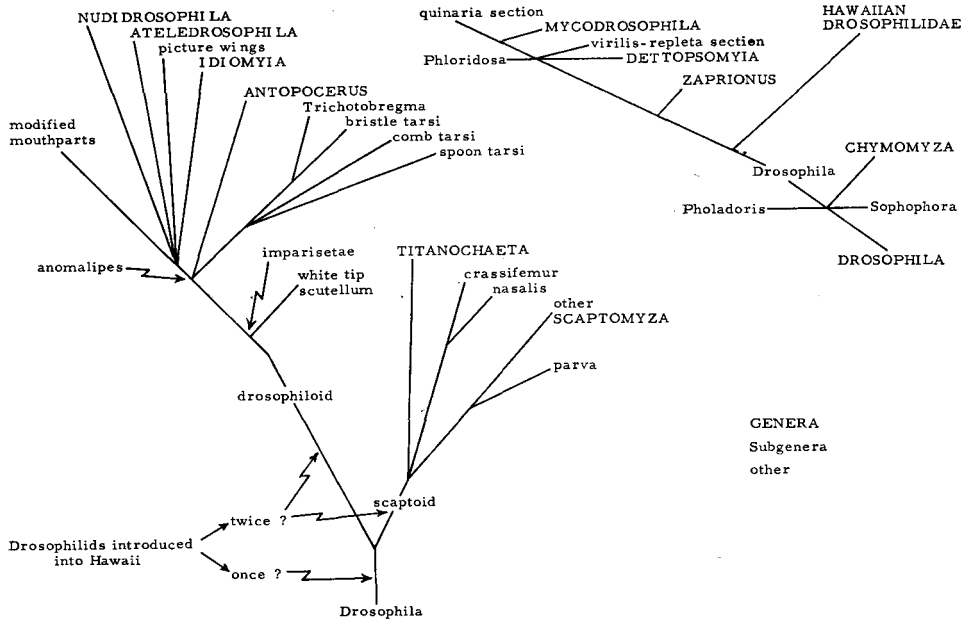
Fig. 18. Left. Preliminary phylogeny of the Hawaiian Drosophilids. Right. The phylogenetic position of the Hawaiian Drosophilids within the genus *Drosophila*

from the Hawaiian Scaptoids for this position will not be recapitulated. The reader should note from Figure 17 that all of the considerations cited for the phylogenetic position of the Drosophiloids apply equally well for the Scaptoids, since these two groups have characters that are very much the same in most cases. Hence, it is possible to indicate a single position for the Hawaiian Drosophilidae, and this is shown to the upper right in Figure 18.

Of itself, the observation that the Scaptoids and Drosophiloids have the same phylogenetic position need be of no great significance. It is quite possible for extant species groups having rather diverse arrays of characters to be derived from nearly the same level in a phylogeny. However, the problem of the origin of the Scaptoids is complicated by the fact that, for most of the characters of phylogenetic significance, the Hawaiian Drosophiloids and Scaptoids overlap broadly. This can be seen very plainly in Figure 17 where their characters are summarized. For only two characters, the ejaculatory bulb (not shown in Figure 17, see Figures 14 and 15) and the paragonia (Figures 17.35–.44) is there a rather sharp difference between the Scaptoids and the Drosophiloids. The paragonia actually do overlap in characteristics more broadly than a cursory inspection of Figures 11–13 might indicate, since Drosophiloid types are rare among the Scaptoids and Scaptoid types rare among Drosophiloids. The significant thing is that both types exist in each group (Figures 17.35–.44) and their frequency of occurrence is irrelevant. The types seen in Figure 17.36–.37, and in 17.40–.41, are apparently found only in Hawaii, and it is remarkable that they are also found in *both* major groups from Hawaii. Much the same situation holds for many of the other characteristics. In some cases there is a simple overlap (sperma-

