This is to certify that the

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By

John Jenkins

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ABSTRACT

SYSTEMATIC STUDIES OF *RHAGOLETIS* AND RELATED GENERA
(DIPTERA: TEPHRITIDAE)

By

John Jenkins

Two traditional sources of taxonomic characters, male genitalia and wing patterns, were examined in detail, and relationships among *Rhagoletis* and 16 related genera were analyzed. The genitalia of 278 males in 90 species was examined. A detailed description of the male genitalia based on these examinations is given. A ground plan for the phallus is proposed, and homology of genital structures is discussed. Elements of banded wing patterns are identified using structural landmarks instead of their relative position on the wing. A model of wing pattern evolution is presented, and a transformation series for wing patterns in *Rhagoletis* is given. A phylogenetic analysis of 50 species of *Rhagoletis* and 38 species in 17 other trypetine genera was performed. During the character analysis, 247 characters were examined, resulting in 91,942 recorded observations. Characters used in the cladistic analysis are detailed, and the use of polymorphisms as cladistic characters is discussed. Results of the cladistic analysis indicate that *Rhagoletis* is not monophyletic; that the subtribe Carpomyina is monophyletic and the subtribe Trypetina is paraphyletic; and that previously unplaced trypetines may be closely related to the Trypetina.

To my Folks

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And then there was my Jude...

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INTRODUCTION

The genus *Rhagoletis* includes 62 described species occurring in temperate areas of the Holarctic, Oriental, and Neotropical regions (Bush, 1966; Hardy, 1977; Foote, 1981, 1984; Berlocher, 1984; Hernández-Ortiz, 1985, 1993; Norrbom, 1989). The genus is placed in the subtribe Carpomyina (tribe Trypetini) (Foote et al., 1993) which also includes the Palearctic genera *Carpomya*, *Goniglossum*, and *Myiopardalis*; the Nearctic genus *Zonosemata*; and the Neotropical genera *Cryptodacus* (=*Lezca*), *Haywardina* (=*Cryptoplagia*), *Rhagoletotrypeta*, and *Stoneola* (Norrbom, 1989).

Members of Carpomyina whose biology is known breed in the fleshy fruits of plants from a wide variety of families (see Foote, 1981; White and Elson-Harris, 1992; Hernández-Ortiz, 1993; Norrbom, 1994; Smith and Bush, in review). A number of these flies are serious agricultural pests, especially species of *Rhagoletis* (Boller and Prokopy, 1977; Foote, 1981; White and Elson-Harris, 1992). Species of *Rhagoletis* also have been the subject of numerous studies in the field of evolutionary biology (Feder et al., 1988; Bierbaum and Bush, 1990; Frey and Bush, 1990; Bush 1992; Berlocher et al., 1993; Johnson et al., 1996; McPheron and Han, submitted; Smith and Bush, in review).

Comparative studies of fruit flies in general, and *Rhagoletis* in particular, are hindered by the current state of the classification of the family. Recent classifications of the Tephritidae (e.g., Hardy, 1973; Foote et al., 1993) have changed little since the one proposed by Herring in 1947 (Hardy 1980, 1983; Hancock, 1986; Foote et al., 1993). These classifications are untested, intuition-based arrangements, and the degree to which they reflect phylogenetic relationships is uncertain.

Phylogenetic systematics, or cladistics, is currently the most widely accepted method for inferring phylogenetic relationships (Forey et al., 1992; Kluge and Wolf, 1993). Recent studies have done little to improve the classification of the family, and most suffer from what Kluge and Wolf (1993) called "*ad hoc* methods that only bear the label, not the meaning, of phylogenetic systematics."

In Hancock's (1986) classification of the Trypetinae, characters were polarized using an "outgroup comparison with other subfamilies" without specifying which subfamilies. Further, many of his defining characters are polymorphic (e.g., "Female typically with three spermatheca, two in a few species and genera, and a variously shaped aculeus [segment 8];"), tautological (e.g., "Leg with a row of bristles on fore femora present or absent."), or noncharacters (e.g., "...; stigma [wing cell sc] not vestigial;..."). Hancock stated that, "Character trends therefore need to be applied if a workable classification is to be achieved, accepting that various anomalies may occur." However, trends are highly subjective and dividing them into meaningful characters can be quite arbitrary.

Discussing the classification of North American fruit flies, Foote et al. (1993) concluded that "homoplasy (convergent evolution) appears to be common in many morphological characters that have been the main basis of classification." Their conclusion was based on the assumption that the family is "a relatively recent, rapidly radiating group" (Foote et al., 1993). However, demonstrating homoplasy depends on a resolved cladogram because homoplasy is a property of characters only within the framework of ancestor-descendant relationships (Wiley, 1981). Similarly, Foote et al.'s (1993) use of "monophyly," "synapomorphy," and "pleisiomorphy" is often inappropriate because these terms are relative only in conjunction with a testable hypothesis of relationships (cladogram).

Another problem has been the assumption that widely distributed characters are primitive. In a phylogenetic study of selected tephritid flies using ribosomal DNA, Han

and McPheron (1994) stated that, "When two equally parsimonious interpretations of ancestral states were possible..., the state more common within the Tephritidae was arbitrarily assigned as ancestral" (reference to specific characters omitted). However, when relationships are not resolved, the assumption that common equals primitive does not ensure that the most recent common ancestor to the study group had the primitive state, especially in groups where homoplasy is common (Wiley, 1981; Watrous and Wheeler, 1981). In addition, the cladogram upon which they based their outgroup relationships (Han and McPheron, 1994, figure 1) misrepresented the phylogeny proposed for the Tephritoidea by McAlpine (1989). McAlpine (1989, figure 116.3) places the Piophilidae in a clade that is a sister taxon to the clade containing the Tephritidae, not basal to the Tephritidae as shown by Han and McPheron (1994, figure 1).

What should be apparent from the above discussion is the central role that characters play in reconstructing phylogenetic relationships (see also Neff, 1986; Pimentel and Riggins, 1987; Bryant, 1989). During a phylogenetic analysis, it is only in the character analysis that hypotheses can be proposed and tested by deduction (Bryant, 1989). No matter what cladogram we generate, it can, in principle, be explained by induction. Because we can never know when we hit upon the true phylogeny, one scenario is, in principle, as good as another. The confidence that we can have in any phylogeny depends directly upon the characters used to infer it.

The work reported herein attempts to make character analysis the central issue. Male genital characters are used extensively in fruit fly taxonomy, but much remains unknown about their structure and homologies. Chapter 1 deals with the morphology of the genitalia of male trypetines in anticipation of their use in phylogenetic analysis. Wing patterns also provide important characters, and, like male genitalia, much of what is known about them is based on taxonomic utility rather than sound morphological study. To stimulate interest in the historical development of wing patterns, and to

stabilize the nomenclature of pattern elements, a heuristic model of trypetine wing pattern evolution is presented in Chapter 2. The results of a phylogenetic analysis of relationships among *Rhagoletis* and related genera are reported in Chapter 3. The phylogenetic analysis consists of two parts: an extensive qualitative analysis of morphology, and a cladistic analysis based on the resulting characters.

Throughout this dissertation the terms "figure," "table," and "character" are used to refer to the figures, tables, and characters of other authors while "Figure," "Table," and "Character" refers to those herein.

CHAPTER 1

MALE GENITALIA IN THE TRYPETINI (DIPTERA: TEPHRITIDAE)

"...man makes nothing so complex as an ant or a fruit fly, and if he did, it would surely be subject to errors of construction and assembly..." — Garcia-Bellido et al. (1979)

Characters of the male genitalia are commonly used in the taxonomy of fruit flies, and much of what we know about genital morphology is a result of taxonomic studies (e.g., Benjamin, 1934; Aczél, 1955; Bush, 1966; Hardy, 1973; Novak, 1974; Stoltzfus, 1977; Freidberg and Mathis, 1986; Korneyev, 1986; Norrbom et al., 1988; Stoltzfus, 1988; White, 1988; Hernández-Ortiz, 1993; Merz, 1994). In particular, Munro (1947) summarized terminology up to 1947 and gave an extensive description of tephritid genitalia based on a revision of African species. More recently, Munro (1984) gave a detailed account of genitalia in his revision of dacine fruit flies.

Despite this long-standing familiarity with the genitalia of male tephritid flies, there are surprising gaps in our knowledge of the structures. This is in part because descriptions are often based on taxonomic convenience rather than well-reasoned morphological study. As a result, terms are applied as a matter of personal preference or taxonomic tradition, and there is often more than one term for a given structure or the same name is given to structures that are not homologous.

Another barrier to understanding tephritid genitalia has been disagreement over interpretation of homologies in the male genitalia of the Diptera (summarized by Cumming et al. [1995]). In a recent series of papers (Wood, 1992; Sinclair et al., 1994; Cumming et al., 1995), however, competing hypotheses were evaluated and new homologies proposed. This important body of work codifies terminology and uses

phylogenetic analysis to corroborate homologies to a greater extent than previous studies (e.g., Griffiths 1972; McAlpine, 1981a, 1989; Wiegmann et al., 1993).

Interest in cladistic analysis of tephritid taxa (e.g., Berlocher, 1981; Han, 1992; Norrbom, 1993, 1994; Han et al., 1993) accentuates the need for phylogenetically informative characters. Male genitalia is a potentially rich source of characters for phylogenetic studies, however, absence of uniform terminology and established homologies presently precludes many comparisons. Therefore, following Wood (1992), Sinclair et al. (1994), and Cumming et al. (1995), I present a comprehensive description of male trypetine genitalia; discuss homologies within the family; and propose a ground plan for the phallus of tephritid flies.

Materials and Methods

Species and number of specimens examined are listed in Table 1. Specimens used for dissection were relaxed in a humidor overnight. About two-thirds of the abdomen was excised and macerated in sodium hydroxide (ca. 10%) heated to 60° C until structures cleared (ca. 20—90 min). Abdomens were then acidified in glacial acetic acid for at least 30 min, rinsed in distilled water and stored in micro vials containing glycerin; microvials were attached to the pin below the fly. Stereo and phase-contrast microscopes were used to examine genitalia. Glycerin was used to make temporary microscope slide mounts. Drawings were made using a drawing tube attached to the microscope.

When available, frozen or recently killed flies were used for preparations studied with scanning electron microscopy. Specimens were cleaned by soaking in enzymatic laundry detergent (Procter and Gambel's ERA®, 5% v/v) for 30 min with brief (10 sec.) sonication followed by three rinses in double distilled water. Flies were fixed in FAA (2 formalin:1 glacial acetic acid:10 80% EtOH:7 water) for 12—24 h, rinsed three times in 70% EtOH with a 15 min soak between rinses, and dehydrated in a graded

alcohol series. Flies were either air dried or dried in a critical point drier, then coated with gold and examined in a JEOL JSM-35CF scanning electron microscope at the Center for Electron Optics, Michigan State University.

Terminology follows Wood (1991), Sinclair et al. (1994) and Cumming et al. (1995) unless noted otherwise. For the purpose of discussion, orientation of the phallus is fully extended posteriorly.

Description

Genitalia was examined from 278 specimens in 90 species (Table 1). The following description is based on these examinations.

Segments 1—5 (Preabdomen). Terga 1 and 2 are fused and form syntergum 1+2 (tergites 1 and 2). The remaining preabdominal sclerites are free. The pleura are usually unmodified, but an invaginated sac-like structure occurs in the pleural membrane between segments 4 and 5 in *Myoleja limata.*

Segments 6—8 (Postabdomen). Syntergosternum 6+7 is formed by fusion of segments 6 and 7 on the left side of the abdomen (Figure 1—2). Fusion of segments 7 and 8 form a lobe, syntergosternum 7+8, that is continuous with syntergosternum 6+7 (Figures 1—2). Sterna 6 and 7 are narrow and free medially and broad and free on the right. Sternum 7 sometimes has a sharp bend near its middle. The right end of sternum 7 is narrowly attached to the anteromedial edge of the hypandrium (Figure 2, arrow). Sterna 6 and 7 each have a pair of sensory setulae. These sensilla are named here according to the sternum and side on which they occur. For example, sensilla 6R and 7L occur on the right and left sides, respectively, of sterna 6 and 7 (Figure 2).

A small blister- or sac-like structure of unknown function sometimes occurs medially in the membrane between sterna 6 and 7 (Figure 1). This structure varies from a low swelling that is just detectable to a conspicuous lobe. The structure is evidently an evagination of the intersegmental membrane; it is most easily seen in

abdomens treated with NaOH prior to removing genitalia. The membrane between sterna 6 and 7 is taut and flat in specimens without the structure.

Epandrium. Tergum 9, the epandrium, is convex dorsally and bears a pair of posteroventrally directed surstyli ventrally (Figures 1, 3—6). Posterior to the epandrium is the anus-bearing segment, the proctiger (Figures 1, 3—6). The epandrium is closed ventrally by the subepandrial membrane which runs anteriorly from the proctiger to the base of the phallus (Figure 6). The epandrium bears a number of macrotrichia and often sparse to dense microtrichia.

Surstyli. Surstyli vary in length (Figures 7—31) and have the outer surface relatively flat to strongly convex. Apically, surstyli vary from more or less blunt to sharply pointed. Each surstylus bears one to three lobes. The anterior surstylar lobe (Figure 31) occurs on the anteromedial surface of the surstylus near the level of the prensisetae (e.g., Figures 8, 15, 22, 28, 30); it is identified by numerous denticles and one or more (rarely none) sensory setulae on its posterior surface (Figure 32). The posterior surstylar lobe (e.g., Figures 10, 15, 21, 26, 28) may be a small posteroapical lobe (e.g., Figure 31) or a major portion of the entire surstylus (e.g., Figure 21). It bears a number of setae that are often larger than the sensory setulae on the anterior lobe (Figure 32); in *Rhagoletis berberidis*, there also are a number of small peg-like sensilla distally (Figure 17). Denticles sometimes occur on the posterior surstylar lobe, where they may be confluent with those on the anterior lobe (Figure 15). The medial surstylar lobe (Figures 28, 31), when present, is between the anterior and posterior lobes and is similar in size to the anterior lobe. The medial lobe also bears denticles.

Bacilliform sclerites. A bacilliform sclerite is closely associated with the inner surface of each surstylus (Figure 6). In lateral view (Figures 6, 33—34), the bacilliform sclerite is a more or less rod-shaped structure with a twist (often indicated by a notch or groove) usually anterior to midlength and with a pair of apical or

subapical prensisetae. The inner and outer prensisetae usually occur at about the same level, but in some species one or the other may be more distal (Figures 35—36). The portion of the bacilliform sclerite posterior to the twist lies in a depression on the inner surface of the surstylus (Figure 37). The bacilliform sclerite and surstylus are connected across the depression by the subepandrial membrane, which usually bears microtrichia (Figure 37). The dorsal edge of the bacilliform sclerite is fused for a variable distance along the posteromedial edge of the surstylus (Figures 32, 38). A dorsal keel that is often erose or serrate sometimes occurs distally on the bacilliform sclerite (Figures 16, 19).

A sclerotized bridge between the posterior portion of the right and left bacilliform sclerites is often present (Figures 14, 39). This posterior bridge is formed by an arm running dorsomedially from each bacilliform sclerite to the subepandrial sclerite (Figures 6, 14). In *Epochra canadensis*, a membranous connection extends from the bridge to an internal sclerotized process at the base of the surstylus (Figure 8, arrow); externally the process is indicated by a sulcus (Figures 7, arrow).

Another sclerotized bridge always occurs anteriorly between left and right bacilliform sclerites (Figures 14, 39). The bridge was fractured medially in a number of specimens (e.g., Figure 22) suggesting the presence of a suture or area of weakness. The subepandrial membrane runs from the proctiger and base of the surstyli to the posterior bridge, and from there to the anterior bridge and phallus (Figures 6, 39). The portion of the subepandrial membrane running from the bridge to the anterodorsal base of the phallus nearly always bears denticles (Figure 6).

The anterior end of the bacilliform sclerite usually forms a lobe that projects forward beyond the anterior bridge for a short distance (e.g., Figure 16, "bacilliform sclerite"); this lobe is absent in the *Oediacarena*, *Paraterellia* (Figures 9, 12), and *Strauzia* species. The lobe usually has fibers attached to it from muscles removed during dissection. A muscle runs obliquely forward from the ventral surface of the bacilliform

sclerite to the lateral wall of the epandrium.

Subepandrial sclerite. The subepandrial sclerite (e.g., Figures 6—10, 40) lies within the epandrium above and between the bacilliform sclerites and usually just ahead of the hypoproct. The sclerite is usually small, but in *P. immaculata* it is quite large (Figure 12). A muscle runs laterally or dorsolaterally from each side of the subepandrial sclerite (Figure 40) to the inner surface of the epandrium; these muscles help identify the sclerite.

Phallus. The intromittent organ, the phallus, arises anteromedially to the epandrium (Figures 3—6). When at rest, most of the phallus is concealed beneath tergum 5 (Figure 38) in a pouch that is formed by the intersegmental membrane. A small portion of the phallus is normally visible to the right of the epandrium where it is held against the abdomen by the pregonite (Figure 38).

The phallus can be divided into a proximal basiphallus and distal distiphallus (McAlpine, 1981a) (Figure 3—5, 41). The basiphallus and distiphallus can usually be distinguished: they join at an angle, the phallus narrows at their junction (Munro, 1947), and the ventral sclerotized strips of the basiphallus terminate at its apex. The parameral sheath forms the external wall of the phallus and encloses the aedeagus; it has both sclerotized and membranous components. The aedeagus is continuous with the sperm sac via the ejaculatory duct (Figures 3, 6). The aedeagus is membranous for the length of the basiphallus and upon entering the distiphallus, but it often terminates in a sclerotized acrophallus (Figure 41).