thecae and egg filaments for example). In other cases there is an overlap, and unique features are shared by the Scaptoids and Drosophiloids. The cleft and suture of the ventral egg surface (Figures 17.21–.29) is an example of the latter. So also are the characteristics of the ventral receptacle. The "white tip scutellum" species have vasa of the Scaptoid type and they share one type of spermatheca with them. (This type of spermatheca is primitive and cannot be taken as evidence of close relationship.) The existence of a unique type of pupal spiracle in Hawaii, and the more or less complete intergradation of spiracle types between Drosophiloids and Scaptoids is very suggestive of a close common origin for these forms. The ejaculatory apodeme of the Scaptoids is distinctive, yet some of the Hawaiian *Scaptomyza* (*articulata* and *inaequalis*, Figures 15.39, .42) have normal *Drosophila* types, and the characteristics of *crassifemur* and *nasalis* have already been mentioned in this respect. Also, most *Scaptomyza* have reduced and "fleshy" ovipositors, but in Hawaii some forms have ovipositors that are unreduced (Figure 17.32). These also have the normal Drosophiloid complement and arrangement of bristles. In short, for virtually all of the characters treated here there is a broad overlap, and often there is a sharing of characteristics that are, for the present, unique to Hawaiian forms.

This does not seem to be a situation that can be dismissed simply as due to convergence. Too many characters are involved, these characters are virtually identical in many cases, and apparently unique types are shared by Drosophiloids and Scaptoids. Under the circumstances, the simplest and most parsimonious conclusion to be reached from the existing anatomical data is that the Scaptoids originated in Hawaii from the same stock as did the Drosophiloids. Alternately, however, Drosophilids might have been introduced into Hawaii twice (see Figure 18, lower left), and if this second alternative is correct a most remarkable set of coincidences was involved in the origin of the Hawaiian Drosophilid fauna. If the first alternative is correct, then both *Titanochaeta* and *Scaptomyza* originated in Hawaii, and *Scaptomyza* subsequently escaped to the mainland, either directly or through the islands of the Pacific, or both. This escape must have taken place rather early, since the genus *Scaptomyza* has a world-wide distribution with many species endemic to continental areas.

If we envision the introduction of two forms into Hawaii, the Drosophiloid species must have been one that was so closely related to *Scaptomyza* that its descendents in Hawaii possess substantially the same complex of characters as do the Scaptoids. This is no mean coincidence. For the characteristics treated herein, the range of variation among the Hawaiian Drosophilids (Drosophiloids *plus* Scaptoids) is of the same order of magnitude as that encountered within some *species groups* from elsewhere in the genus *Drosophila*. It is considerably less than is encountered within the major subgenera, and some species groups (*e.g.*, the *repleta* group) seem to be more variable, for more of these characteristics, than are the Hawaiian Drosophilids (see Throckmorton, 1962 for supporting data). Elsewhere in the genus, then, such cohesive character complexes are strong evidence of close common descent, and they must be interpreted as indicating the same thing here. Regardless of the geographical point of origin of the Scaptoids, present evidence requires that they share a close common ancestor with the Hawaiian Drosophiloids. If the origin of the Scaptoids occurred outside of

Hawaii, then two successful trans-Pacific colonizations are needed. Each one of these was, in itself, an improbable event. That a successful introduction be made twice from the same family of Diptera is even less probable, and that the two successful introductions from the same family should involve species so closely related (but presumably already generically distinct) as to produce the existing patterns of variation in Hawaii is less probable still. And if we do not postulate extremely close relationships between the two original colonizers, we must then explain the broad overlaps between the Drosophiloids and Scaptoids as due to convergent evolution. This requires that we explain why the Scaptoids should have diverged in the direction of *Drosophila* (while they were competing with them among the vacant niches of Hawaii), and why, for some character states at least, they have happened to diverge specifically in the direction of the *Hawaiian* Drosophiloids. And why do the Hawaiian Drosophiloids, of all the Drosophiloids in the world, include a group of species ("white tip scutellum" forms) that share characters with the Scaptoids, their nearest (geographical) relatives? Finally, Spieth (this Bulletin) concludes, on the basis of his studies of behavior, that the "white tip scutellum" species are Scaptoid and that the genus *Scaptomyza* probably originated in Hawaii. For the present, then, Hawaii must be considered to be the only place in the world where the otherwise sharp distinctions between *Scaptomyza* and *Drosophila* tend to disappear.