The basiphallus (Figure 3—5, 41) is relatively long and narrow, and coiled or convoluted. It usually has numerous transverse grooves dorsally and a pair of sclerotized strips ventrally that run its length and which may be fused proximally (Figure 41). A narrow ring-shaped sclerite encircles the base of the basiphallus (Figures 6, 41). The ejaculatory duct and accessory gland enter the basiphallus through the center of the sclerite (Figure 6). The sclerite articulates ventrally with the

phallapodeme and is connected to the subepandrial membrane dorsally (Figure 6). In several species, the basiphallus bears a small dorsal or dorsolateral bladder-like structure distally, here termed the basiphallic vesica (Figure 42). A small, irregularly-shaped sclerite sometimes occurs near the apex of the basiphallus (Figures 42—43, 45—46). A pair of membranous ventral keels (Figure 41) occur on the basiphallus in several species. *P. immaculata* has a pair of small, sclerotized tubercles on the ventral surface of the basiphallus proximally.

The distiphallus (Figures 3—5, 41—70) usually is distinctly swollen and much shorter than the basiphallus. The apex of the aedeagus is usually enclosed by the distiphallus, but in *E. canadensis* (Figures 48—49), *O. latifrons*, and *P. superba*, the aedeagus terminates externally. There is an appressed flap laterally ("ventral flap" of Munro, 1984) formed by a longitudinal invagination of the parameral sheath (e.g., Figures 42, 45, 48, 69). This appressed flap is part of a sclerotized plate that makes up a variable portion of the external wall of the distiphallus. The flap wraps around the distiphallus and the position of its distal edge varies from right lateral to dorsal (c.f. Figures 42 and 45). The distal edge of the flap usually can be identified by microtrichia along its length (e.g., Figures 42, 45, 62, 69). The microtrichia may run the entire length of the flap (Figure 56) or be limited to it's edge near the base of the distiphallus (Figure 68).

A membranous flap of variable size occurs apically (Figures 42—70). This apical flap may be cleft (Figure 70), and in most species examined it is microtrichiose (Figure 69) or has fine striations on its internal surface; in some species (e.g., *R. suavis* group), the flap is also arenose.

A variously shaped lobe occurs subapically on the left side of the distiphallus (odd numbered Figures 43—59, 63—67). This subapical lobe varies considerably among the species examined. In some it appears as a simple membranous lobe (Figures 51, 61, 65), while in others it bears additional lobes (Figure 52), microtrichia (Figures 56—

60, 62—63, 66—67, 69—71), or sclerotized denticles or hooks (Figures 42 inset, 68). Sclerotized plates or strips are sometimes present in the wall of the lobe (Figure 48—49, 57, 62—63), and a lumen could be seen within the lobe in a number of specimens. In the *Zonosemata* species, the subapical lobe is continuous with the apical flap and does not form a separate lobe as in the other species examined.

Structures that appeared to be campaniform sensilla (Figure 64) occurred in a few specimens and in no specific location on the parameral sheath. Some specimens of *E. canadensis* (Figure 49), *O. latifrons*, and *Trypeta inaequalis* (Figure 46) had a minute setiform sensillum ventrobasally on the sheath.

Internal structure of the distiphallus is complex and affinities are uncertain. In nearly all specimens examined, the course of the aedeagus through the distiphallus could not be traced (see also Munro, 1947, p. 78). The apex of the aedeagus forms sclerotized tubes or strips in species where it terminates beyond the parameral sheath (Figures 48—49). When the aedeagus is enclosed, its apex often forms a sclerotized acrophallus that resembles either a corrugated plate (Figure 72) or two to three troughs (Figures 50, 62). In several species, however, the apex of the aedeagus could not be discerned.

A small, sclerotized loop (= "valve" of Munro, 1984 and [?] "basalring" of Merz, 1994) within the base of the distiphallus on the left side occurs in number species (e.g., Figure 63).

The sclerotized plate within the parameral sheath usually has at least a small amount of weak striate, crenulate or rugose sculpturing (inset, Figures 54—56, 58—59, 62—67). In some species, however, the sculpturing is quite extensive and much more elaborate, forming distinctive polygons, striations and denticles (inset, Figures 42—44, 46—50, 68). A serrate sclerite (Korneyev, 1986) occurs in the distiphallus of *S. intermedia* and *S. longipennis* (c.f. Stoltzfus, 1988, figure 36).

Sperm pump. The ejaculatory duct runs from the sperm sac to the ring-shaped sclerite at the base of the phallus (Figures 3, 6). Entering the phallus with the

ejaculatory duct is an elongate accessory gland (Figures 6, 41); the gland is delicate and easily damaged during dissection. A large, spatulate apodeme, the ejaculatory apodeme, attaches to the sperm sac anteriorly (Figures 3—5). The distal edge is usually thin and coplanar with the blade (Figure 3), but it is flattened perpendicular to the blade in a few species.

Hypandrium. Sternum 9, the hypandrium, is a simple, U-shaped sclerite that articulates with the anterior edge of the epandrium (Figure 4—5). A laterally compressed, anteriorly projecting lobe, the hypandrial apodeme, occurs medially in several species. A small piece of sternum 7 sometimes remains attached to the hypandrium after dissection and may be mistaken for the hypandrial apodeme in species where the apodeme is absent. Specimens of some species (e.g., *R. cingulata* and *R. suavis* groups) sometimes have the anterior edge of the hypandrium more or less U-shaped in the transverse plane. An invaginated sac ("genital ring membrane pouch" of Bush, 1966, figure 75) sometimes occurs in the hypandrial membrane anteriorly. This hypandrial sac varies from relatively shallow and ill defined (Figure 6) to deep and decidedly sac-like; it is lined with numerous, well-sclerotized denticles in the *R. suavis* species group (Bush, 1966, figures 72—73, 75—76, 78).

Pregonites. A small rod-shaped pregonite occurs proximally on both sides of the hypandrium (Figures 3—5, 38). The rods articulate with the medial bases of the hypandrium and the lateral arms of the phallapodeme. Both pregonites are deflected ventrally, but the right one usually more so. When the phallus is not in use, its base is held against the abdomen by a small lobe formed by the membrane that runs between the right pregonite, hypandrium, and right lateral arm of the phallapodeme (Figures 3, 38).

Phallapodeme. The phallapodeme (aedeagal guide + aedeagal apodeme of McAlpine, 1981a) is a more or less cruciform sclerite (horizontal plane) occurring in the hypandrial membrane (Figures 4—6). It articulates posteriorly with the ring-shaped

sclerite at the base of the phallus and laterally with the pregonites. The more or less spatulate anteromedial projection of the apodeme (aedeagal apodeme of McAlpine, 1981a) serves for muscle attachment.

Proctiger. The terminal abdominal segment, the proctiger (Figures 1, 3, 6), bears the anus apically and the hypoproct ventrally. The proctiger varies from relatively short (e.g., Figure 14) to relatively long (e.g., Figure 13). In most species studied, the hypoproct forms a somewhat ill-defined sclerite running the length of the proctiger (e.g., Figures 7, 16, 30, 40). The hypoproct typically becomes wider distally and varies in length from about as long as wide to decidedly longer. Apically, the sclerite may be rounded, truncate or bilobed. The hypoproct is divided medially for most or all of its length in the *Oedicarena* and *Paraterellia* species (Figures 10—11). In some species, (e.g., *Acidia cognata*, *Chetostoma* spp., *Strauzia* spp.) the hypoproct extends dorsally and forms lateral plates that cover much of the proctiger (Figures 27, 31). The rectal lining within the proctiger of several species has numerous bumps and folds; the rectal lining is smooth in most species.

Discussion

Segments 1—5. The function of the invaginated pleural sacs in male *My. limata* are unknown. Male *Anastrepha suspena* extend pleural pouches during courtship (Nation, 1972); glands associated with the pouches appear to be a source of male sex pheromone (Nation, 1981). Pleural glands, known or suspected to produce courtship odors, occur in a number of male tephritid flies (Jenkins, 1990 and references therein).

Segments 6—8. A sharp bend near the middle of sternum 7 occurred in some or all specimens of about half of the species of *Rhagoletis*, but only four of the 39 non-*Rhagoletis* species examined. The sensory setulae on sterna 6 and 7 are found throughout the Diptera, usually occurring on the anterior margin of the sclerites where they serve as landmarks of segmentation (Griffiths, 1972; McAlpine, 1981a). In species studied

here, some specimens had one or more sensilla in the intersegmental membrane behind the sterna. Sensillum 7R was the most likely to occur in the membrane. In some specimens, one or more sensillae were missing.

Surstyli. The term surstylus is used here for the structure referred to in the recent literature (e.g., McAlpine, 1981a) as the outer surstylus. Surstyli are secondarily derived articulated clasping structures in the Eremoneura (Cumming et al., 1995). The cyclorrhaphan surstylus is a lateral outgrowth of tergum 9, the outer surface of which is formed by the epandrium and the inner surface by the bacilliform sclerite (Cumming et al., 1995). Surstyli are not articulated in the Tephritidae, but published illustrations indicate that articulation occurs in several sister groups (e.g., Steyskal, 1958, figures 8, 10, 20, 22 [Richardiidae]; McAlpine, 1987, figures 14—15 [Lonchaeidae]; Steyskal, 1987a, figure 9 [Platystomatidae]; Steyskal, 1987b, figure 7 [Pyrgotidae]; McAlpine, 1981b, figures 3—4 [Pallopteridae]). Non-articulated surstyli could be a result of the fusion of articulated lobes, or the secondary gain of non-articulated lobes. The sulcus at the base of the surstylus of *E. canadensis* (Figure 7, arrow) may represent a line of fusion between the epandrium and a once articulated surstylus. Further, the membrane running from the internal apodeme formed by the sulcus to the posterior bridge between the bacilliform sclerites may represent a primitive connection between the surstylus and the subepandrial membrane. However, more study, including detailed evaluation of musculature, is needed to determine which course of evolution occurred in the Tephritidae.

Homology of surstylar lobes has not been well established. Benjamin (1934, figure 6) described the anterior surstylar lobe as "a pad (a small soft structure, presumably sensory)." Stoltzfus (1977) used the "dorsal lobe" (=posterior surstylar lobe?) extensively in his taxonomic study of *Eutreta.* Munro (1984) described anterior and posterior surstylar lobes and detailed the variation in the lobes of dacines. Munro (1984) identified the anterior lobe by presence of a "papillose patch or rugose area,"

but did not mention whether sensilla also are present. Norrbom et al. (1988) noted that the "*Rhagoletis* type" surstylus is longer than the "inner surstylus" (=bacilliform sclerite) and has the "mesal" (=anterior) lobe near the level of the prensisetae; parenthetically, they state that the "*Rhagoletis*" type surstylus is secondarily absent in *Zonosemata*.

Anterior and posterior lobes were present in most species examined here. In the *Zonosemata* species (Figure 30) and *E. canadensis* (Figure 8) only the anterior lobe was present. All three lobes were present only in *A. cognata* and *T. inaequalis* (Figure 28, 31).

An anterior surstylar lobe was present in all species examined. Its homology is established by its position relative to the prensisetae and by the presence of denticles and usually one or more sensillae. From specimens studied, Munro's (1984) work cited above, and illustrations in the literature (e.g., Munro, 1947; Bush, 1966; Drew, 1972; Hardy, 1973; Stoltzfus, 1977; Freidberg, 1980; Stoltzfus, 1988; Jenkins and Turner, 1989; Korneyev, 1991; Condon and Norrbom, 1994; Norrbom, 1994), it is likely that an anterior lobe is a feature of surstyli throughout the Tephritidae. Function of the anterior lobe is unknown, but its close apposition to the prensisetae suggest that it is used in clasping.

The medial and posterior surstylar lobes are more problematical. When both lobes are present, they can be identified simply by their positions. In most species studied, however, only one lobe in addition to the anterior lobe is present. Whether this lobe is derived from the medial or posterior lobes, or both, could not be determined. However, development of the posteroapical portion of the surstylus in a number of species (e.g., Figures 11, 15, 23—24) suggests derivation from the posterior lobe. Loss or reduction of medial and posterior lobes may result in surstyli like those found in *Zonosemata* (Figures 29—30) and numerous tephritines (e.g., Jenkins and Turner, 1989; Novak, 1974; Stoltzfus, 1977).

Bacilliform sclerites. The structures referred to here as bacilliform sclerites are the inner surstyli of McAlpine (1981a). Munro (1947, 1984) termed the structures "twisted rods" in reference to their characteristic twist. The bacilliform sclerites are formed by secondary sclerotization of the subepandrial membrane (Sinclair et al., 1994; Cumming et al. 1995). It is very likely that the bridges and denticles described for the species studied here are also derived from the subepandrial membrane by secondary sclerotization. The anterior bridge appears to be widespread within the Tephritidae (see Bush, 1966; Drew, 1969; Stoltzfus, 1977; Freidberg and Mathis, 1986; Condon and Norrbom, 1994; Norrbom, 1994). Following Griffiths (1972), Korneyev (1985) and Norrbom and Kim (1988) termed the anterior bridge "interparameral sclerite." However, Griffiths' (1972) term is inappropriate if the structure is derived from the subepandrial membrane, which is likely (see Cumming et al., 1995). The posterior bridge in the species studied ranged from well-developed, sclerotized structures to a simple membranous connection between the bacilliform subepandrial sclerites.

Phallus. There has been much confusion over the naming and homology of structures of the phallus. The structure herein termed basiphallic vesica has been described as a "gland-like tubular sac" near the apex of the basiphallus (Bush, 1966); a "membranous bladder" at the base of the distiphallus (Drew, 1969); a "basal gland" of the distiphallus (Munro, 1984); a "fold or ligule" at the "place of articulation" of the distiphallus with the basiphallus (Korneyev, 1985); a "membranous lateral lobe" at the base of the distiphallus (Norrbom et al., 1988); and a "basal lobe" of the distiphallus (Condon and Norrbom, 1994). Neither Bush (1966) nor Munro (1984) stated why the structure should be considered glandular. Eberhard (1990, figure 6) showed that the structure is expandable (like a vesica) in *Ceratitis capitata* . Confusion exists over which part of the phallus the vesica belongs to because the extent of the distiphallus and basiphallus has not been clearly defined. Distinction between basiphallus and

distiphallus is usually apparent when using the limits listed above.

The terms distiphallus and glans are often used synonymously, but the latter is more appropriate for the terminal portion of the vertebrate penis. Similarly, the term prepuce and its derivatives (see Korneyev, 1986) are more appropriate to vertebrate morphology.

The structure described herein as the subapical distiphallic lobe is widely distributed and has been referred to as "apical appendage" (Bush, 1966), "apical process", (Foote, 1981), "apicodorsal rod" (Munro, 1984; Han, 1992), "juxta" (Korneyev, 1986; Merz, 1994), "accessory sclerite" (White, 1988), "tubular structure" (Eberhard, 1990), and "apical spinose appendage" (Hernández-Ortiz, 1993; Condon and Norrbom, 1994). In all specimens examined, the base of the lobe is subapical, although the apex may extend beyond the tip of the distiphallus. Except for Nearctic *Chetostoma*, the apex of the subapical distiphallic lobe in the non-carpomyines examined is trumpet-shaped (but it is often flattened in preparations). This shape is similar to the "tubular structure" of *Ce. capitata* (Eberhard 1990, figure 6) and the "apicodorsal rod" of dacines (Munro, 1984), in which the subapical lobe appears to be well sclerotized. Nearctic *Chetostoma* have the subapical lobe elongated and with a pair of sclerotized hooks apically. The subapical lobe of the carpomyines studied is usually an attenuated lobe or flattened flap; it is usually bare but is sometimes fimbriate or bears microtrichia that vary in size and density. Position of the lobe on the distiphallus of carpomyines is similar to that of the other species examined.

Function of the subapical distiphallic lobe is unknown. Eberhard (1990, figure 6, caption) states that inflation of the apical membranous portion of the distiphallus ("second expandable sac," labeled "b") of *Ce. capitata* drives the subapical lobe ("tubular structure," labeled "c") into "a cone in the wall of the vagina" (=ventral receptacle?). Eberhard (1990) implies that sperm is transferred through the subapical lobe; unfortunately, no reference or further discussion is given. However, because the

subapical lobe is an outgrowth of the parameral sheath, and because the aedeagus is often recognizable as a definite acrophallus, it seems more likely that sperm is transferred through the aedeagus. Further, in all material examined the subapical lobe appeared to be closed distally, which substantiates Munro's (1984) observation of a "concavo-convex cap at the tip" of the lobe in dacines.

Munro (1947, p. 79) called the "terminal membranous part of the aedeagus [=distiphallus]" the "vesica." This is equivalent to the apical membranous flap described herein and the "second expandable sac" illustrated by Eberhard (1990). In the species studied here, the apical membranous flap varies from small to large (e.g., Figures 62 and 68).

Han's (1992) "dorsal sclerite" is an area of the sclerotized plate within the parameral sheath of the distiphallus and not an actual sclerite. Like the dorsal sclerite, the "median granulate sclerite" (Han, 1992) is not a sclerite, but a sclerotized area of the phallotheca that bears denticles or papillae, the extent of which is quite variable.

The epiphallic sclerite of Korneyev (1985) is interpreted here as the acrophallus. The term epiphallic sclerite is better applied to the small, bilobed plate that occurs at the extreme base of the phallus in some tephritines (e.g., *Tephritis* spp.).

The phallus of tephritid flies is a potential source of characters for phylogenetic studies. However, little progress will be made towards understanding evolution of the phallus until a ground plan is proposed. I therefore propose the following model.

The phallus is in the form of a tube within a tube (Figure 73). The outer tube is derived from the parameral sheath and the inner tube from the aedeagus (Cumming et al., 1995). The phallus can be further divided along its proximal-distal axis into two more or less well defined regions: a proximal basiphallus and a distal distiphallus. The aedeagus is mostly membranous, but may terminate in a sclerotized acrophallus; it is fused to the parameral sheath within the distiphallus. The parameral sheath consists of membranous and sclerotized elements. A sclerotized plate occurs within the parameral

sheath of the distiphallus where it makes up a variable portion of the outer wall and internal structure. Longitudinal infolding of the parameral sheath of the distiphallus produces an appressed lateral flap. This flap wraps around the distiphallus and its extent determines the size of the terminal opening of the parameral sheath. A variously-shaped subapical lobe is formed by an outgrowth of the parameral sheath near the apex of the distiphallus. The wall of the subapical lobe may be completely or partially sclerotized, or entirely membranous. The lobe may bear various superficial processes such as microtrichia, denticles, and supernumerary lobes. The apex of the distiphallus forms a membranous apical flap that may bear microtrichia, denticles or other superficial outgrowths (e.g., arenosity).