The pattern of variation seen among the Hawaiian Drosophilids is so readily interpreted as being the uncomplicated consequence of divergence from a single ancestral colonizer that alternative explanations seem labored and uncalled-for. If we accept this interpretation, a simple and logical sequence of evolution is seen for the species in Hawaii. This last interpretation does require that at least one species of *Scaptomyza* escaped from Hawaii, but this is not a serious drawback. Both of the major alternatives require two trans-Pacific colonizations. One requires two separate introductions into Hawaii. The other requires one introduction into Hawaii and one introduction from Hawaii to a continent. There is no reason to think that one of these trips is inherently more difficult or more improbable than the other, and such considerations cannot help us establish the relative merits of the two major alternatives. Another consideration, that of time, has yet to be broached.

The most recent and informative treatment of the ages of the Hawaiian volcanoes is that of McDougall (1964). He has determined the potassium-argon ages of these as follows: (in millions of years) Kauai, 5.6–3.8; Oahu, 3.4–2.2; Molokai, 1.8–1.3; Maui, 1.3–0.8; Hawaii, <1. He interprets these ages as showing the order of extinction. However, the evidence also indicated that the eruption of the presently exposed lavas was very rapid, so the order of extinction may well represent the order of commencement. One of the most interesting observations was that one sample (Mauna Kuwale trachyte) from West Oahu had an age of about eight million years (two readings of 8.26 and 8.46, respectively). This suggests that two volcanoes differing in age by five million years were active in West Oahu, with the earliest known activity dating from the early to middle Pliocene. The activity that produced the presently existing islands, including the Waianae Range of West Oahu, was late Pliocene to Pleistocene.

The islands from which these datings were obtained belong to the "windward"

group. These are but the southeastern members of a chain that extends for about 1900 miles from Hawaii to a coral atoll off to the northwest. The northwestern members, the "leeward" islands, are thought to be the remnants of earlier high islands (see Zimmerman, 1948) and these presumably would have been older than the existing islands of the "windward" group. Bearing these factors in mind, an estimate of ten million years as the age of the older members of the archipelago seems justified. It is not unreasonable to assume that the western islands were inhabitable and inhabited at one time, and that some of the evolution of the endemic Hawaiian Drosophilidae occurred on them. If we grant the first five million years for the development of a flora adequate to support the Drosophilids and assume the successful colonization toward the end of this period, then there would be about five million years available for the development of the endemic Drosophilid fauna. If we assume only three generations per year as a probable minimum estimate for the species and climate involved, then perhaps fifteen million generations of evolutionary change were possible. Since the western-most islands may have been much older than the eight million years estimated for West Oahu, and since less than five million years may have been required for the original successful introduction, fifteen million generations is probably a minimum estimate. At any rate, it is a conservative estimate, and hopefully it does not err in the wrong direction.

If one were to generalize about evolutionary rates, the best that can be said is that they vary widely, both from lineage to lineage and at different times within the same lineage. There is almost no concrete evidence from which we might estimate evolutionary rates in *Drosophila* (Simpson, 1945). The recent description of a fossil Drosophilid about thirty million years old (Wheeler, 1963) gives us an indication of the age of the genus *Drosophila* and of the major phyletic branches within it, but it does not tell us much about rates of evolution. Simpson (1949) suggests 50,000 years or more for the production of species "fully distinct genetically and morphologically," and he indicates that this may be for cases of rather rapid evolution. For lack of a better, we can take this estimate and see where it leads us.