Identification of these structures or their derivatives will provide characters for phylogenetic analysis. For example, the trumpet-shaped subapical distiphallic lobe of the trypetines studied is likely due to descent rather than chance (see Chapter 3). Moreover, the position and shape of the lobe is very similar to that of the lobe in dacines (c.f. Munro, 1984; Han, 1992). As another example, membranous and sclerotized portions of the parameral sheath of the distiphallus are more or less coextensive in the species studied here. In the putatively derived genus *Tephritis*, however, the membranous component of the sheath is much larger than the sclerotized portion (Jenkins, 1985; Jenkins and Turner, 1989; Merz, 1994). Evidently, during the evolution of *Tephritis*, the membranous component of the parameral sheath has become enlarged relative to the sclerotized portion.

Ejaculatory apodeme and phallapodeme. Shape and size of the ejaculatory apodeme and the anteromedial portion of the phallapodeme (= aedeagal apodeme of McAlpine, 1981a) is age-dependent. These structures continue to grow for a period of time after adult emergence (Pickett, 1937; Drew, 1969; Drew, 1972; Kamali and Schulz, 1974; Berube, 1978; Munro, 1984). With a few exceptions (e.g., *R. ribicola*—see Bush, 1966), use of these structures as taxonomic characters (e.g., Bush, 1966; Novak

1974; Stoltzfus, 1977; Foote, 1981) should be viewed with skepticism (Drew, 1972; Munro, 1984).

Hypandrium. The invaginated sac occurring in the hypandrial membrane of some species has been termed "genital ring membrane pouch" by Bush (1966) and "membranous process of the hypandrium" by Korneyev (1986). Munro (1984) reported a "fultella [=hypandrium] gland" in dacines with free terga and, in dacines with fused terga, the gland is replaced by a sac that is setulose or bare. The terms "hypandrial sac" or "hypandrial gland" would be more consistent with current terminology. A hypandrial sac is widespread in the Tephritidae, occurring in Dacines (e.g., Munro, 1984), trypetines (e.g., Bush, 1966), and tephritines (e.g., Korneyev, 1986).

Pregonites. The rod-like structure associated with the base of the hypandrium and articulating with the phallapodeme laterally (herein termed pregonite) has been called "inferior rod" (Munro, 1947), "lateral sclerite of the hypandrium" (Korneyev, 1986), "intermediate rod" (Munro, 1984), and "lateral sclerite" (Han, 1992). Homology of the structure is not clear. In the ground plan of the Diptera, gonocoxites are closely associate with, but separate from, the hypandrium (Wood, 1991). Many Nematocera and some Lower Brachycera retain this primitive condition (Wood, 1991; Sinclair et al., 1994). In many other Lower Brachycera, the gonocoxites are partially to completely fused to the hypandrium (Sinclair et al., 1994). The hypandrium and gonocoxites are completely fused in the Eremoneura, and structures that are secondarily derived from gonopods in the Schizophora are termed pregonites (Cumming et al., 1995). The position of the rod-like structures at the base of the hypandrium in tephritid flies suggests a gonopodal origin. Articulation of the rods with the lateral arms of the phallapodeme, which is itself secondarily derived from the gonocoxal portion of the hypandrium (Cumming et al., 1995), indicates that the rods are secondarily derived. The term pregonite should therefore be used for these rod-like structure.

Proctiger. The portion of the rectum lying within the proctiger is convoluted or papillate in the *Chetostoma*, *Eulia*, *Myoleja*, and *Strauzia* species. These convolutions and papillae are similar to those seen in a specimen of *Ce. capitata* examined. Rectal glands in male *Ce. capitata* are the source of a sex pheromone (Nation, 1981) that is produced during courtship and is highly attractive to females (Prokopy and Hendrichs, 1979).

Although based on relatively few trypetines, most of the results of this study should be applicable to the entire family. In order for knowledge of genital morphology to expand, a unified system of terminology must be settled upon, and refinement of homologies sought. As more is learned about the structure and function of tephritid genitalia, previously untested characters can be incorporated into phylogenetic studies.

CHAPTER 2

A HEURISTIC MODEL OF WING PATTERN EVOLUTION IN THE TRYPETINI (DIPTERA: TEPHRITIDAE)

"The primary value of models is heuristic. ...the establishment that a model accurately represents the 'actual processes occurring in a real system' is not even a theoretical possibility." —Oreskes et al. (1994)

The wings of tephritid flies often bear color patterns. Wing patterns may consist of dark bands on a hyaline field, hyaline spots on a dark field, or a combination of bands and spots. The relative ease with which wing patterns are observed has long made them a useful character in tephritid taxonomy (Cole, 1969). Patterns are often characteristic of a species and many flies can be identified on the basis of wing pattern alone. Patterns also are useful for identifying seasonal color morphs within species (Jenkins and Turner, 1989), and for distinguishing some genera and tribes.

Although wing patterns are very useful for identification, a system based on taxonomic utility presents challenges to systematists wanting to use wing patterns for phylogenetic analysis. Phylogenetic relationships usually are overlooked by taxonomists interested in finding taxonomic differences rather than characters that unite taxa (i.e., synapomorphies). Unfortunately, taxonomic differences are often homoplasious or autapomorphic. One problem in using a taxonomically based system for phylogenetic research is that the names of pattern elements are inconsistently applied (Table 2), sometimes even within a single work (e.g., White and Elson-Harris, 1992, figures 37—38, 97; Foote et al., 1993, pp. 129, 248, 325). Taxonomists also devise systems of wing pattern nomenclature for particular groups (e.g., White and Elson-Harris, 1992, figures 35—36; Condon and Norrbom, 1994), but such esoterica make comparing patterns among groups with different systems uncertain at best.

Another important consideration for phylogeneticists is a general lack of demonstrated (or even proposed) homology of wing pattern elements. In species with banded wing patterns, bands are named based on their relative position, and as a result, bands with the same name may not be homologous. In Foote et al. (1993), for example, the subbasal and discal bands of *Epochra canadensis*, *Chetostoma californicum*, and *Ch. rubidium* are the discal and intercalary bands, respectively, of *Rhagoletis*.

A heuristic model of the evolution of banded wing patterns like those found in the Trypetini is presented below. The purpose for presenting such a model is to stabilize nomenclature for banded wing patterns and to provide a hypothetical basis for constructing transformation series of pattern evolution for phylogenetic analysis. A discussion of possible mechanisms involved in pattern formation follows the model.

Evolution of Banded Wing Patterns in the Trypetini

> *As it becomes evident, that between these different types of design a genetic connection really exists, so that they can be arranged in a series, leading from the most primitive and regular to the farthest modified and most capricious, and that this series is the same for different interrelated genera and families, the conclusion, that this correspondence roots in relationship, is a natural one.*
> — van Bemmelen (1917)

The fundamental difference in wing patterns is the extent and position of pigmented and hyaline areas of the wing membrane. Different wing patterns evolve by the expansion and contraction of these areas (*Aciurina* provides a compelling example of this [see Foote et al., 1993, figures 112—124]). For simplicity, only the expansion of hyaline areas will be considered in the hypothetical model presented here. Although the model is described in terms of the expansion of hyaline areas, it should be borne in mind that it is the pigmented portions of a pattern that determine the extent of the hyaline areas.

To avoid comparing non-homologous bands, names used here (Figure 74), except for the apical band, are based on morphological landmarks instead of their relative position on the wing. Figure 75a gives a hypothetical wing pattern from which other

patterns are derived. Choice of the positions of hyaline areas for the hypothetical pattern was based on requirements of the model and actual patterns with extensively pigmented areas and relatively few small hyaline marks (e.g., *Aciurina* spp. [Steyskal, 1984], *Xanthaciura* spp. [Aczél, 1950, 1952], Acanthonevrini [Hardy, 1973, 1974, 1986], and African spp. [Munro, 1947]). Relatively few hyaline areas are needed to derive patterns of the species studied. New patterns are the result of the inward expansion of marginal hyaline areas and the enlargement of discal hyaline spots. Patterns illustrated in Figure 75 show some of the changes in the ground plan that are needed to obtain banded wing patterns. The patterns were not taken from particular species, but elements of each can be found in real patterns in the taxonomic literature.

Band h (humeral band). Band h runs posteriorly from the costa at or near the level of vein h usually to the level of vein CuA_2; vein h is its landmark (Figure 74). Band h is sometimes indistinct, especially in species where the proximal portions of the wing are extensively pigmented (e.g., *Euleia* spp. [Figure 78], *Myoleja* spp., *Strauzia* spp.), or the pattern is generally lightly pigmented (e.g., *Carpomya incompleta*, *R. juglandis* [Figures 88—89]).

The humeral band is formed by the inward expansion of hyaline spots in cells c and bc and the anal lobe and alula (Figure 75). Additional hyaline spots in the extreme wing base (e.g., the base of cell br) also may be involved. In most carpomyines studied, band h is free, crosses cells bm and cup, and covers vein CuA_2 (e.g., Figures 82—87). In *E. canadensis* (Figure 76), *Ch. californicum*, and *Ch. rubidium*, band h runs to or across the base of cells bm and cup and does not cross vein CuA_2. The humeral band is truncated posteriorly or interrupted by a hyaline area or spot in cell bm in a number of non-carpomyines. In several of these (e.g., *Acidia cognata*, *Ch. curvinerve* [Figure 77], *Oedicarena latifrons*, *Paraterellia ypsilon* [Figure 80]), the posterior portion of both band h and the proximal subcostal band (described below) converge on vein CuA_2. It is unclear whether the posterior portion of band h actually belongs to that band or to the

posterior portion of the proximal subcostal band (see below).

Band sc (subcostal band). The subcostal band runs posteriorly from cell sc (its landmark) usually to the wing margin or nearly so (Figure 74). The band may be entire or divided into proximal and distal bands. Each band may be partially fused to other wing bands (e.g., Figures 78—79).

The proximal edge of the subcostal band is formed concomitantly with the distal edge of the humeral band. Coalescence of a hyaline spot in cell br with a hyaline area in cell cua_1 divides the band into proximal and distal portions (Figure 75). The distal edge of band sc is formed by the inward expansion of hyaline areas in cell r_1 and cua_1 and their coalescence with spots in cells br or dm. When the proximal hyaline area in r_1 and the hyaline area in cua_1 converge on and coalesce with the spot in br, the distal portion of band sc is reduced or obliterated forming a prominent proximal band sc (Figure 75b—d). The proximal subcostal band runs posteriorly from cell sc usually to the level of vein CuA_2 (Figures 76—77). When the hyaline areas in r_1 and cua_1 converge on and coalesce with the spot in dm, both the proximal and distal portions of band sc are prominent (Figure 75e—f). Subsequent loss of the proximal portion results in a prominent distal band sc (Figure 75g). The distal band runs posteriorly from cell sc to cell cua_1 or the posterior wing margin, and at least its distal edge crosses vein r-m (Figures 79—89). Both subcostal bands are prominent in *Ch. curvinerve* (Figure 77), but in most species seen only one band is prominent although a second faint or incomplete band can sometimes be traced (e.g., Figures 76, 79—80).

Norrbom et al. (1988) suggested that the pigmented spots lying on vein h and cell "bcu" (=cell cup) in *Oedicarena* (e.g., Figure 81) may be an "incomplete subbasal band" (=humeral band) and, as such, a possible synapomorphy. However, as interpreted here, the spot on the humeral crossvein is part of the humeral band and the spot on cell cup is either part of the humeral band or proximal band sc; similar spots occur in *Paraterellia*. Foote et al. (1993) did not recognize a proximal subcostal band and as a

result their "discal" band is actually the distal subcostal band in *Rhagoletis* and band r-m (described below) in *Epochra* and *Chetostoma*. Norrbom (1993) also identified band r-m in *E. canadensis* and *E. mexicana* as the "discal" band.

It is important to keep in mind the distinctions between proximal and distal subcostal bands in phylogenetic studies because they are not strictly homologous.

Band r-m (radial-medial band). Band r-m runs posteriorly from the costa in cell r_1 across vein r-m, its landmark (Figures 74, 76, 80). In a number of species, however, the band extends posteriorly only to vein R_{4+5} (e.g., Figures 79, 81) or is absent (e.g., Figures 82—89).

Band r-m is formed by the inward expansion of hyaline areas in cells r_1 and cua_1 and their coalescence with spots in cells br, dm, or both (Figure 75). If the proximal hyaline area in cell r_1 coalesces with the spot in cell br, band r-m crosses vein r-m (Figure 75b—d). If the hyaline areas in cell r_1 converge on and coalesce with the spot in cell dm, band r-m is truncated and does not cross vein r-m (Figure 75e—f). In both cases, the distal edge of band r-m is formed by the coalescence of the distal hyaline area in cell r_1 with the hyaline areas in cells dm and cua_1. When band r-m crosses vein r-m it either runs as a free band to the posterior wing margin (or nearly so) (e.g., Figure 76), or it joins distal band sc (e.g., Figures 78, 80). When the band is truncated, it extends posteriorly only to vein R_{4+5} (e.g., Figures 79, 81).

Band r-m joins the apical band anteriorly in several species (e.g., *P. varipennis*, *P. immaculata*, *P. superba*, *Euleia* spp. [Figure 78] and specimens of *E. canadensis*). It joins the apical band anteriorly and band dm-cu posteriorly in *P. superba* and the *Euleia* species (Figure 78). Band r-m is absent in a number of species, especially North American *Rhagoletis* (e.g., Figures 82—89), and some specimens of *Rhagoletotrypeta rohweri* and *Rh. uniformis*.

Norrbom (1989) reported that the truncated band r-m is rare in the Tephritidae and that it may be a synapomorphy for a taxon that includes the Carpomyina and

Oedicarena. Foote et al. (1993) did not recognize the homology of a band crossing vein r-m with the truncated band r-m (their "intercalary" band; Table 2). Norrbom (1994) suggested that the "apical fork" (=band r-m) in the "discal" band (=band sc + band r-m) of *P. ypsilon* (Figure 80) may be homologous to the "accessory" band (=truncated band r-m) of some carpomyines, but did not recognize this homology in other *Paraterellia* species.

Band dm-cu (discal medial-cubital band). Band dm-cu runs from the posterior wing margin across vein dm-cu, its landmark, and usually joins the apical band anteriorly (Figure 74).

The proximal edge of band dm-cu is formed concomitantly with the distal edge of band r-m. Expansion of a hyaline area in cell m forms the distal edge of band dm-cu (Figure 75). Anteriorly, band dm-cu usually is continuous with the apical band (Figures 77, 79—80, 83—87, 89). In a number of species, band dm-cu may join band r-m, band sc (e.g., Figure 79), or both (e.g., Figure 78). Band dm-cu is incomplete in several species (e.g., Figure 81).

Because band dm-cu and the apical band are usually joined anteriorly, it is unclear whether they evolved as a single pattern element or separately. However, some evolutionary independence is needed to explain differences (e.g., reduction) observed in apical bands without complementary changes in band dm-cu.

Foote (1981) identified the subcostal band as the "preapical" band (=band dm-cu, Table 2) and band dm-cu as the posterior apical band in the *R. pomonella* species group. Further, Foote et al. (1993) did not recognize the homology of band dm-cu (their "subapical" band) in the *R. pomonella* group with this band in other *Rhagoletis* species. They considered the "subapical" band to be absent in the *pomonella* group, and the band crossing vein dm-cu to be a posterior apical band (Foote et al., 1993). This is despite having defined their "subapical" band as the band crossing vein dm-cu (Foote et al., 1993, p. 325), which is clearly crossed by a band in the *pomonella* group. In none of

the species studied here is a posterior apical band present and band dm-cu simultaneously absent.

Apical band. The apical band, unlike the other bands, has no structural landmark. Distally, the band ends in the wing margin beyond the wing apex; anteriorly, it usually joins band dm-cu (Figure 74). The apical band may occur as a definite band occupying much of the wing apex (e.g., Figure 76), or as small, variously shaped marks (e.g., Figure 81). The band may be continuous with the wing margin (e.g., Figure 79) or separated from it by a narrow hyaline area (Figure 82). It may be entire (e.g., Figures 79—80) or divided into anterior and posterior bands (e.g., Figures 78, 84—87).

The posterior edge of the apical band is formed concomitantly with the distal edge of band dm-cu by the inward expansion of a hyaline area in cell m (Figure 75). Inward expansion of a second hyaline area in cell m divides the band into anterior and posterior apical bands.

In all species studied except *C. incompleta*, the apex of the wing is at least partially pigmented; in *C. incompleta*, the wing apex is hyaline. The apical band in *E. canadensis*, *P. varipennis*, *P. immaculata*, *P. superba*, and the *Euleia* species joins band r-m (at least narrowly) or is continuous with an area of pigment along the costa. It joins bands dm-cu and sc anteriorly in the *R. pomonella* group (Figure 82) and *R. zernyi*.

Assuming that a divided apical band joined to band dm-cu anteriorly and continuous with the wing margin is the pleisiomorphic condition (as in Figure 75d, f—g), the following changes may occur to produce apical bands like those observed in this study. A pleisiomorphic apical band has the distal corner of the posterior band ending well behind vein M and the distal corner of the anterior band ending at or near the apex of M (e.g., Figure 78). Loss of the posterior band results in an apical band that is undivided and continuous with the wing margin (e.g., Figures 77, 79). Several species (e.g., *R. nova* and *R. psalida* groups, *R. magniterebra* and *Eu. uncinata*) have the posterior apical band reduced to varying degrees. Secondary division of the remaining (anterior) apical band

may result in an apical band like that in the *R. cingulata* species group (Figure 84). In these species, the distal corner of the new posterior band ends in the wing margin at or near vein M and the distal corner of the new anterior band (or spot) ends at the margin well ahead of M. It is important to keep in mind that anterior and posterior apical bands that are the result of secondary division are not homologous to the pleisiomorphic apical bands. Loss of the anterior band in a *cingulata*-like pattern would result in a hyaline area between the posterior band and wing margin (Figure 82). The resulting apical band would be like that of *C. schineri*, *C. vesuviana*, *Goniglossum wiedemanni*, *Myiopardalis pardalina*, and several *Rhagoletis* species.

Bush (1966) suggested that the wing pattern of *R. ribicola*, which has an undivided apical band separated from the wing margin by a hyaline area, could be derived by loss of the anterior apical band from a *cingulata*-like pattern. Bush (1966) also suggested that the pattern of *R. berberis* could be derived by loss of the posterior apical band of a *cingulata*-like pattern. However, the single, undivided apical band of *R. berberis* is continuous with the wing margin and its distal corner is at or near the apex of vein M. If derived from a *cingulata*-like pattern, the distal corner of the band would be well ahead of vein M and at least a small hyaline area would lie between the band and wing margin in cell r_1 and r_{3+4}. A simpler explanation of the pattern of *R. berberis* is that the posterior band has been lost from a pleisiotypic apical band as described above.

Foote et al. (1993) refer to any single undivided apical band as the anterior apical band, whether it is continuous with the costa or separated by a hyaline area, and without regard to precisely where it ends in the wing margin. The posterior apical band is defined by Foote et al. (1993) as originating on either the "subapical" band (=band dm-cu, Table 2) or the "discal" band (=distal subcostal band) and ending on or between the tip of veins CuA_1 and M. They consider the apical band of the *R. cingulata* group to be divided, presumably secondarily so.

The apical band of some species of walnut-infesting *Rhagoletis* (*R. boycei*, *R.*

juglandis, *R. ramosae*, *R. zoqui*) provides yet another modification. In these flies, streaks of pigment lay along or between veins R_{4+5} and M (Figure 83). Because apical bands typically cross the radial and medial veins obliquely, these streaks are likely novel marks rather than a result of the reduction of pre-existing bands.

Figure 90 provides an example of a transformation series showing changes in wing patterns of *Rhagoletis*. The pleisiotypic pattern (Figure 90a) has all wing bands observed in the genus and is represented by species like those in the *ferruginea* species group. Loss of band r-m results in the pattern found in the *striatella* group (Figure 90b), while loss of the posterior apical band results in patterns like that in several Eurasian species (e.g., *R. berberidis*, *R. cerasi* [Figure 90c], *R. caucasica*). Loss of both bands (Figure 90d) is seen in species such as those in the *suavis* group, *R. berberis*, *R. emiliae*, *R. flavicincta*, and *R. reducta*. Secondary division of the apical band results in a *cingulata* group pattern (Figure 90e—f). Loss of the anterior arm of the apical band in the *cingulata* group produces patterns like those in the *tabellaria* group (Figure 90g), *R. batava*, *R. flavigenualis*, *R. mongolica*, and *R. ribicola*. Fusion of the distal three bands in the anterior half of the wing produces the *pomonella* group pattern (Figure 90h). Within the series additional modifications may alter patterns. For example, fusion of the humeral and subcostal bands posteriorly in the *pomonella* group (Figures 82, 90h) and some *tabellaria*-like patterns (Figure 90g).

It is one thing to arrange wing patterns into plausible transformation series, but it is quite another to assert that such evolution has occurred in nature. After all, hypothesis testing, not judging plausibility, is the task of science. In order to test hypotheses of character evolution systematists require hypotheses of phylogeny. It is the interplay between these two types of hypotheses that determines the veracity of each. It now appears that *Rhagoletis* is not monophyletic, and not all monophyletic groups in this assemblage have been identified (McPheron and Han, submitted; Smith and Bush, in review; Chapter 3 herein). However, portions of the above transformation series

pertinent to established monophyletic groups could be used to test relationships within and between those groups.

Mechanisms of Wing Pattern Formation

The mechanisms of wing pattern formation in tephritid flies is unknown, but some inferences may be made from observations of adult wings. In order to discuss pattern formation, however, it is necessary to have in mind some general features of wing development and models for pattern formation in animals. Therefore, a brief summary of each is given below. Because details of wing development in tephritid flies sufficient for studying pattern formation have not been reported, the wing development of *Drosophila melanogaster* has been summarized; the summary is based on the works of Waddington (1941), Bainbridge and Bownes (1981) and Johnson and Milner (1987).

Wings develop from imaginal discs. Many of the structures of the wing, including dorsal and ventral surfaces, sensilla, basal sclerites, and some veins, are determined in the imaginal disc (Campuzano and Modolell, 1992, figure 1). The dorsal and ventral surfaces of the wing each develop as a two-dimensional cellular monolayer of epidermis. Basement membranes of the wing surfaces are fused except where blood lacunae form. Lacunae run longitudinally through the disc and around its margin, and provide the only means by which material enters and leaves the developing wing. Tracheae invade lacunae during the prepupal period and form the primary venation of the wing. Evagination of the disc occurs during the prepupal stage. Shortly after evagination and onset of the pupal stage, the wing epidermis undergoes a period of rapid growth by cell division. Near the middle of the pupal period, secondary tracheae that will form the adult wing veins replace the primary tracheae. A second period of growth occurs at about the middle of the pupal stage and as a result the wing becomes pleated and folded upon itself. The wing expands by enlargement of epidermal cells during this second period of growth. Chitin is deposited during the last half of the pupal period. After emergence, wing

epidermis degenerates leaving only the nonliving cuticle, and the wing expands to its adult form. The pupal period of *D. melanogaster* lasts about 93—105 h at 26° C.

Current models of pattern formation propose that cells destined to produce integumental pigment are determined by a prepattern formed early in development (Bard, 1977; Murray, 1981, 1988; Nijhout, 1985, 1991). Prepatterns are the result of reaction-diffusion systems that generate stable patterns of activators and inhibitors of varying concentrations in the developing integument (Murray, 1981, 1988; Meinhardt, 1982; Nijhout, 1985, 1991; Pool, 1991; see also Lengyel and Epstein, 1991). Timing and the geometry and scale of the integument where chemical interactions occur strongly influence prepatterns (Murray, 1981, 1988). Once established, prepatterns may be modified by allometric growth of the integument; however, the characteristic pattern of a species is to a large extent determined by the prepattern (Bard, 1977; Murray, 1981, 1988; Nijhout, 1991). Patterns become visible when pigment is produced in cells determined by the prepattern. The amount of pigment produced by cells, and therefore the intensity of pigmentation, is determined by the interaction of pigment-inducing morphogens and the prepattern.

Two observations suggest that wing patterns in tephritid flies are determined early in development. First, flies with an abnormal wing shape have the same pattern as flies with the normal wing shape (Figures 84—89). In *D. melanogaster*, shape of the adult wing emerges after the wing has undergone its final period of growth (45—60 h postpupariation) (Waddington, 1941). If the prepattern is established after wing shape is attained, then differences in shape should affect wing pattern because even small changes in the geometry of a developmental field can alter the prepattern (and thence the final pattern) (Murray, 1981, 1988).

Second, wing pattern and distribution of the three distal campaniform sensilla on vein R_{4+5} dorsally (Figure 90) are strongly correlated. In *Rhagoletis*, the distal two sensilla are situated very close to one another in species with band r-m present or with

a pleisiotypic (as described above) apical band, or both (Figure 90a—c). Species without band r-m or with a derived apical band, or both, have the middle sensillum decidedly proximal to the distal sensillum (Figure 90d—g), and in the *R. pomonella* group, the proximal two sensilla are situated very close to one another (Figure 90h). This correlation may be the result of pattern and sensilla simultaneously tracking wing growth. If so, then pattern and sensilla may be established at about the same time. Development of these sensilla has not been documented for tephritid flies, however, in *D. melanogaster*, precursor cells of the sensilla are established in the wing bud by 12 h after pupariation (Murray et al., 1984; Palka et al., 1986), which is well before expansion of the wing at around 45—60 h. Also, position of the sensilla relative to one another does not appear to be affected by wing growth after precursor cells are established (Murray et al., 1984, figures 1—2; Palka et al., 1986, figures 1—2).

These observations conform to the expectation of current models (Bard, 1977; Murray, 1981, 1988; Nijhout, 1985, 1991) that patterns are established early in ontogeny. In lepidopterans, insects for which wing pattern has been most studied, pattern determination begins in the imaginal wing discs during the last larval instar (Nijhout, 1985, 1991). It is reasonable then to suspect that wing patterns in tephritid flies are determined early in wing development, perhaps in the imaginal disc.

Allometric growth may affect the arrangement of elements in some wing patterns of tephritid flies. The closely related *R. pomonella* and *R. tabellaria* species groups (Berlocher and Bush, 1982; McPheron and Han, submitted; Smith and Bush, in review) have wing patterns that are essentially the same except for fusion of the three distal bands (sc, dm-cu, apical) in the anterior half of the wing in the *pomonella* group (Figures 82, 90h). Fusion of these bands may be the result of retarded growth in that area of the wing. Spacing of the campaniform sensilla on vein R_{4+5} (Figure 90g—h) and orientation of vein dm-cu also suggests differential growth rates occur. The proximal displacement of the anterior portion of band dm-cu in *Euleia* species (e.g.,

Figure 78) may be another example of allometric growth affecting arrangement of pattern elements.

Examples of the effect of allometry on the shape of pattern elements may be the step-like distal edge of the apical band in the *R. pomonella* group (Figure 82). Another example may be the relationship between the condition of the anterior apical band and spacing of distal sensilla on vein R_{4+5} in the *R. cingulata* species group (Figure 90e—f). The anterior apical band is usually broken in *R. cingulata* but complete in *R. indifferens*, *R. chionanthi* (Figure 84), and *R. osmanthi* (Bush, 1966, table 8; Foote et al., 1993). The ratio of the distance between the distal two sensilla to the distance between the distal most sensillum and apex of vein R_{4+5} of 16 flies (8 ♂♂ and 8 ♀♀) each of *R. cingulata* and *R. indifferens* was very significantly different (arcsine [(A/B) - 1] transformation; d.f. = 1, $F = 22.87$; $p = 0.00004$) (Microsoft EXCEL, 1992—1993, single factor ANOVA). Condition of the apical band is not determined solely by allometric proportions, however, as 4 specimens of *cingulata* had the band complete and 2 of the *indifferens* had the band broken (Figure 91).

Wing patterns of insects have been studied in greatest detail for Lepidoptera, and the excellent work of Nijhout (e.g., 1985, 1991) and his coworkers provides a valuable paradigm for the study of wing patterns in fruit flies. There are, however, distinct differences in the wing patterns of lepidopterans and tephritid flies. A fundamental difference is wing morphology and location of pigment. Pigment of the wings of lepidopterans is found exclusively in the wing scales—modified macrochaetae covering the external surface of the wing (Nijhout, 1985, 1991). Macrochaetae are absent from the wings of tephritid flies except as setae or campaniform sensilla on some anterior wing veins; the wing membrane is bare or covered with microtrichia—acellular superficial outgrowths of the integument (McAlpine, 1981a). Microtrichia may contribute somewhat to the color pattern, as for example the whitish apical spot of euphrantines and the white apical crescent of *Eutreta* species (see Foote et al., 1993),

or as general infuscation of the wing membrane (e.g., *R. alternata* species group). Microtrichia may also produce structural colors. Munro (1947) described "shining silvery spots or areas" that he termed "argents" on the wings of a number of African tephritid flies. He reported that argents are caused by "greatly attenuated and colourless" microtrichia. Nevertheless, the vast majority of color making up tephritid patterns lies within the wing, not in surface structures as in Lepidoptera. In some species, it appears that pigment is laminated between hyaline upper and lower wing surfaces, rather than the cuticle itself being pigmented. This is especially so for the proximal streaks and spots in the wings of species of *Ceratitis*. Because pigment is a product of the epidermal cells of a wing, the laminated appearance may be explained as pigment left between hyaline cuticle after epidermal cells degenerate. Debris from epidermal cells has been reported between the wing surfaces in *Drosophila* (Johnson and Milner, 1987, figure 4f).

Another essential difference between Lepidoptera and tephritid flies is the form of the patterns themselves. In lepidopterans, two distinct systems combine to form wing patterns: a system of discrete pattern elements is superimposed on a second system that forms a background pattern (Nijhout, 1991). Pattern elements develop along the midline of wing cells (in the venational sense) and veins act as boundaries to the elements (Nijhout, 1985, 1991). Pattern elements in wing cells on either side of vein M_3, which approximates the boundary between the anterior and posterior developmental compartments of *Drosophila*, are often different (Nijhout, 1991). Wing cells are serially homologous with respect to wing pattern, and pattern elements within each cell develop and evolve independently of those in other cells and the background pattern (Nijhout, 1991). Different areas of the background pattern may evolve independently and there is no correspondence between background and wing structures, such as veins (Nijhout, 1991). Also, overall patterns on upper and lower surfaces of a wing are often different.

The patterns of tephritid flies generally are simpler than those of lepidopterans. It appears that the patterns of fruit flies are formed by a single system similar to the background pattern of Lepidoptera. Pigment is deposited on an essentially colorless field without additional elements superimposed on the pigmented areas, and patterns are identical on upper and lower wing surfaces. The roles of wing cells and veins are unclear, but it does not appear that they necessarily influence pattern. An exception may be the truncated form of band r-m which may run to vein R_{4+5}, but was never seen to cross that vein. The wing margin does, however, seem to be involved in organizing patterns. In numerous species there is a series of hyaline spots running around the margin. Fusion and expansion of these spots appear to be responsible for many of the differences observed in patterns. Interestingly, nearly 80 years ago Van Bemmelen (1917) suggested that banded wing patterns in some Diptera may be derived by expansion and coalescence of marginal spots like those found in tephritid flies with irrorate wing patterns. Unlike lepidopterans, the wing patterns of tephritid flies are not visibly disrupted across the anterior-posterior developmental boundary, which lies between veins R_{4+5} and M in *Drosophila* (Garcia-Bellido et al., 1979). Also, the wing cells of tephritid flies do not appear to be serially homologous with respect to wing pattern. However, as in Lepidoptera, it appears that portions of tephritid wing patterns evolve independently. In South American *Rhagoletis*, for example, (see Foote, 1981; Frias et al., 1987) the anterior apical band may be lost to varying degrees without affecting the presence of the posterior apical band and vice versa.

The model presented here stabilizes wing band nomenclature, and provides a framework for constructing transformation series of wing patterns for phylogenetic analysis. The model will not fit all tephritid fly wing patterns nor is it intended to do so. It is hoped that interest will be stimulated for systematically sorting out the remarkable variation in fruit fly wing patterns. An essential step in this process will be delineating a ground plan pattern. Van Bemmelen (1917) suspected that a ground plan exists for

the color patterns of dipteran wings, but empirical study is needed to evaluate his rather vague conclusions. Information on the development of tephritid wings and wing patterns is also needed; modern molecular techniques will be invaluable in this regard. The coplanar nature of wings and their distinctive landmarks (veins) should facilitate morphometric analysis. The wing patterns of tephritid flies should provide an ideal system for studying pattern formation in animals; perhaps this intriguing problem will not be left to smolder for another 80 years.

CHAPTER 3

PHYLOGENETIC ANALYSIS OF *RHAGOLETIS* AND RELATED GENERA (DIPTERA: TEPHRITIDAE)

"...the search for lost things is hindered by routine habits and that is why it is so difficult to find them." — Márquez (1991)

Hypotheses of phylogenetic relationships among organisms provide the basis for much of comparative biology (Kluge and Wolf, 1993). Phylogenies are especially important to studies of evolution because they provide a historical framework from which to ask questions and direct research (Miles and Dunham, 1993).

Active interest in evolutionary studies of *Rhagoletis* (e.g., Berlocher et al., 1993) underscores the need for a phylogeny of the genus. Norrbom (1989) placed *Rhagoletis* in his subtribe Carpomyina, stating that the "monophyly of the genus has not been demonstrated and its relationships to other Carpomyina are poorly understood" (see also Foote et al., 1993; Norrbom, 1994). Phylogenetic analyses of Nearctic *Rhagoletis* species have been reported by Berlocher (1981) (morphology and allozymes), Berlocher and Bush (1982) (allozymes), Ming (1996) (ribosomal DNA), McPheron and Han (submitted) and Smith and Bush (in review) (mitochondrial DNA). There has been no phylogenetic analysis of the genus on a worldwide basis to date.

A problem in constructing a phylogeny for *Rhagoletis* has been the choice of an outgroup. Because supergeneric classifications of the Tephritidae (e.g., Hering, 1947; Hardy, 1973; Hancock, 1986; Foote et al., 1993) are untested intuition-based hypotheses, little can be said with confidence about the evolution of major groups within the family. Foote et al. (1993) stated that one reason relationships are poorly resolved for higher taxa is that homoplasy is common in the morphological characters used to

construct classifications. However, their conclusion is largely anecdotal because the critical character and cladistic analyses necessary to establish family-wide homoplasy have not been carried out.

The purpose of this study was to 1) conduct a detailed analysis of the morphology of *Rhagoletis* and related genera; 2) test the monophyly of *Rhagoletis*; and 3) identify an outgroup for use in subsequent analyses of intrageneric relationships.

Materials and Methods

> *"...[systematists] devote very little effort, in most cases no effort whatever, to the* methods *by which characters are recognized or defined." (emphasis in original)* — Neff (1986)

Morphological terminology follows that of McAlpine (1981a) unless otherwise noted. The term species is used herein for the nominal taxa normally dealt with by taxonomists and represented by museum specimens; it was from these specimens that morphological data were obtained. I follow the supergeneric classification of Foote et al. (1993), summarized in Table 3.