If speciation can occur within 50,000 years, and if five million years are available, then 100 speciation events in sequence are "possible." For the sake of arithmetic, if we assume all speciation to have been synchronous and dichotomous, then 2^{100} species could have been produced in the time available. However, we need time only to produce about 2^{10} species (say 600 endemic Drosophilids plus less than 200 *Scaptomyza* from elsewhere in the world), for which only 500,000 years might have been sufficient. Apparently the rate could be tenfold slower and still produce the requisite number of species. And while speciation would certainly not be synchronous, it most probably would not be strictly dichotomous either. In many instances speciation would almost certainly produce more than two products. Given environmental opportunity, and such opportunity does seem to have existed in Hawaii, a thousand surviving species in five million years may be a very reasonable estimate. In fact, environmental opportunity may be by far the most critical factor regulating rates of speciation. In its absence the rates of change would be low, but in its presence they may be far higher than educated guesses suggest. At any rate, and granting that we are vastly ignorant of specia-

tion rates in *Drosophila*, time does not provide us with a critical means for distinguishing between the two major alternatives. Certainly considerations of time alone do not force us to reconsider the implications of the anatomical data for the origin of the genus *Scaptomyza*.

The final resolution of this question must depend on very thorough anatomical studies, particularly of the continental species of *Scaptomyza*. One bit of evidence of this nature tends to cast some doubt on the interpretation of an island origin for *Scaptomyza*. Wheeler (1952, p. 204) reports that the male of *Scaptomyza montana* ('western U.S.) has elliptical testes. This seemingly trivial observation is of some consequence for the present discussion. To date no species of Hawaiian *Scaptomyza* are known to have elliptical testes. This condition is primitive, and if *Scaptomyza* originated in Hawaii it is surprising that some Hawaiian species do not also have elliptical testes. It is true that some of the "white tip scutellum" species have less than one complete coil in the testis, and these species are Scaptoid in other respects, but still the absence of elliptical testes among Hawaiian forms is puzzling if *Scaptomyza* originated there. The entire sequence would require that the original colonizer of Hawaii carried genetic variability sufficient to produce either coiled or elliptical testes. Subsequently species were produced that had coiled testes, but no species with elliptical testes survived in Hawaii. However, the colonizer from Hawaii to the continent still carried genetic variability that could produce elliptical testes, and one of its descendents on the mainland does have elliptical testes. In short, the genetic variability for testis form must have survived two bottlenecks if it is to be expressed in mainland forms, and it is not known to have been expressed at the first stopping point in Hawaii.

It is possible, of course, to rationalize these observations. In the first place, only a fraction of the Hawaiian Scaptoids have been investigated. Species in which the male has elliptical testes may yet be discovered there. Second it is not absolutely necessary that a Hawaiian form with elliptical testes survive to the present. All that is required is that one persisted to the time when the *Scaptomyza* colonizer *left* the islands. Evolution in Hawaii may well have involved the sequential replacement of one species by several derivative descendent species, and hence we have no definitive evidence regarding the contents of the Hawaiian gene pools at the time the second colonization occurred. Finally, it is not strictly necessary that the reappearance of an ancestral character result from segregation. Atavistic recurrences may well be due to segregation of rare complex genotypes from gene pools in which the ancestral genetic elements still persist at low frequencies. They may also be due to a simple mutational change, say in a regulator gene, that suppresses, or fails to induce, more derivative developmental sequences. Hence, an ancestral trait may reappear through mutation, and its appearance may not be critical evidence of the evolutionary history of the species. Rationalizations are never very satisfactory for deciding issues, and they indicate only that the question must remain open until more concrete evidence is available. For the purposes of discussion, and because the bulk of the existing evidence so indicates, an origin of *Scaptomyza* in Hawaii will be assumed in the next section.