Species examined and their distribution and larval hosts are given in Table 4. Two undescribed species, *Rhagoletis "florida"* and *Rhagoletis* nr. *tabellaria* (Table 4), also were included. Whenever possible specimens for study were selected from throughout their species' range. If available, specimens used to study genitalia were in addition to those used for other structures because removing genitalia often destroys characters on other portions of the abdomen (see Chapter 1 for details on preparing genitalia for study). Light (stereo and compound) and scanning electron microscopes were used to examine specimens (see Chapter 1 for details on scanning electron microscopy).

Character Analysis. A list of morphological structures was compiled from McAlpine (1981a), and a preliminary list of qualitative attributes was generated by screening these structures in one to several specimens of each species. Attributes that appeared to vary discretely were retained for further analysis while those that were invariable or

appeared to vary continuously were omitted. This initial, cursory survey was necessary because of the large number of species and attributes examined. Variation of each attribute was then partitioned into provisional states, and the attributes were scored for 1—27 specimens of each species (Table 1). Distribution of states within and between species was summarized, and attributes with more than one state for a given species were re-evaluated. Re-evaluation consisted of re-examining the study specimens and, if necessary, redefining the attribute, its states, or both. After re-evaluation, attributes were retained if their states were found to be discrete even though coextensive within a species. These attributes were the characters used in the cladistic analysis. If an attribute could not be objectively parsed into discrete states or was found to vary continuously it was eliminated from the study.

Cladistic Analysis. The data set was analyzed with PAUP 3.1.1 (Swofford, 1993) on a Power Macintosh® 7100/66 personal computer with 10,000K RAM allocated to the software. Redundant taxa (Table 5) and characters occurring in single species (Table 6) were removed to increase search speed (but see Yeates, 1992). Species represented by a single specimen also were excluded because of the large number of genital characters (27 male, 15 female) that would have to be coded as missing. All characters were unordered and only missing characters were coded as "?." The effect of polymorphisms was tested by searching on the data set with polymorphic characters included and removed.

Multiple searches were performed using starting trees generated with random and simple addition sequences and Tree-Bisection-Reconnection branch rearranging (Maddison, 1991; Maddison et al., 1992). Random addition searches performed 1,000 replicates with no more than 2 or 3 trees saved during each replicate (Maddison et al., 1992). Searches were allowed to run to completion or were aborted when there was insufficient computer memory to store new trees or the search became excessively slow. MacClade 3.0 (Maddison and Maddison, 1992) was subsequently used to trace character

evolution.

The monophyly of *Rhagoletis* was evaluated by filtering all minimal length trees with a user-defined constraint tree where *Rhagoletis* was monophyletic. To identify an outgroup for *Rhagoletis*, 37 species in 16 genera from the Trypetini were included in the analysis (Table 5). Trees were rooted using *Epochra canadensis* as the outgroup because it is from the Euphrantini (Table 3), a tribe considered to be primitive to the Trypetini (Hering, 1947; Hardy, 1973; Foote et al., 1993).

Results and Discussion

> *"A hypothesis, after all, is no better than the evidence that supports it, and hypotheses without evidence are mere wishful thinking."* — Barber (1994)

Character Analysis

A total of 101 species and 879 specimens were included in this study (Table 1). One-hundred and sixty-five morphological structures were examined, and from these 534 attributes were screened for use in the character analysis. Two-hundred and forty-seven of the attributes were analyzed for cladistic characters resulting in 91,941 recorded observations. The final data set (Table 5) included 88 species and 77 characters (Table 7), 28 of which were polymorphic for one or more species. Characters not included in the cladistic analysis are listed in Table 8. Thirteen characters were autapomorphous (Table 6).

Head (Characters 1—10, Tables 5, 7)

Antenna. A number of species have a dorsoapical point on the flagellum (Character 1). Dorsoapical points range from minute (e.g., *Euleia fratria*) to relatively large (e.g., *Rhagoletis flavigenualis*), and size usually varies within species. Most species of *Rhagoletis* have at least a small dorsoapical point, but *Rhagoletis caucasica*, *Rhagoletis kurentsovi*, and some specimens of several other species lacked a point. A dorsoapical point also occurs in some specimens of *Carpomya*, *Goniglossum*, *Haywardina*, and *Myiopardalis*.

Bush (1966) reported that the flagellum usually bears a dorsoapical point in North American *Rhagoletis*, but that some Palearctic and Neotropical species have the apex rounded. Foote (1981) also noted the tendency for some Latin American *Rhagoletis* to have the apex rounded. Berlocher (1981) scored only the pointed state for *Rhagoletis boycei*, *Rhagoletis fausta*, *Rhagoletis pomonella*, *Rhagoletis ribicola*, and *Rhagoletis tabellaria*, species that I found to be polymorphic for the character. Norrbom et al. (1988) and Norrbom (1989, 1990) considered the dorsoapical point to be a possible synapomorphy for *Rhagoletis* and related genera. Norrbom (1989) noted that a dorsoapical point occurs in *Carpomya*, *Cryptoplagia* (=*Cryptodacus*), *Haywardina*, *Myiopardalis*, *Zonosemata*, and most *Rhagoletis*. He also suggested that the point is lost in *Goniglossum*, but a minute point was seen in four of the five specimens of *Goniglossum wiedemanni* examined here. Norrbom (1994) scored *Haywardina cuculi* and *Haywardina cuculiformis* as having a "distinct dorsoapical pointed lobe" whereas I scored these species as polymorphic and without a point, respectively.

Most species examined have a microtrichiose arista (Character 2), with the microtrichia ranging from very short (e.g., *Paraterellia immaculata*) to relatively long (e.g., *Rhagoletis striatella*). Except for *Rhagoletis lycopersella*, *Rhagoletis tomatis*, and *Rhagoletis macquarti*, South American *Rhagoletis* species had the arista bare. In *R. lycopersella* and *R. tomatis*, a few microtrichia occurred in the proximal half or less of the arista. In addition to sparse proximal microtrichia, specimens of *R. macquarti* also had 1—6 microtrichia in the distal half. South American *Rhagoletis* species often have the arista sinuous, especially distally, and shiny in addition to being bare.

Facial Ridge. Comparison of the width of the facial ridge to the parafacial (Character 3) is made at the level of the ventral end of the facial suture. A narrow facial ridge commonly occurs in species that also have the facial ridge about as wide as the parafacial. The facial ridge of *Euleia* species is distinctly wider than the parafacial. The broad facial ridge in *Chetostoma curvinerve* is probably due to the extreme

enlargement of the setae on the parafacial (Character 9). In *Chetostoma californicum* and *Chetostoma rubidium*, these setae are not enlarged and the facial ridge is similar in width to the parafacial. Because of this, the broad facial ridge in *Ch. curvinerve* is not considered to be homologous to the broad facial ridge in the *Euleia* species and was scored the same as *Ch. californicum* and *Ch. rubidium*.

Chaetotaxy. Color of the genal, gular, postocellar and postocular setae (Characters 4—7) is often lighter than the color of other principal head setae in many of the species studied here. Although there is a trend for these setae to be lighter, there is also considerable intraspecific variation. One or more pair of setae may be lighter in a given specimen, and in a few cases, left and right setae vary in color. In the *Carpomya* species and *Myiopardalis pardalina*, the upper orbital and inner and outer vertical setae may also be lighter than other principal setae.

Within the Tephritidae, color of principal head setae varies from nearly white to black. Color of these setae is often used taxonomically to help separate subfamilies (e.g., Hardy, 1973, 1974; Foote, 1980), genera (e.g., Munro, 1947; Richter, 1970; Foote and Steyskal 1987), and species (e.g., White, 1988; Foote, 1981; Foote et al., 1993). Berlocher (1981) used "light" and "dark" states for postocellar, postocular, genal and gular setae. (Berlocher listed postocular setae twice [characters 25 and 31]. Based on the distribution of his states and my own observations, it is likely that he mistakenly used "postocular" for "postocellar" in character 25.)

Like Berlocher (1981), I originally recorded the color of the genal, gular, postocellar and postocular setae as "light" or "dark." Using relative color appeared to be a good strategy because absolute color may vary depending on lighting (see below). However, deciding if setae are "light" or "dark" can be quite arbitrary. In specimens of some species (e.g., *Rhagoletis alternata*), the difference in color was very slight or some setae were intermediate in color. On the other hand, frontal, orbital and vertical setae were always the darkest (except as noted above for *Carpomya* spp. and *M. pardalina*),

often black. Therefore, the color of genal, gular, postocellar and postocular setae was based on a comparison to the color of other principal setae. In this way, character states reflect whether colors are the same (concolorous) or not, without regard to the degree to which the colors differ.

It is well known among fruit fly taxonomists that the color of setae often changes with viewing angle, thus making determination of setal color imprecise. This is especially so for light colored setae. It is likely that variable setal color is due in part to the surface ultrastructure of setae. Oblique striations lying in longitudinal grooves of the setae (Figure 92—93) may reflect light differentially as the specimen is turned. Surface structure and the quality of the light reflected from these setae are very similar to that of certain scales on the wings of the moth, *Diachrysia* (=*Plusia*) *balluca* (Ghiradella, 1984, figure 6). Ghiradella (1984) reported that in *D. balluca* "patches of shiny, satiny scales...brighten and darken with movement of light." Ghiradella (1984) explained that this brightening and darkening is due to microribs that extend between longitudinal ridges in the scale so that "[t]he scale thus presents to the incoming light a series of parallel rodlets that selectively reflect or scatter light, depending on their orientation." Further evidence for a structural role in setal color comes when flies are examined in fluid preservatives such as ethanol. Under such conditions the color of setae ceases to vary, probably because of the difference in the refractive index of air and ethanol (see Nijhout, 1991, plate 2). Another source of setal color may be from pigment or some other substance in the lumen of setae. When generally lightly pigmented species like *Rhagoletis basiola* are viewed in fluid, a dark colored substance is sometimes visible in the lumen of the larger setae.

The number of frontal and orbital setae is used extensively in tephritid fly taxonomy (e.g., Hardy 1973, 1974, 1980, 1986, 1988; Foote, 1980; Foote et al., 1993; Foote and Steyskal, 1987). Bush (1966) considered three frontal and two orbital setae to be diagnostic characters for *Rhagoletis*, and Norrbom (1994) regarded

four frontal setae to be apomorphic for *Zonosemata*.

For species studied here, the most common number of frontal setae was three, but the number ranged from one to seven per side and overlapped continuously. Scores for this character by Berlocher (1981) and Norrbom (1994) reflect its polymorphic nature. Because of the high level of intraspecific variation, the number of frontal setae was not used in the cladistic analysis.

The number of orbital setae (Character 8) for most species studied was two. The upper orbital seta is absent in *E. canadensis*, two of the four specimens of *H. cuculi*, and females of the *Strauzia* species. (Contrary to Foote et al. [1993, p. 373], only male *Strauzia* lack all orbital setae.) Absence of the upper orbital seta was scored as the derived state even though it is absent in the outgroup, *E. canadensis*. This is because absence of the seta probably represents a true loss and is therefore derived (Pimentel and Riggins, 1987). In a few specimens where the number of orbitals varied from right to left sides, the most common number of setae in the species was used.

Setae on the parafacial, gena, or both, of the *Chetostoma* species were larger or more numerous, or both, than setae in these areas in other species (Character 9). Enlarged frontal setae (Character 10) occurred in only males of the species of *Strauzia* examined.

Thorax (Characters 11—20, Tables 5, 7)

Coloration. The scutum proper is uniformly yellowish, brownish to black (most species), or it has a distinct color pattern (e.g., *Carpomya schineri*, *Strauzia* spp., *Zonosemata* spp.).

Ground color of the scutum (Character 11) usually does not vary within species. In *Rhagoletis completa*, the ground color is typically yellowish, but very rarely (2/1,062 specimens examined) there are dark brown morphs. Ground color in four of the six specimens of *Rhagoletis blanchardi* examined is black; in the remaining two it is yellowish. In *Euleia heraclei*, there are both yellowish and black flies, and the color

difference is quite dramatic (see Foote, 1959, p. 149; White, 1988). In *Oedicarena latifrons*, color varies from yellowish to dark brown. Ground color is polymorphic within the *Rhagoletis suavis* and *Rhagoletis ferruginea* groups. Bush (1966) considered ground color of the thorax to be "highly variable" in *Rhagoletis*, ranging from yellow to black. Norrbom (1994) likewise commented that the thorax color is "highly variable" in the Tephritidae. The states used here for scutal ground color are essentially the same as those used by Norrbom for thoracic color (1994, character 15), and species common to each study have identical scores.

Scutal patterns are often quite distinctive. The *Carpomya*-like scutal pattern (Character 12) consists of a pair of dark postpronotal, notopleural, supra-alar, postalar, scutellar and subscutellar maculae, and a single dark interacrostical macula (see White and Elson-Harris, 1992, figures 210, 233). Extent of the maculae varies somewhat and adjacent maculae may be discrete or fused. Maculae are at least partially covered with velvety black microtrichia that may be worn off in some specimens. The interacrostical macula is divided into anterior and posterior portions in *M. pardalina* and *G. wiedemanni*; the posterior portion forms a dark spot on the disc of the scutellum. Only the subscutellar marks are present in *Carpomya incompleta*. The *Carpomya*-like scutal pattern is similar to the scutal pattern of a number of ceratitines (e.g., White and Elson-Harris, 1992, figures 208, 211).

A whitish or yellowish scutal mark occurs medially in several species (Character 12). In the *Rhagoletotrypeta* and *Zonosemata* species, the mark is a claviform stripe extending anteriorly from the prescutellar area. In *Cryptodacus tau*, *H. cuculi*, *H. cuculiformis*, *P. immaculata*, *Paraterellia varipennis* and *Paraterellia ypsilon*, the mark is a prescutellar spot or blotch. Additional light and dark markings occur in *Cr. tau*, *Rhagoletotrypeta pastranai*, and the *Haywardina* and *Zonosemata* species. Norrbom (1994) hypothesized that the four carpomine genera with a scutal white spot (i.e., *Cryptodacus*, *Haywardina*, *Rhagoletotrypeta*, and *Zonosemata*) form a monophyletic

group, but results of his analysis indicated that the group is paraphyletic.

A few species have dark scutal marks or stripes that are intraspecifically variable. Specimens of the *R. ferruginea* group have three or five dark scutal stripes extending forward from the prescutellar area: one medially, a pair sublaterally, and in some specimens, a pair laterally. The stripes vary in width and may be fused anteriorly or posteriorly or both. A single specimen of *R. pomonella* from Mil Cumbres, Michoacan, Mexico also had scutal stripes.

One or more of the following scutal marks are usually present in the *Strauzia* species: a medial pair of dark maculae extending posteriorly from the pronotum to the level of the postpronotal setae or a little beyond; a pair of sublateral dark maculae extending from the level of the presutural supra-alar seta anteriorly to about the level of the posterior extent of the anterior medial maculae; a pair of sublateral dark stripes extending anteriorly from the level of the intra-alar setae to the transverse suture; and a pair of lateral dark stripes extending anteriorly from the level of the postalar setae to the transverse suture and passing over the postsutural supra-alar setae (see Steyskal, 1986, figure 8; Stoltzfus, 1988, figure 16). All marks were present in the *Strauzia intermedia* specimens examined. Some specimens of *Strauzia longipennis* had all maculae except the lateral most stripes, while others had only the anterior-most maculae. In *Strauzia perfecta*, only the anterior-most maculae were present, but in some specimens even these were absent.

Specimens of *Oedicarena beameri*, *O. latifrons*, and *Oedicarena nigra* have a dark central spot occupying a variable portion of the scutum. The spot is contained within the area circumscribed by the presutural supra-alar and intra-alar setae in the specimen of *O. beameri*, while in the other two species the spot occupies essentially the entire scutum.

Coloration of other portions of the thorax have been used extensively in taxonomy and to infer relationships and thus warrant discussion here. The postpronotal lobe in

most species is lighter (whitish or yellowish) than the ground color of the scutum. In a few species (e.g., *Ch. rubidium*, *Myoleja lucida*, and the *Rhagoletis psalida* group), the lobe is concolorous with the scutum. Norrbom (1994) used the states "mostly or entirely white" and "mostly or entirely brown" for the postpronotal lobe.

The scutellum is uniformly pigmented and concolorous with the scutum (e.g., *Chetostoma* spp.) or uniformly pigmented and lighter (whitish or yellowish) than the scutum (most *Rhagoletis* spp.), or has a color pattern. Scutellar patterns range from a simple, dark central spot (sometimes vague) in *E. canadensis* to relatively elaborate patterns with light and dark elements, as in *C. schineri*. Bush (1966) and Foote (1981) use coloration of the scutellum throughout their taxonomies of *Rhagoletis*. Norrbom (1994) considered a generally white scutellum to be pleisiomorphic in his analysis of *Cryptodacus*, *Haywardina*, and *Rhagoletotrypeta*.

A whitish or yellowish pleural stripe runs from the postpronotal lobe to the wing base in most species. The stripe usually includes the postpronotal lobe, a variable amount (usually 1/5—1/3) of the upper portion of the proepimeron and anepisternum, a small sclerite (=paratergite?) above the anepisternum, and the pleural wing process including the greater ampulla. In *Cr. tau*, the stripe is interrupted by a dark brown wedge-shaped mark extending from the proepimeron and anepisternum, and is continuous with the transverse suture and anepisternal cleft. Bush (1966) considered a pleural stripe as one of several diagnostic characters for *Rhagoletis*. The pleural stripe in *Oedicarena* species may be indistinct or absent, especially in *persuasa* and *tetanops* (Norrbom et al., 1988; Foote et al., 1993). Color of thoracic pleura is sexually dimorphic in *R. completa*, *Rhagoletis ramosae* and *Rhagoletis zoqui* (see Bush [1966] and Hernández-Ortiz [1985] for descriptions).

A whitish or yellowish band occurs dorsally on the katepisternum of specimens of *C. schineri*, *Cr. tau*, *G. wiedemanni*, and the *Haywardina* and *Zonosemata* species. Presence of the band was ambiguous in *C. incompleta*, *Carpomya vesuviana*, *M. pardalina*, *P.*

varipennis, *S. intermedia*, and the *Euleia* species. Except for *Eu. heraclei*, a dorsal band is most apparent in species with relatively more pigmentation on the lower portion or disc of the katepisternum. In lightly pigmented color morphs of *Eu. heraclei*, a faint band is present, especially anteriorly, while in the melanic forms the band is absent. This character was not used in the cladistic analysis because of the difficulty in scoring it. Presence of a dorsal white area on the katepisternum was included in Norrbom's (1994) analysis of Latin American carpomyines.

Although determining the color of the postpronotal lobe scutellum, and pleuron is usually simple in darkly pigmented flies (e.g., most *Rhagoletis* spp.), the color in lightly pigmented species can be ambiguous. This may be due to little contrast between the color of these areas and ground color of the thorax, preservation artifacts (decomposition of subcuticular structures—see below), or both. For example, the postpronotal lobe, scutellum, and pleural stripe were lighter than the yellowish ground color of live specimens of *Eu. fratria* and *R. basiola*, but there was usually no difference in the color of these areas in pinned specimens. Another factor affecting color is the method of killing specimens. Specimens killed by freezing often have these areas grayish or brownish, whereas specimens killed by chemical agents or preserved in fluid usually retain the natural color of the areas.

Coloration of the thorax may be the result of cuticular pigments, subcuticular structures, or both. Brownish to black elements of scutal patterns appear to be due to cuticular pigments, and in some instances may be associated with areas of muscle attachment. For example, the dark medial presutural marks in the *Strauzia* species are at the approximate position of the anterior insertion of the dorsal longitudinal flight muscles. Sites of muscle attachment may provide convenient landmarks for homologizing maculae. Other dark markings, such as the stripes in the *R. ferruginea* group, simply appear to be melanized portions of the integument.

Color of the whitish or yellowish pattern elements may be due to subcuticular

structures seen through the integument. Scutal cuticle is nearly colorless in newly emerged adults of *R. pomonella*, and whitish membranous structures are clearly visible through the integument of the postpronotal lobe and scutellum and in the area of the pleural stripe. The structures initially look like collapsed sacs, but within about a day they enlarge and become closely appressed to the inner surface of the integument. As the black ground color of the thorax develops, the cuticle of the postpronotal lobe, scutellum and pleural stripe remains nearly colorless. These subcuticular structures form a soft amorphous mass in specimens preserved in FAA. In pinned specimens treated with NaOH, the integument of the postpronotal lobes, scutellum, and pleural stripe rapidly loses its whitish color while the remainder of the thorax remains darkly pigmented. The yellowish dorsal band on the katepisternum of several species (e.g., *C. schineri*, *H. cuculi*, and the *Zonosemata* spp.) and the yellowish or whitish elements of the more elaborate scutal patterns (e.g., the *Carpomya*-like pattern, *Cr. tau*, and the *Zonosemata* spp.) also may be due to the visibility of subcuticular structures.

Munro (1984) discussed at length yellow areas of the thorax of dacines that he termed "xanthines." My observations above are very similar to those reported by Munro (1984). According to Munro, the xanthines of dacines may be discolored by preservation and become similar in color to the adjacent integument. Further, he reported essentially the same results that I obtained for specimens treated with caustic (potash) and specimens preserved in fluid (alcohol).

What are the subcuticular structures that lend whitish and yellowish colors to thoracic patterns? Adult Muscamorpha are characterized as having well developed tracheal air sacs in the thorax, head, and abdomen (McAlpine, 1989). In *Drosophila*, air sacs in newly emerged flies are collapsed, but within 24 h after emergence they expand to occupy a large portion of the body cavity (Wigglesworth, 1963). Within the thorax of *Drosophila*, air sacs occur in the postpronotal lobe, scutellum, and along the pleuron (Wigglesworth, 1950)—the precise locations where the subcuticular

structures in trypetines are visible. The internal surface of air sacs is hydrophobic and the taenidia are often reduced (Nation, 1985). Microscopic examination of the subcuticular structure removed from the scutellum of an anesthetized *R. pomonella* showed the structure to be a delicate hydrophobic membrane studded with small granular objects. Circumstantial evidence suggests that the subcuticular structures seen through the integument of tephritid flies are air sacs, but further study is clearly needed.

Vestiture. Scutal setulae vary from dark brown or black to yellowish or white. In a number of species that possess microtrichiose stripes, scutal setulae are a mixture of whitish and brownish or black setulae (Character 14), with the whitish ones mostly associated with the microtrichiose stripes. However, in the *Zonosemata* species (except *Zonosemata vidrapennis*), and *Cr. tau*, species without microtrichiose stripes, color of scutal setulae correspond, at least in part, to the yellowish, or brownish to black color of the integument from where they arise. In species with predominantly light colored setulae (e.g., *R. suavis* and *R. tabellaria* groups), the peripheral setulae are often darker than the discal ones. In *R. pomonella* and *Zonosemata vittigera*, there were specimens with uniformly dark setulae and specimens with a mixture of light and dark setulae; these were the only instances of intraspecific variation. The precise distribution of light and dark scutal setulae in species with the mixed state suggests that the state is not homologous among species. Bush (1966) and Foote (1981) make extensive use of patterns formed by scutal setulae in the taxonomy of *Rhagoletis*.

The *Oedicarena* species are peculiar in having bare spots at the inner ends of the transverse suture and base of dorsocentral setae (Character 20). Norrbom et al. (1988) considered this character to be a synapomorphy for *Oedicarena*. They also reported that, within the Tephritidae, these bare spots are unique to *Oedicarena*. However, *Orellia falcata* has bare spots in the same locations as *Oedicarena*, and setulae, microtrichia, or both, are reduced or absent in one or both of these locations in other terelliines and ceratitines.

Setulae on the postpronotal lobe are uniformly colored or a mixture of whitish and brownish or black setae. Both conditions occurred in 17% (17/101) of the species examined. The character was not used in the cladistic analysis because it was sometimes difficult to judge the color of the setulae (see discussion of setal color in section on head characters above). Berlocher (1981, character 44) divided color of postpronotal setulae into only dark and only light states, but I observed mixed setulae in eight of the species common to his and my studies.

Microtrichia are distributed over the entire scutum or limited to its periphery (Character 13). When only peripheral microtrichia are present, they are relatively small and difficult to see. When discal microtrichia are present, they, as well as peripheral microtrichia, are easily observed. When viewed from behind at a low angle, scutal microtrichia are uniformly distributed or form stripes. There are five faint stripes in *E. canadensis*: one medially, a pair sublaterally, and a pair laterally. In the other species, the medial stripe is absent and only the sublateral and lateral stripes are present. Further, the dorsocentral seta lies within the sublateral stripe in *E. canadensis*, but in other species the dorsocentral lies between the sublateral and lateral stripes. Stripes may be free or fused anteriorly, posteriorly, or both; sublateral and lateral stripes are separated by only a narrow line in *R. striatella*. In *R. pomonella*, microtrichia from stripes are bent near their base and somewhat dilated, while interstripe microtrichia are straight and more or less evenly tapered (Figures 94—95)

Microtrichiose stripes are used extensively in descriptions and identification of *Rhagoletis* species (e.g., Bush, 1966; Foote, 1981). Berlocher (1981, character 49) referred to scutal microtrichia as being "complete," "partial," or "absent." From the distribution of these states in Berlocher's data matrix, he evidently was referring to the presence or absence of microtrichia, and whether they are uniformly distributed ("complete") or occur in stripes ("partial"). Norrbom (1994) divided the character into microtrichia absent, microtrichia evenly distributed, two states with microtrichia

forming stripes, and one state with stripes and bare areas.

Although scutal microtrichia is a distinctive feature of a number of species, it is not a suitable cladistic character for species studied here for at least two reasons. First, presence of a medial stripe only in *E. canadensis* and the position of sublateral and lateral stripes relative to the dorsocentral seta suggest that different patterning systems operate to form scutal stripes (see discussion of tergal pattern systems in section on abdominal characters below). Thus, stripes of *E. canadensis* may not be homologous with stripes of the remaining species. Second, the absence of microtrichiose stripes in species with microtrichia that do not form stripes is not equivalent to the absence of microtrichiose stripes in species without discal microtrichia. This is actually an amalgam of states from two characters: 1) Presence or absence of microtrichia, and 2) the arrangement of microtrichia (stripes or no stripes). Because absence of microtrichiose stripes depends on the presence of microtrichia, the character is valid only for the subset of species that have discal microtrichia.

As noted above, species with the *Carpomya*-like scutal pattern have black, velvety microtrichia on the dark pattern elements. This type of microtrichia is found elsewhere only in the *R. psalida* group where it occurs only on the supra-alar area (Character 15). Homology of the velvety microtrichia in the two groups is uncertain. If the microtrichia are considered an integral part of the *Carpomya*-like pattern, then it arose independently in the *R. psalida* group. If the microtrichia evolve independent of scutal pattern then it could be retained on the supra-alar area and lost elsewhere.

Vestiture of the mediotergite (Character 16) varies from sparse, simple microtrichia occurring only laterally (e.g., *G. wiedemanni*, *R. basiola*, *R. psalida*), to moderately dense, simple microtrichia covering the entire sclerite (most species), or dense pollenose microtrichia throughout (*Carpomya* spp. and *M. pardalina*).. Berlocher (1981) refers to the "Polinosity [sic] on the postscutellum" (=mediotergite + laterotergites), which he scores as present in *E. canadensis* and absent in the other

species in his analysis. The microtrichia in *E. canadensis* are simple and decidedly not like the pollenose microtrichia of *Carpomya* and *Myiopardalis*. Further, at least some microtrichia are present on the mediotergite or laterotergites of all the species common to his and my analyses.

Chaetotaxy. Position of the dorsocentral seta has traditionally been used as a key character of the Tephritidae and most, if not all, contemporary taxonomists consider its position taxonomically or phylogenetically important. Hardy (1973, 1974) and Foote (1980) used dorsocentral seta usually behind the supra-alar seta to help separate the Trypetinae (except Adramini) from the Tephritinae (in which the dorsocentral is before or near the supra-alar). Foote and Steyskal (1987) and Foote et al. (1993) used relative position of the dorsocentral to help separate trypetine and tephritine genera. Hancock (1986) and White (1988) considered the position of the dorsocentral relative to the supra-alar to be of importance in the higher classification of the family.

Berlocher (1981) divided the position of the dorsocentral seta into three states relative to the supra-alar seta: "slightly behind," "far behind," and "ahead" of the supra-alar. Berlocher (1981) did not specify the distinction between "slightly" and "far" behind the supra-alar. Norrbom (1994) used the states dorsocentral seta closer to the level of the postalar seta, and dorsocentral seta closer to the level of the supra-alar seta.

In species examined here, position of the dorsocentral seta varies from just behind the transverse suture (e.g., *C. schineri*, *R. psalida* group) and well ahead of the level of the postsutural supra-alar seta to near the level of the acrostichal seta and well behind the postsutural supra-alar (e.g., *Zonosemata* spp.). Further, the ratio of the distance of the supra-alar seta from the transverse suture to the distance of the dorsocentral seta from the transverse suture varies continuously across species (Figure 96; the dorsocentral seta is even with the supra-alar seta when the ratio = 1, behind the supra-alar when the ratio is < 1, and anterior to the supra-alar when > 1). Although the

character may be useful in taxonomy, it is phylogenetically uninformative for species studied here.

Principal thoracic setae are of uniform color except for the scapulars and proepisternal in some species. Color of the outer scapular seta and proepisternal setae (Characters 18 and 19) varies from whitish or yellowish to dark brown or black; both are polymorphic for a number of species. Berlocher (1981; characters 41 and 48) divided color of thoracic setae into "light" and "dark" states. Factors affecting the color of thoracic setae are probably the same as those for head setae (see above).

Halter. Halteres are wholly yellowish or brownish, or with the stem yellowish and the knob dark brown or black (Character 17). Brownish halteres occur infrequently in species with yellowish ones and it is likely that the difference in color is a preservation artifact. The bicolored state is distinct from either wholly yellowish or brownish halteres, and occurred only in the *R. pomonella* species group, *O.* beameri and *O. nigra.* Bush (1966) considered halter coloration diagnostic for the *pomonella* group. Norrbom et al. (1988) scored the halter knob as "dark" (versus "light") for *O. nigra* and *O. beameri*, and stated that this character suggests a close relationship between the two species.

Wing (Characters 21—26, Tables 5, 7)

Wing Pattern. A detailed discussion of wing pattern, including the terminology used here, is given in Chapter 2.

Band r-m is present (Character 21) in about half of the species examined (e.g., Figures 76, 79—81). In *Rhagoletis cerasi*, some specimens have the band fused with band dm-cu or the apical band. Two of four specimens of *Rhagoletotrypeta rohweri* and one of three specimens of *Rhagoletotrypeta uniformis* lack band r-m. Norrbom (1994) scored the band as present in both of these species, but absent in *Rhagoletotrypeta argentinensis* and *Rhagoletotrypeta parallela.* In *R. striatella*, there is a very faint mark in cell r_1, about where band r-m should occur, but it may be due to an area of dense

microtrichia. The anterior portion of band dm-cu may be confused with band r-m in *Trypeta inaequalis*, but based on a comparison of wing patterns of North American *Trypeta* (Foote et al., 1993, figures 475—481), band r-m is absent in this species. There is a band passing over vein r-m in the *Eulia* species (Figure 78), but it is not clear that it is only band r-m. In these species, it appears that band dm-cu anterior to vein M and the proximal end of the apical bands are displaced proximally and have coalesced to form a compound band that may include band r-m. Berlocher (1981, character 13) unknowingly compared proximal band sc of *E. canadensis* with distal band sc of his other species. Norrbom (1989) stated that the "accessory costal band" (=band r-m) is present in "about half the species of Carpomyina, but rare in other Tephritidae."

The subcostal band crosses vein r-m (e.g., Figure 79) in most species examined (Character 22). It is reduced in *Trypeta fractura* and *T. inaequalis* to a pigmented area extending from cell sc into cell r_1 and a pigmented area surrounding vein r-m. A pigmented spot lying on vein CuA_1 is also sometimes present in *T. inaequalis*. The band is unbroken and well developed in *Trypeta tortile* (see Foote et al., 1993, figure 476).

A hyaline spot is enclosed in band sc within cell br (Character 24) in *Acidia cognata*, and the *Euleia* (Figure 78) and *Strauzia* species. The aberrant wing pattern of *S. longipennis* (see Steyskal, 1986, figure 2c; Foote et al., 1993, figure 413) was not included in the character analysis.

Members of the *R. pomonella* group are distinguished by having bands sc, r-m, and dm-cu fused anteriorly, and bands h and sc fused posteriorly (Bush 1966) (Character 25, Figure 82). Anterior fusion of bands also occurs in *Rhagoletis zernyi*, but bands h and sc are free posteriorly.

Wing pattern is also unique for species of the *Rhagoletis cingulata* group (Bush, 1966) (Character 26, Figure 84). Secondary division of the anterior apical band places the posterodistal corner of the anterior arm of the apical band well ahead of the

apex of vein M in these species (see Chapter 2). The anterior apical band in other species is either entire or absent.

Calypter. Hairs of the calyptral fringe (Character 23) are usually whitish in *Rhagoletis*, but in the outgroup species they are usually dark brown or blackish, at least proximally. Color of the calyptral fringe is polymorphic for five outgroup and five *Rhagoletis* species.

Venation and Chaetotaxy. The position of vein r-m and the presence of setae on vein R_{4+5} are used extensively in tephritid systematics. These characters were not included in the cladistic analysis here for the reasons given below.

Bush (1966) considered the position of r-m near the middle of vein M to be one of several diagnostic characters for *Rhagoletis*. Han et al. (1993) reported that r-m is located beyond the apical 0.40 of cell dm-cu in most genera of the Trypetini. Norrbom (1994) narrowly divided the character into two states (<0.60 and >0.63) using the ratio of the length of vein M between veins bm-cu and r-m to the length of M between veins bm-cu and dm-cu. Using Norrbom's ratio, the position of r-m in species studied here is usually near the middle of vein M (mean = 0.52;). However, position of r-m varies continuously (Figure 97) and can not be objectively divided into discrete states. The average range (0.06) for species where more than one specimen was measured overlaps the difference between Norrbom's (1994) states.

Bush (1966) regarded the "setulose" condition of vein R_{4+5} to be primitive, and stated that the condition demonstrated an affinity between the Holarctic *R. alternata* group and most Neotropical species of *Rhagoletis*. Foote (1981) reported that setae on R_{4+5} are present almost to crossvein dm-cu in most Latin American *Rhagoletis*. One or more setae occur on the dorsal surface of vein R_{4+5} beyond Rs in at least some specimens of most species examined here. Within *Rhagoletis* the number of setae on R_{4+5} varies continuously from zero to 15 setae per wing (Figure 98). Number of setae for all species studied varied continuously from zero to 24 setae per wing (Figure 99).

Eighteen (18.2%) of the species had specimens with and without setae. Therefore, the distribution of setae could not be objectively parsed into discrete states, as is required of cladistic characters (Pimentel and Riggins, 1987). Further, the range in the number of setae for many of the species (Figure 99), suggests that there is a large component of individual variation.

Although the position of vein r-m and presence or absence of setae on vein R_{4+5} may have taxonomic utility, they are of no value as cladistic characters in the species studied.