The evolution of the Hawaiian Drosophilids—If we assume a single colonization of Hawaii, the following general outline of events can be adduced. We would expect that the first individual encountered an environment that was not only

hospitable but full of empty niches and empty of competitors. Under the circumstances, its immediate descendents probably were not under strong selection pressure, and they probably found two major habitats open to them. One of them was the usual *Drosophila* habitat, woodland with its associated fungi, flowing sap, fruits, rotting vegetation, etc. The other was the open and semi-open grasslands whose niches elsewhere in the world are filled by species from other families of Diptera (the leaf-mining Agromyzidae, the Chloropidae, etc.). Under these circumstances, the first major separation may well have involved a dichotomy between the major habitats, leading to two groups, one primarily woodland, the other grassland. The woodland habitat is characteristically that of *Drosophila* and probably required little in the way of modification to adapt to it. These forms retained the basic *Drosophila* way of life and also retained the general *Drosophila* morphology and behavior. They became the Drosophiloids of this paper. The other forms adapted to a new environment (grassland and semi-grassland) and became modified accordingly. In making the transition from one way of life to another, and from one food source to another, some forms switched to become parasitic on spider eggs (*Titanochaeta*) and others eventualy became *Scaptomyza*. This adaptive shift was accompanied by morphological changes and the distinctive *Scaptomyza "gestalt"* was the result.

The occupation of the leaf-mining niche by *Scaptomyza* has always puzzled me, since other families of Diptera seem to be firmly established in at least superficially similar niches. (This assumes that adaptations of families are more ancient than those of genera, which may not be the case in this instance.) However, if *Scaptomyza* first entered this niche in the comparative seclusion of Hawaii, and if it perfected its adaptation to this niche in the absence of competition from already well-adapted species, then its position may not be surprising. Once established in the niche, it may have been able to compete successfully with other Dipteran species when it finally came in contact with them, and this may account for its wide distribution on the mainland. Physiologically it would have been quite different from its competitors in other families, and its adaptations could hardly have precisely duplicated those of continental competitors. Hence, when it "returned" to the mainland it may have "seen" many niches that may not have been accessible to an earlier Drosophilid.

Be that as it may, the next significant event was the separation of the "white tip scutellum" line. The nature of the events that produced the rather pronounced differences of these species is, of course, unknown. Apparently they are fungus feeders (Hardy, 1965), and they may reflect a second major partition of the available food sources. The first would have been between woodland and grassland; the second, within woodland, between fungus feeders and non-fungus feeders. It is probable that a bottleneck of some kind was passed at their origin. At least, the sharp differences in egg filaments and spermathecae implicate something of the sort, and their distinctive external *gestalt* is perhaps indicative of the same thing.

Subsequent to the separation of the "white tip scutellum" forms, the evolution of the Drosophiloids appears to have involved two major patterns, not necessarily sharply distinct from each other. One of these patterns, most evident among the more recent forms, is the orthodox one of differentiation in isolation. This is par-

ticularly clear for the subgenus *Exalloscaptomyza*, where there may be one species for each of the major islands. There are also a number of species pairs (or triplets, etc.) whose distribution indicates much the same thing. Thus we find, for example, *conjectura* from Kilauea (Hawaii), and "conjectura-like" from Mauna Kea on the same island. We also find *fungicola* and "fungicola-like," *mimica* and "mimica-like," etc., in the same two localities, as if the same original "community" had been established in each place, with subsequent species divergence producing the present faunas. Alternately, this situation could have been produced by independent colonizations from several sources. The Drosophiloids of Hawaii offer unusual opportunities for studying the evolution of community relationships, niche separations and adaptations together with an analysis of speciation events involving forms whose genetic relationships are very close and which may ultimately be determined.

The second major pattern follows from the wide, and almost random, distribution of many of the character states peculiar to Hawaiian Drosophiloids. It is as if a population originated, became widespread, developed a great store of genetic variability, and then fragmented. The resulting populations, regardless of their mode of origin or the factors keeping them separate, had much of the original genetic variability in common. They could not and did not utilize it all, and different lineages used different combinations. Thus, no strong evolutionary trends are apparent among the more recent Drosophiloids. A pattern of reticulate evolution of this sort might also be produced by the differentiation of populations in semi-isolation (imperfect isolation by distance), and the Hawaiian environments and the habits of *Drosophila* are particularly well suited to this type of evolution. One might visualize an original population slowly spreading to occupy the available geographic range of niches open to it. Local populations of considerable size might build up, but favorable environments might be rather widely separated from each other, as many, if not most of them, are today. Thus, gene flow between the local populations would be slight and sporadic at best. The general situation could be visualized as a net, with each knot a local population, each thread the evidence of gene flow between them. Early in the sequence gene flow might be reasonably constant between the populations, but as time passed, gene flow, as distinct from immigration, might gradually diminish as a consequence of the genetic divergence of the populations involved. Alien genes might be selectively eliminated from each gene pool, or alien behavior patterns (regional dialects) might reduce the probability of mating even if immigrations occurred at appropriate seasons. Under such circumstances, and even with continued introduction of *individuals* from other populations, divergence and eventual speciation might occur. In the net visualized earlier, the knots would persist but the webs between might gradually and sporadically break. Some would break earlier than others, and some might never break. Newly originating genotypes might diffuse readily through some populations, but only poorly or not at all to others. And at various times along the way some populations might themselves begin to spread and establish new local populations of their own (without necessarily displacing the originals) so that new cycles might well be under way long before the original cycle, with well-established reproductive isolation between all the remaining populations, had been completed. The net effect of such

a system would be to produce complexes of species only slightly differentiated from each other, and with the complexes themselves only partially distinct. One group would overlap another for some character states, have certain other states in common with a second group, and have still others in common with a third group, etc., etc. This is substantially what exists in Hawaii today, and such a product seems more likely to have been produced by highly multiplicative splittings and fragmentations than through conservative dichotomies.

SUMMARY

Various anatomical features of the Hawaiian Drosophilids are described and discussed. Two major groups are indicated, the Drosophiloids and the Scaptoids. Phylogenetically, both of these groups are very closely related to each other and they are derived from near the base of the major branch leading to the subgenus *Drosophila* of the genus *Drosophila*. Evidence is presented indicating that the genus *Scaptomyza* originated in Hawaii and arguments for and against this interpretation are discussed. If *Scaptomyza* originated in Hawaii, then the available evidence favors the introduction of only a single individual (basically a *Drosophila*) as the progenitor of the more than 400 endemic species of Drosophilids. At most, two introductions, presumably of a single individual each, are required if the Scaptoids are thought to have originated from an introduction separate from that for the Drosophiloids. Existing evidence indicates that the Drosophiloid introduction was from east Asia, perhaps from Japan, but this problem is still under investigation. Some general patterns of evolution in Hawaii are also discussed.

ACKNOWLEDGMENT

APPENDIX

The species dissected for this study are listed below. Their present classification is indicated, together with informal designations that serve to clarify general groupings. The identification number relates specific individual specimens in my collection to the notes on their dissection. When specimens from more than one locality were dissected, the number given is that for the specimens whose characteristics are reported in this paper.