Legs (Characters 27—33, Tables 5, 7)

Coloration. Preliminary observations suggested that generally yellowish flies have wholly yellowish legs while flies that are generally brownish or black have yellowish legs with dark markings (infuscations). Specimens were initially scored as having infuscate legs if one or more legs had brownish or black markings on one or more segments (excluding the tarsus); or as having wholly yellowish legs if none of the segments had dark markings. Tarsi were scored separately because it was noticed that infuscation of distal tarsomeres varied independently of the color of the rest of the leg. Initial scores showed that leg coloration is polymorphic for a number of species and is not necessarily correlated with general body color. For example, many specimens in the *R. cingulata* group, which contains species with generally black bodies, have wholly yellowish legs. Conversely, *R. zoqui* and *R. completa* are generally yellowish but often have infuscate legs. Leg coloration also can be sexually dimorphic. Males of *R. ribicola* have wholly yellowish legs, or if dark markings occur they are limited to the coxae, while females have infuscated coxae and femora. Legs of male *R. completa*, *R. ramosae*, and *R. zoqui* often are more infuscate than females (see Bush [1966] and Hernández-Ortiz [1985] for detailed descriptions of leg coloration).

To determine if there is a pattern to leg coloration, each segment was scored for the presence or absence of infuscation (Table 9). These scores showed that there is no clear

transformation from wholly yellowish to wholly infuscate legs, despite ordering the scores by leg or by segment. Infuscation of one segment does not ensure that other segments will be infuscate. The most frequently infuscated segments are the coxae and femora, particularly the hind coxa and hind femur (Table 9). In species with one or more segments infuscated, coxae or femora were not infuscate only in the *R. ferruginea* species group, *Rh. uniformis*, and the *Zonosemata* species; in these species, one or more tibiae (but usually the hind tibia) are infuscate. Based on these observations, it was decided that the hind coxa or hind femur would be used as an indicator of coloration. Infuscation of the hind coxa and hind femur occurred with equal frequency, but, because it is sometime difficult to see the entire hind coxa, the hind femur was chosen (Character 27). Despite limiting variation to this single segment, leg coloration was still polymorphic, although less often than when all segments are taken together.

Bush (1966) used coloration of the fore coxa to differentiate *R. cingulata* and *Rhagoletis indifferens*. According to Bush (1966), the entire fore coxa is yellowish in *R. cingulata* while in *R. indifferens* the posterior surface of the fore coxa is infuscate. Two of the eight specimens of *R. indifferens* examined here lacked infuscation. Berlocher (1981, character 56) scored infuscation of the fore femur as "complete," "restricted to a thin line," or "absent." In specimens examined here, the amount infuscation of the fore femur varied continuously from none to essentially complete. I found that the fore femur in three of the species Berlocher (1981) scored with complete or restricted infuscation (*Rhagoletis cornivora*, *R. pomonella* and *R. ribicola*) were polymorphic. I also found that three species Berlocher (1981) scored as having no dark markings on the fore femur were polymorphic (*R. completa* and *Rhagoletis mendax*) or had the fore femora infuscate (*O. latifrons*). Foote (1981, table 1) showed that the amount of infuscation of femora and tibiae overlaps broadly in the *Rhagoletis nova* group.

As with other leg segments, there is considerable intraspecific variation in color of the tarsi (Character 28). One or more legs may have the distal tarsomeres infuscate,

and there is no strict correspondence between infuscation of distal tarsomeres and general body color. For example, *Rhagoletis electromorpha*, *R. tabellaria*, and *R.* nr. *tabellaria* have generally black bodies and heavily infuscated legs, but have tarsi that are wholly yellowish. On the other hand, specimens of *S. intermedia*, *P. immaculata*, and several *Rhagoletis* species that have legs and body generally yellowish, have tarsomere 4 or 5 or both dark brown. Judging color may be influenced by pubescence or a specimen's age, and is generally more of a problem with tarsomeres than other leg segments. Bush (1966) reported dark distal tarsomeres for *R. completa*, but I found the state more widely distributed among the North American species (Table 5). Foote (1981) states that the tarsi of all legs of Latin American species are yellow, but several of the species examined here had some or all specimens with dark distal tarsomeres.

Chaetotaxy. About a third of the species examined lacked a distinct posterodorsal row of setae on the mid tibia (Character 29). (A row is "distinct" if the setae forming it are definitely larger than surrounding setae. Further, the setae are often semierect, and there is often a bare, narrow strip on one or both sides of the row.) In some species (e.g., *R. fausta*, *R. cerasi*, *Rhagoletis berberidis*), the posterodorsal row of setae can be located, but the setae are questionably different from surrounding setae; such species were scored as not having the row. In other species (e.g., *A. cognata*, *Oedicarena* spp.), no posterodorsal row could distinguished.

Most species have a distinct anterodorsal row on the hind tibia (Character 30). The row is indistinct or lacking in *My. limata*, *S. intermedia*, and *T. inaequalis*, and polymorphic in *S. longipennis* and *S. perfecta*.

Enlarged setae are lacking on the mid or hind femora or both in most species examined (Character 31). In *A. cognata*, *Oedicarena persuasa*, and *Oedicarena tetanops*, enlarged setae occur on both femora only in males. Norrbom et al. (1988) scored the posteroventral and anteroventral femoral setae as "weak" for *O. persuasa* and *O. tetanops*, and considered the setae in these two species to be "no stronger than in many

other Trypetini." Both sexes of *O. latifrons* and *O. nigra* have enlarged setae on both femora. Males of *P. immaculata* have enlarged setae on the mid femur and probably also the hind femur. Setae in *Paraterellia superba*, *P. varipennis*, and *P. ypsilon* intergrade from unmodified to enlarged with a tendency for males to have slightly larger setae than females. Enlarged setae are in indefinite rows on the ventral surface of the mid and especially hind femora in *A. cognata* males. In the *Paraterellia* species, enlarged setae are on the posteroventral surface of the mid femur, and are largest in about the distal one-third. Enlarged setae are mostly confined to the posteroventral and anteroventral surfaces of the mid and hind femora of the *Oedicarena* species. Enlarged setae also occur ventrally on the fore femur of *O. beameri*, *O. latifrons*, and *O. nigra* (see Character 32 below).

Enlarged setae in the anteroventral row of the fore femur occur only in males of *My. lucida* and the *R. ferruginea* species group (Character 32). Foote (1981) noted that the "longest and heaviest" setae of the fore femur occur distally in *ferruginea* and *adusta* and medially in *blanchardi*. The enlarged ventral setae on the fore femur of *O. beameri*, *O. latifrons*, and *O. nigra* are in addition to setae in the anteroventral row, which are unmodified.

Shape. The fifth tarsomere of *R. lycopersella*, *R. tomatis*, and one of the three specimens of *Rhagoletis acuticornis* is relatively small, cylindrical, and about twice as long as its maximum dorsal width (Character 33). The fifth tarsomere in other species examined is larger, flattened, and less than twice as long as its maximum dorsal width.

Abdomen (Characters 34 —35, Tables 5, 7)

I restrict the terms tergite and sternite to subdivisions of the sclerotized plate that forms a tergum or sternum, respectively (see McAlpine, 1981a). For example, the basal abdominal tergum (syntergum 1+2) is formed by tergum 1 and tergum 2 and a suture usually can be traced where the sclerites have fused. Thus, the consolidated tergum can be divided into an anterior tergite 1 and posterior tergite 2.

Coloration. Terga are either uniformly pigmented or patterned. Uniformly pigmented terga vary from yellowish (e.g., *R. alternata* species group, *Rhagoletis meigeni*, *O. persuasa*) to brownish or black (e.g., *O. latifrons*, *R. fausta*, dark morphs of *Eu. heraclei*). Tergal patterns consist of dark, regular or irregular shaped marks on predominantly light colored terga, and dark or light colored terga with yellowish or whitish bands along the posterior margin (Figure 100). Species with maculate patterns include *E. canadensis*, the *Paraterellia* species, *S. intermedia*, and the *Zonosemata* species. The *Rhagoletotrypeta* species and most *Rhagoletis* species have terga with marginal bands; however, both maculate and banded patterns occur in *Rh. uniformis*, *R. caucasica*, *Rhagoletis chionanthi*, *R. cingulata*, *R. completa*, *R. ferruginea*, *Rhagoletis flavicincta*, *R. ramosae*, and *R. zoqui*.

The evolutionary relationship between maculate and banded patterns is not known. If wholly yellowish terga and wholly black terga represent extremes of coloration, then maculate and banded patterns may represent intermediate stages, and transformation from one extreme to the other would be by expansion or contraction of pattern elements (Figure 100). An example of intermediate forms in such a transformation can be seen in species where both maculate and banded patterns occur (e.g., see Bush, 1966, figures 49—56; 59—64).

Maculate patterns can be further divided into those with dark marks lying on the median line and those with dark marks lying laterally to the median line. The first arrangement of dark marks is here termed the *medial pattern system* and the second arrangement is termed the *sublateral pattern system* (Figure 100); both systems are symmetrical about the median line. Markings may be discrete spots on each tergum or may form part of a more extensive pattern, such as stripes running the length of the abdomen (e.g., *Cr. tau*).

Of the species included in this study, only *E. canadensis* has the medial pattern system. Out of 34 specimens of *E. canadensis* examined, the tergal pattern could be

completely discerned for 18 (unctuous substances and discoloration partially or entirely obscured the pattern in the other 16 specimens). Out of these 18, all have a dark mark on the median line of tergite 1 and tergite 2, and nine had a dark mark on the median line of one or more additional terga. There is no indication that the marks are a result of the fusion of sublateral pattern elements. Specimens of several *Rhagoletis* species (*ferruginea*, *caucasica*, *completa*, *kurentsovi*, *magniterebra*, *zoqui*, *cingulata*, *chionanthi*, *osmanthi*) have a medial dark mark on tergite 1 or tergite 2 or both, but, in some of these the mark appears to be the result of the fusion of sublateral marks. Further, a dark medial mark was observed on preabdominal terga distal to tergite 2 only in *E. canadensis*.

The sublateral pattern system occurs in the *Paraterellia* species, *S. intermedia*, and perhaps the *Zonosemata* species. In the *Zonosemata* species, the pattern is limited to a pair of lateral (not sublateral) spots on tergum 5 of males and tergum 6 of females. There is some evidence that species with lateral maculae can be derived from species with the medial pattern system or vice versa (see Aczél, 1955a, 1955b, figures 97 and 102).

Interestingly, within the Tephritidae, many tergal patterns can be grouped into one of these two systems, and there is a strong tendency for only one pattern system to occur in a subfamily. Results of a preliminary survey of the literature and specimens in the Michigan State University Entomological Museum and my personal collection are given in Figure 101 and Tables 10—11. If pattern systems are independently distributed with respect to subfamily then, on average, each subfamily will have equal numbers of species for each pattern system. However, my sample of tergal patterns differs significantly from this hypothesis (Dacinae: $\chi^2 = 113.03$, $p << 0.001$; Trypetinae: $\chi^2 = 23.15$, $p << 0.001$; Tephritinae: $\chi^2 = 47.08$, $p << 0.001$). The distinctiveness of these systems is taken as evidence that two different developmental processes are involved in determining tergal patterns. Similar processes may regulate patterns of

microtrichiose stripes on the scutum and pigmentation of the scutellum and mediotergite.

Tergal patterns were not used as cladistic characters. As discussed above, maculate patterns may be developmentally different in the medial and lateral pattern systems, and are therefore not strictly homologous. Instead of pattern, ground color of terga (Character 34) was used, but not without some difficulty (see also Norrbom et al., 1988, table 1, character 2). In *O. beameri*, *R. completa*, and *R. suavis* the distinction between brownish and yellowish terga is not always clear. In specimens of several species with patterned terga (e.g., *Rh. uniformis*, *R. flavicincta*, *R. cingulata*, *Rhagoletis osmanthi*), the proportion of light and dark pattern elements is about equal, making the choice of ground color equivocal. The most extreme case of polymorphism is in *Eu. heraclei* where specimens with wholly black and wholly yellowish terga occur (see also Foote, 1959, p. 149; White, 1988). Norrbom (1994) noted that abdominal color is "highly variable" in the Tephritidae.

Vestiture. Tergal microtrichia intergrades continuously from nearly absent, with only a small amount basolaterally on one or more terga (e.g., *E. canadensis*, *Euleia* spp., *Chetostoma* spp., *Paraterellia* spp., *Zonosemata* spp.), to densely microtrichiose (e.g., *R. flavigenualis*, *Carpomya* spp., *M. pardalina*). Setae are always present, with the largest ones occurring on the posterior margin of terga. Except for females of *E. canadensis*, setae along the posterior margin of terga grade from relatively short medially to relatively long laterally. Tergal setae of female *E. canadensis* are unusual (Table 6) because they are relatively long medially and grade into decidedly shorter setae laterally, especially those on syntergum 1+2 to tergum 4.

Excluding tergite 1, tergite 2 plus one or more terga have bands of light and dark colored setae, or the setae are uniform in color (Character 35). The large marginal setae were not scored because they are usually dark colored regardless of the color of other setae. When setae occur in bands, the proximal band is dark and the distal band is

light. Bands are sometimes limited to the central area of the terga. Setae are usually concolorous in *R. flavicincta*, *Rhagoletis juniperina*, *Zonosemata electa* and *Z. vittigera*, but specimens of each species had one or more terga with the banded state.

Male Genitalia (Characters 36—62, Tables 5, 7).

See Chapter 1 for a detailed description of male terminalia and discussion of the terminology adopted here.

Pregenital Segments. The broad, right lateral portion of sternum 7 (Figure 2) in some specimens of *R. alternata*, *R. chionanthi*, *R. indifferens*, and *R. tabellaria*, and all specimens of *R. cerasi* had polygonal surface sculpturing (Character 36); other species lack sculpturing.

Most species have one or more setae on syntergosternum 7+8 (Character 46). The character is polymorphic for *Rhagoletis berberis* and *R. cerasi* where eight of nine and two of nine specimens, respectively, have setae.

A small blister- or sac-like structure (Figure 1) occurs in the intersegmental membrane between sterna 6 and 7 in the *Rhagoletotrypeta* species and a number of *Rhagoletis* species. Norrbom (1994) described this structure as a "mostly membranous lobe" on sternum 6 and found its presence to be a synapomorphy for the *Rhagoletotrypeta annulata* group. The character was not included in the cladistic analysis here because it was ambiguous for a number of the *Rhagoletis* species.

Epandrium. In the *Oedicarena* and *Paraterellia* species, the epandrium is produced posteriorly and the angle formed by its posterior edge below the proctiger and the long axis of the surstyli is less than 90° (Character 39, Figures 9, 12). The subepandrial sclerite and the lateral sclerotized arms that attach it to the bacilliform sclerites are also shifted posteriorly. In other species (e.g., Figures 7, 16, 23, 27, 29), the epandrium is not markedly produced posteriorly and the angle formed by the epandrium and surstyli is about or more than 90°; the sclerotized arms that attach the subepandrial sclerite to the bacilliform sclerites are more or less vertical. Norrbom et al. (1988)

regarded *Oedicarena* and *Paraterellia* to be sister taxa based, in part, on the unusual shape of the epandrium and surstyli.

The epandrium has numerous evenly distributed microtrichia in most Nearctic and several Palearctic *Rhagoletis*, *Rh. pastranai* and *Rh. rohweri* (Character 45). Other species lack microtrichia or have at most a few distributed randomly. The character is polymorphic in *R. suavis* and *Rhagoletis zephyria*. This character appears to be taxonomically useful for separating *R. basiola* (which has numerous microtrichia) from its sister species *R. alternata*, and separating *R. cornivora* (which lacks dense microtrichia) from other *R. pomonella* group species.

Surstyli. Microtrichia are present at the base of the surstyli anteriorly (Character 43) in a number of *Rhagoletis* and outgroup species. The character is polymorphic in 15 of the 37 species for which it was recorded. Because of the delicate nature and location of the microtrichia, they may be easily rubbed away during copulation, and therefore some of the polymorphism may be due to scoring artifacts.

The membrane connecting the bacilliform sclerite to the surstylus (Figure 37) has microtrichia (Character 44) in all Carpomyina except *Cr. tau*. The membrane lacks microtrichia in all other species except *Ch. curvinerve*.

The tips of the surstyli have a cluster of noticeably longer setae in species of the *R. cingulata* and *R. suavis* species groups (Character 48). The setae tend to be curved in the *R. cingulata* group (Figures 19—20) and more or less straight in the *R. suavis* group. The *Chetostoma* and *Euleia* species and *R. berberis* have one or a few setae at the tip of the surstyli but not a cluster as in the *suavis* and *cingulata* groups. Bush (1966) considered the apical surstylar setae to be diagnostic only for the *R. cingulata* group. Similarly, Berlocher (1981) scored the character as present for *R. cingulata* and *R. indifferens*, but not for the *suavis* group species.

Carpomya species have relatively short, stout, proximally directed, setae on the surstyli distally (Character 49, Figure 13). Setae in this region of the surstyli are not

different from adjacent setae in all other species examined. Bush (1966) suggested that *Rhagoletis* is synonymous with *Carpomya*, but could find no "suitable" characters to distinguish the two genera. The surstylar setae described here are unique to the three species of *Carpomya* studied. However, before this character is considered a synapomorphy for the genus (see Cladistic Analysis below), the taxonomic status of *C. caucasica*, the fourth and only other *Carpomya* species listed in the current Paleartic Catalog (Foote, 1984), must be established. (V. Korneyev, [pers. comm.] has suggested that *C. caucasica* is a *nomen dubium*.)

Norrbom (1989) considered a surstylus with the posterior lobe elongated beyond the anterior lobe to be a possible synapomorphy for the Carpomyina. Norrbom et al. (1988), Norrbom (1989), and Foote et al. (1993) felt that a similar surstylar shape in *Paraterellia* indicates a relationship between it and the Carpomyina. In the species studied here, the posterior surstylar lobe varied from absent (Figures 7—8, 29—30) to relatively very long (Figures 21—22). Visual estimates indicate that across all species length of the posterior lobe beyond the anterior lobe varies continuously. Further, length of the posterior lobe is similar in species where the epandrium and surstyli are decidedly different in shape. For example, the relative length of the posterior lobe in the *Paraterellia* and *Euleia* species is similar to that of several *Rhagoletis* species, but other aspects of shape vary widely (c.f. Figures 12 and 14). As Norrbom (1989) pointed out for *Paraterellia* and carpomyines, similarity in shape of the surstylus may be due to homoplasy.