APPENDIX

Species	Identification number	Locality

DROSOPHILOIDS

Genus: IDIOMYIA
    obscuripes Grimshaw   85   Paliku, Maui
    perkinsi Grimshaw   53   Waikamoi, Maui
    picta Grimshaw   99   Waikamoi, Maui
Genus: ANTOPOCERUS
    aduncus Hardy   55   Waikamoi, Maui
    diamphidiopodus Hardy   54   Waikamoi, Maui
    diamphidiopodus Hardy   . .   Puu Kolekole, Molokai
    longiseta (Grimshaw)   134   Puu Kolekole, Molokai
    orthopterus Hardy   98   Paliku, Maui
    orthopterus Hardy   . .   Waikamoi, Maui
    tanythrix Hardy   73   Kilauea, Hawaii
    villosus Hardy   59   Waikamoi, Maui
Genus: NUDIDROSOPHILA
    aenicta Hardy   19   Drum Drive, Oahu
    lepidobregma Hardy   94   Kipuka Ki, Hawaii
Genus: ATELEDROSOPHILA
    preapicula Hardy   135   Opaeula Ridge, Oahu
Genus: DROSOPHILA
  Subgenus: *Drosophila*
  Miscellaneous species
    anomalipes Grimshaw   43   Kokee State Park (Mohihi Stream), Kauai
    caccabata Hardy   89   Puu Kolekole, Molokai
    hirtitibia Hardy   20   Drum Drive, Oahu
    imparisetae Hardy   83   Kilauea, Hawaii
    imparisetae Hardy   . .   Kipuka Puaulu, Hawaii
    quasianomalipes Hardy   30   Kokee State Park (Halemanu Valley), Kauai
    truncipenna Hardy   61   Waikamoi, Maui
  picture wings
    adiastola *Hardy*   72   Waikamoi, Maui
    crucigera Grimshaw   136   Mt. Tantalus, Oahu
    engyochracea Hardy   93   Kipuka Puaulu, Hawaii
    fasciculisetae Hardy   105   Waikamoi, Maui
    grimshawi Oldenberg   2   East Molokai
    musaphilia Hardy   137   Kipuka Puaulu, Hawaii
    picticornis Grimshaw   138   Kokee State Park, Kauai
    pilimana Grimshaw   139   Mt. Tantalus, Oahu
    punalua Bryan   140   Pupukea, Oahu
    villosipedis Hardy   141   Kokee State Park (Kumuwela Ridge), Kauai
  modified mouthparts
    aquila Hardy   76   Kilauea, Hawaii
    araiotrichia Hardy   6   Puu Kolekole, Molokai
    asketostoma Hardy   95   Haleakala Crater, Maui
    chaetopeza Hardy   24   Kipuka Puaulu, Hawaii
    comatifemora Hardy   34   Waikamoi, Maui

Species	Identification number	Locality
conjectura Hardy	22	Kipuka Puaulu, Hawaii
dissita Hardy	78	Kilauea, Hawaii
eurypeza Hardy	142	Kokee State Park (Alakai Trail), Kauai
flavibasis Hardy	143	Kokee State Park, Kauai
freycinetiae Hardy	144	Mt. Tantalus, Oahu
furvifacies Hardy	38	Kokee State Park (Mohihi Stream), Kauai
hirticoxa Hardy	113	Paliku, Maui
infuscata Grimshaw	23	Mud Lane, Hawaii
involuta Hardy	145	Paauilo Experiment Station, Hawaii
ischnotrix Hardy	151	Pupukea, Oahu
ischnotrix Hardy	1	Mt. Tantalus, Oahu
kauluai Bryan	63	Pupukea, Oahu
mimica Hardy	146	Kipuka Puaulu, Hawaii
mimica Hardy	. . .	Paauilo Experiment Station, Hawaii
mycetophila Hardy	147	Mt. Tantalus, Oahu
pychnochaetae Hardy	9	Pupukea, Oahu
residua Hardy	103	Kipuka Ki, Hawaii
scolostoma Hardy	96	Paliku, Maui
bristle tarsi		
apodasta Hardy	41	Kokee State Park (Alakai Trail), Kauai
basimacula Hardy	44	Kokee State Park (Mohihi Stream), Kauai
expansa Hardy	68	Waikamoi, Maui
perissopoda Hardy	40	Kokee State Park (Mohihi Stream), Kauai
prodita Hardy	112	Paliku, Maui
redunca Hardy	87	Puu Kolekole, Molokai
seclusa Hardy	3, 91	Puu Kolekole, Molokai
torula Hardy	69	Waikamoi, Maui
trichaetosa Hardy	77	Kilauea, Hawaii
spoon tarsi		
conformis Hardy	27	Mud Lane, Hawaii
conformis Hardy	. .	Kilauea, Hawaii
contorta Hardy	66	Waikamoi, Maui
disticha Hardy	10	Puu Kolekole, Molokai
disticha Hardy	. .	Waikamoi, Maui
incognita Hardy	82	Kilauea, Hawaii
neutralis Hardy	148	Kilauea, Hawaii
polliciforma Hardy	28	Mud Lane, Hawaii
sordidapex Grimshaw	81	Kilauea, Hawaii
sordidapex Grimshaw	17	Kulani Road, Hawaii
split tarsi		
ancyla Hardy	49	Waikamoi, Maui
clavata Hardy	26	Pupukea, Oahu
fundita Hardy	48	South of Hanalilolilo, Molokai
pectinitarsus Hardy	25	Kipuka Puaulu, Hawaii
white tip scutellum		
cilifemorata Hardy	52	Waikamoi, Maui
fungicola Hardy	14	Paauilo Experiment Station, Hawaii
fungicola Hardy	152	Kipuka Puaulu, Hawaii

Species	Identification number	Locality
haleakalae Grimshaw	107	Paliku, Maui
iki Bryan	65	Waikamoi, Maui
melanoloma Hardy	108	Paliku, Maui
melanoloma Hardy	. . .	Puu Kolekole, Molokai
melanosoma Grimshaw	33	Kokee State Park (Halemanu Valley), Kauai
melanosoma Grimshaw	46	Kokee State Park (Kumuwela Ridge), Kauai
nanella Hardy	31	Kokee State Park (Halemanu Valley) Kauai
nigra Bryan	50	Waikamoi, Maui
bipolita Hardy	149	Mt. Tantalus, Oahu
canipolita Hardy	150	Pupukea, Oahu
demipolita Hardy	16	Paauilo Experiment Station, Hawaii
Subgenus: *Trichotobregma*		
petalopeza Hardy	97	Paliku, Maui

SCAPTOIDS

Genus: DROSOPHILA		
crassifemur Grimshaw	79	Kilauea, Hawaii
crassifemur Grimshaw	80	Puu Kolekole, Molokai
crassifemur Grimshaw	153	Kokee State Park, Kauai
crassifemur Grimshaw	154	Paliku, Maui
nasalis Grimshaw	155	Paliku, Maui
nasalis Grimshaw	156	Puu Kolekole, Molokai
parva Grimshaw	157	Kokee State Park (Mohihi Stream), Kauai
Genus: TITANOCHAETA		
contestata Hardy	13	Drum Drive, Oahu
species C	8	Pupukea, Oahu
Genus: SCAPTOMYZA		
Subgenus: *Alloscaptomyza*		
longisetosa Hackman	158	Mt. Tantalus, Oahu
stramineifrons Hackman	159	Mt. Tantalus, Oahu
Subgenus: *Bunostoma*		
anomala Hardy	160	Kokee State Park (Mohihi Stream), Kauai
palmae Hardy	161	Mt. Tantalus, Oahu
palmae Hardy	162	Kamuela, Hawaii
xanthopleura Hardy	163	Mt. Tantalus, Oahu
Subgenus: *Exalloscaptomyza*		
mauiensis (Grim.)	164	Iao Valley, Maui
species ?	165	Kamuela, Hawaii
species ?	166	Pali Highway, Oahu
species ?	167	Molokai
species ?	168	Puu Ka Pele, Kauai
Subgenus: *Parascaptomyza*		
pallida (Zett.)	169	Pohakaloa, Hawaii
Subgenus: *Rosenwaldia*		
abrupta Hackman	120	Waikamoi, Maui
Subgenus: *Tantalia*		
varipicta Hardy	170	Kokee State Park, Kauai

Species	Identification number	Locality
Subgenus: *Trogloscaptomyza*		
argentifrons Hardy	171	Kokee State Park (Mohihi Stream), Kauai
articulata Hardy	172	Pohakaloa, Hawaii
connata Hardy	121	Kokee State Park (Mohihi Stream), Kauai
hackmani Hardy	116	Puu Kolekole, Molokai
hackmani Hardy	. . .	Kipuka Puaulu, Hawaii
inaequalis (Grim.)	174	Pohakaloa, Hawaii
intricata Hardy	125	Waikamoi, Maui
intricata Hardy	. . .	Puu Kolekole, Molokai
latitergum Hardy	139	Haleakala, Maui
levata Hardy	122	Kokee State Park (Mohihi Stream), Kauai
retusa Hardy	127	Waikamoi, Maui
rostrata Hardy	118	Kokee State Park (Kumuwela Ridge), Kauai
silvicola Hardy	126	Waikamoi, Maui

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