Most species have anterior and posterior surstylar lobes, but an additional medial lobe occurs in *A. cognata* and *T. inaequalis* (Character 51, Figures 28, 31). Only the anterior lobe is present in *E. canadensis* and the *Zonosemata* species (Figures 7—8, 29—30). Shape of the surstyli is very different between *E. canadensis* and the *Zonosemata* species and it seems unlikely that their anterior lobes are homologous. Norrbom (1994, character 37) stated that the anterior lobe (="mesal lobe") is absent in

Zonosemata, but noted that the rugose apex of the surstylus may be homologous to the anterior lobe. Norrbom (1994) considered absence of an anterior lobe to be apomorphic for *Zonosemata*.

Bacilliform Sclerites. In *A. cognata* and *T. inaequalis*, the inner prensiseta is on a relatively large tubercle that places it decidedly distal to the outer prensiseta (Character 54, Figure 35—36). Both prensisetae are at about the same level in most species. In *O. persuasa*, *O. tetanops* and *O. nigra*, the inner prensiseta is somewhat more distal than the outer prensiseta, but it is not on a tubercle. In *O. latifrons* and the *Paraterellia* species, the prensisetae are at about the same level, but the larger inner prensisetae gives the illusion that it is distal to the outer prensisetae (Figures 9—12).

Inner and outer prensisetae are similar in size in most species (Character 57). The *Rhagoletotrypeta* species (except *Rh. pastranai*), *R. kurentsovi*, and *R. meigeni* have the inner prensiseta smaller than the outer. The inner prensiseta is larger than the outer in *T. inaequalis* (Figure 28), and the *Myoleja*, *Oedicarena*, and *Paraterellia* species. Han et al. (1993, 1994a) considered the "reduced subapical [=outer] prensisetae" to be the synapomorphy for their *Trypeta* group. The *Trypeta* group contains eleven mostly Palearctic genera and does not include the genera *Myoleja*, *Oedicarena*, and *Paraterellia*, which also have the reduced outer prensiseta. The shape of the inner prensiseta in *Oedicarena* and *Paraterellia* is squarish instead of the usual conical shape, and both prensisetae are mostly or entirely covered by the posterior surface of the bacilliform sclerite.

A dorsal keel or ridge is present at least distally on the bacilliform sclerite of 29 of the *Rhagoletis* species (Character 42). It is usually visible in lateral view and may be erose or serrate (Figure 19). This character was identified only for *R. berberis* by Bush (1966). Presence of the dorsal surstylar keel in *R. cornivora* appears to be useful for separating it from other *R. pomonella* group species, which lack a keel.

Anterolateral lobes on the bacilliform sclerites (e.g., Figure 16) are present in all

species except those of *Oedicarena* (e.g., Figure 9), *Paraterellia* (e.g., Figure 12), and *Strauzia* (Character 58). One specimen of *O. latifrons* had a small extension of the anterolateral corners of sternum 10, but it was not a definite lobe (see also Norrbom et al., 1988).

Phallus. A basiphallic vesica occurs in *R. electromorpha*, *R. ribicola*, *R. tabellaria*, *O. latifrons*, *O. nigra*, and the *Euleia* and *Paraterellia* species (Character 37). In *P. immaculata* (Figures 42—43) and *P. ypsilon*, the vesica is covered with a scale-like pattern. Bush (1966) noted a vesica for *R. tabellaria*, but does not mention one for *R. ribicola*. A basiphallic vesica is widespread in the Tephritidae, occurring in Dacinae (Hardy, 1973, 1974; Munro 1984), Acanthonevrini (Condon and Norrbom, 1994), and Tephritinae (Freidberg and Mathis, 1986).

The subapical distiphallic lobe is either trumpet-shaped or forms an elongate lobe (Character 41). Nearctic *Chetostoma* species have an elongate lobe with large apical hooks (Figure 68) while the other non-Carpomyina species have the trumpet-shaped lobe (Figures 42—49). Species of Carpomyina have an elongate lobe that lacks the large apical hooks (Figures 50—67). The lobe is free, at least distally, except in *Zonosemata* where it is contiguous along its entire length with the parameral sheath (Character 61). The lobe may be bare (e.g., Figure 51), denticulate (e.g., Figure 42), fimbriate with (e.g., Figure 52) or without (e.g., Figure 55) a supernumerary lobe, or microtrichiose (Character 62). Microtrichia range from short and sparse (e.g., Figures 62—63) to long and dense (e.g., Figures 58—59, 70); size and abundance of microtrichia intergrades continuously among species.

Berlocher (1981) reported that an "apical appendage on [the] aedeagus" is absent in several species. However, his interpretation of the phallus is incorrect if by "apical appendage" he meant subapical lobe: a subapical distiphallic lobe is present in all of the species for which he scored its absence.

The parameral sheath of the distiphallus has polygonal sculpturing in a number

species (Character 47). Berlocher (1981) recognized this state as a "scale-like pattern" on the phallus of *E. canadensis*, and Norrbom (1993) referred to "platelike or scalelike sculpture [sic]" for this species. Han (1992) used presence of a pattern of "narrowly fusiform or oblong cells" (=polygonal sculpturing) on the "dorsal sclerite" of the distiphallus as the defining character for the Trypetini and also to help delimit the Trypetina. (See Chapter 1 for clarification of Han's "dorsal sclerite" and "median granulate sclerite.") Foote et al. (1993) reported that the presence of "minute scalelike sculpturing in two areas" of the distiphallus is characteristic of the Trypetina. Variation in markings in this area indicates that there is no qualitative difference between the sculpturing Han (1992) used to define the Trypetini (and Trypetina) and the sculpturing I observed in both Trypetini and non-Trypetini species. Further, the amount of the sculpturing is "highly variable" (Han, 1992) and ranges from "greatly reduced or absent" to extensive (Han et al., 1994b). Eleven species of Trypetinae that have polygonal sculpturing on this area of the parameral sheath, but were not included in Han's (1992) Trypetini, are: *E. canadensis* (Figures 48—49), *O. nigra*, *O. persuasa*, *O. tetanops*, the *Paraterellia* species (e.g., Figures 42—43), and the *R. ferruginea* species group (e.g., Figure 50). Further, the sculpturing may be widespread within the family (e.g., see Munro 1984, p. 10, and figures 11, 70, 76, and 91).

Han (1992) and Han et al. (1993) used presence of a "median granulate sclerite" of the distiphallus to help define the Trypetina and *Trypeta* group, respectively. Freidberg (1994) assigned *Notommoides* to the Trypetina based in part on presence of "the median granulation of the distiphallus." This denticulate area of the distiphallus occurs in *E. canadensis* (Figures 48—49), and the *Oedicarena* (e.g., Figures 44—45) and *Paraterellia* species (e.g., Figures 42—43), none of which are included in Han's (1992) Trypetina or Han et al's. (1993) *Trypeta* group. A similar denticulate area is present in *Blepharoneura* (Condon and Norrbom, 1994, figure 3).

A definite acrophallus (Character 53) is present in all Carpomyina except for the

Haywardina and *Zonosemata* species. The acrophallus occurs as two or three sclerotized troughs (Figures 51, 60, 61, 62) or a corrugated plate. In other species, the gonopores are free distally (e.g., Figures 44—45, 48—49) or there is a single large opening (e.g., Figure 68). Norrbom (1994, figure 4, character 41) described a "sinuous internal tube" for *Cr. parkeri* and *Cr. tau*, which I interpret as the acrophallus (Figure 41).

The aedeagus is usually enclosed by the parameral sheath (Character 59). Enclosure of the aedeagus depends on the extent of the appressed flap of the sheath (see Chapter 1). In *E. canadensis* (Figure 48—49), *O. latifrons* (Figure 44—45), and *P. superba*, about one-half or more of the ventral surface of the distiphallus is not covered by the flap distally, leaving the terminal portion of the aedeagus exposed. In the other species of *Oedicarena* and *Paraterellia* (e.g., (Figure 44), the distal portion of the distiphallus is not completely closed by the flap, but the aedeagus terminates well within the parameral sheath. In most species, the flap extends the entire length of the distiphallus and encloses the aedeagus (e.g., Figures 46—47, 50—69).

The basiphallus has a pair of membranous ventral keels in *Cr. tau* (Figure 41), *H. cuculi*, *O. nigra*, *O. persuasa*, *O. tetanops* and the *Paraterellia* species (Character 60). Keels are usually located on the distal half of the basiphallus, but in *Cr. tau* they occur at about midlength. The keel on the left side in the *Oedicarena* species is expanded into a flat lobe for a distance; keels are delicate and similar from side to side in the other species.

Ejaculatory Apodeme. Most species have the distal edge of the ejaculatory apodeme coplanar with the blade, but the edge is flared in *C. vesuviana*, *Eu. fratria*, *Rhagoletis adusta*, *R. ferruginea*, and *R. ribicola*, and some specimens of *C. incompleta*, *C. schineri*, *R. alternata*, and *R. striatella* (Character 38). The flared edge of the ejaculatory apodeme in *R. ribicola* is diagnostic among Nearctic *Rhagoletis* species (Bush, 1966).

Hypandrium. The intrahypandrial membrane anterior to the lateral arms of the aedeagal guide varies from unmodified, being more or less tightly stretched across the hypandrium, to forming a sac of varying depth. The hypandrial sac in the *R. suavis*

group is lined with numerous heavily sclerotized denticles (Character 40); when present in other species, it lacks denticles. Bush (1966) found the sac to be diagnostic for the *suavis* group. Berlocher (1981) listed an hypandrial sac only for *suavis* group species but it is also present in *R. striatella* (Bush 1966), which was included in his analysis. A hypandrial sac may be widely distributed within the Tephritidae (see Chapter 1).

The hypandrial apodeme is absent in the Carpomyina, *My. lucida*, *T. inaequalis*, and the *Strauzia* species (Character 50). In some specimens lacking the apodeme, the hypandrium is thickened medially, but such thickening is not a hypandrial apodeme. Norrbom et al. (1988) considered the apodeme to be pleisiomorphic in *Oedicarena* and *Paraterellia*, and noted that it is "weak or absent" in *Rhagoletis* and a number of other trypetines.

Pregonites. The right pregonite is displaced farther ventrally than the one on the left (Figures 3, 5) in all species except the *Chetostoma* species (Character 52). In *Chetostoma*, the pregonites are more or less symmetrical from side to side.

Proctiger. The hypoproct forms a single sclerotized plate on the ventral surface of the proctiger, except in species of *Oedicarena* and *Paraterellia*. In *Oedicarena* (e.g., Figures 10—11) and *Paraterellia*, the hypoproct is divided medially (Character 55). In *A. cognata* (Figure 27), the *Chetostoma*, *Euleia*, *Myoleja*, and *Strauzia* species, and *T. inaequalis* (Figure 32), the hypoproct extends dorsally for most or all of the height of the proctiger (Character 56). In other species, the hypoproct extends dorsally for less than half of the height of the proctiger.

Female Genitalia (Characters 63—77, Tables 5, 7)

Spermathecae and Spermathecal Ducts. Number of spermathecae (Character 63) and number of spermathecal ducts (Character 65) each vary from two to four. Species with two spermathecae have two or three spermathecal ducts; species with three spermathecae have three ducts; and species with four spermathecae have three or four

ducts. The number of spermathecae is usually constant for a given species. However, in some species that usually have two spermathecae and three spermathecal ducts, the distal end of the duct that is typically undifferentiated is sometimes dilated or there is a partially sclerotized, presumably nascent, spermatheca (e.g., *R. basiola*, *R. chionanthi*, *Rhagoletis batava*, *R. flavigenualis*, *R. fausta*, *R. meigeni*). Nascent spermathecae were not included in the number of spermathecae for a given species. In the *Oedicarena* species there are four spermathecae, and in *O. persuasa* and *O. tetanops* there are four spermathecal ducts. In *O. latifrons* and *O. nigra*, however, there are only three ducts, one of which is forked distally and bears two of the spermathecae. Two specimens of *R. mendax* and one of *E. canadensis* had two spermathecae attached to the end of a forked duct, similar to *O. latifrons* and *O. nigra*.

Number of spermathecae is often used to diagnose higher taxa. For example, dacines typically have two spermathecae (Hardy, 1973, 1974; Munro, 1984), trypetines have three, and tephritines two (Hancock, 1986; White, 1988). Contrary to the expectation for trypetines, fewer than half (39/88 = 44.3%) of the species examined here have three spermathecae, while slightly more than half (45/88 = 51.1%) have two. Bush (1966) used number of spermathecae and spermathecal ducts to help diagnose Nearctic species groups of *Rhagoletis*. Norrbom et al. (1988) considered the four spermathecae of *Oedicarena* to be a synapomorphy for the genus and also noted that having four spermathecae is unique within the Tephritidae. Norrbom (1989) stated that presence of three spermathecae is pleisiomorphic for the Tephritidae, and used number of spermathecae in his analysis of Latin American carpomyines (Norrbom 1994). Berlocher et al. (1993) considered three spermathecae synapomorphic in the *R. pomonella* group, but also noted that number of spermathecae in *Rhagoletis* is likely homoplasious.

Number of spermathecae and spermathecal ducts can be diagnostic at the species level. In the morphologically homogenous *R. pomonella* group, *R. cornivora* has two

spermathecae (contrary to Bush [1966] and Berlocher [1981]) and three ducts while the other species have three spermathecae and ducts. The sister species *R. alternata* and *R. basiola* have two and three ducts, respectively.

Shape of spermathecae (Character 64) varies from small and spherical (e.g., *Myoleja limata*) to long and cylindrical (e.g., *R. suavis* group). Cylindrical spermathecae are straight (e.g., *R. pomonella*) or convoluted (e.g., *R. ribicola*). In several of the species with three spermathecae, some or all specimens have one spermatheca decidedly smaller than the other two (Character 74); Bush (1966) noted this size difference for the *R. pomonella* group and *R. zoqui*. The external surface of spermathcae is smooth or has wrinkles, bumps or variously shaped papillae. Very small, delicate, and essentially colorless, capitate bodies (Ming, 1989, figures 43—44) also are present. Spermathecae may or may not have a definite neck to which the spermathecal duct attaches. An atrium is present where the duct joins the spermatheca in several of the species. Atria may be distinct, sclerotized structures, but identifying them can be quite arbitrary because the place where the duct attaches to the spermatheca is sometimes dilated, sometimes sclerotized, and sometimes sclerotized and dilated.

Spermathecal shape across all species appears to vary continuously. Shape within species usually varies to a lesser extent, but in *R. tabellaria*, spherical, pyriform, and cylindrical spermathecae were encountered. Mating and oviposition may affect spermathecal shape (White, 1988). Because of the difficulty of precisely determining shape by visual estimate, shape was arbitrarily classified into two broad categories: globular and cylindrical. A spermatheca is globular when its body is less than 3 times as long as its greatest diameter, and cylindrical when its body is more than 3 times as long as its greatest diameter. Unfortunately, this dichotomy does not capture the diversity of shapes and is probably not very phylogenetically informative. For example, spermathecae of the *Zonosemata* species are weakly sclerotized (considered synapomorphic by Norrbom [1990, 1994]), and in *Rhagoletis conversa*, *R. nova*, and

the *R. psalida* group spermathecae have a sharp bend or coil proximally. Berlocher (1981) divided spermathecal shape into "globular," "oval," and "long and cylindrical," but he did not specify the difference between globular and oval.

Spermathecal ducts are usually about as long as the abdomen, but in several species they are distinctly longer (e.g., *R. berberidis*, *R. kurentsovi*, *Rhagoletis mongolica*, *R. psalida*, *S. intermedia*, *S. perfecta*), and across all species may vary continuously. Ducts are usually membranous and distinct from the spermatheca; however, in a few species (e.g., *R. blanchardi*, *R. meigeni*, *R. juniperina*) some specimens have ducts that are sclerotized for a variable length beyond their attachment to the spermatheca. In *R. psalida*, the ducts are sclerotized for a short distance beyond the ventral receptacle. Ducts are usually colorless, but in the some Neotropical *Rhagoletis* (e.g., *R. nova* group) they are lightly pigmented. The external surface of ducts (Character 75) is almost always smooth, but it is definitely annulated in the *Zonosemata* species.

Eversible Ovipositor Sheath. In most species the eversible ovipositor sheath is subequal in length to segment 8 (Character 66). In *E. canadensis*, *O. persuasa*, and *O. tetanops*, however, the sheath is decidedly longer than segment 8.

Norrbom and Kim (1988) reported that "scales" (=denticles) are absent from the apical portion of the eversible ovipositor sheath of *Rhagoletis*. Evidently, they were referring to the large discal denticles, because minute denticles are present at the extreme apex of the sheath in *Rhagoletis*, as well as the other species examined. Denticles on the sheath just proximal to the point of its attachment to segment 8 have either a single point or multiple points (Character 68). These denticles usually are similar dorsally and ventrally, but in the *Euleia* species and *R. cingulata*, ventral denticles have single points and dorsal denticles have multiple points. In *R. ribicola* and *R. batava*, there is a mixture of single and multiple point denticles both dorsally and ventrally. This character is taxonomically useful in the *R. pomonella* species group where *R. cornivora* has denticles with single points and the other species have denticles

with multiple points (Figures 102—103). The large discal denticles on the ventral surface of the sheath usually are triangular and have a single point, but in the *Chetostoma* and *Myoleja* species they are squarish and irregular apically (Character 69). Han (1992) regarded the denticles of these genera to be a reduced form of the normal triangular-shaped teeth and a synapomorphy for his Chetostomina. The eversible ovipositor sheath usually bears only denticles, but several species have microtrichia proximally (Character 67).

The dorsal taeniae of the eversible ovipositor sheath (Steyskal, 1984; Norrbom and Kim, 1988) usually end well ahead of segment 8. In the *Chetostoma* and *Rhagoletotrypeta* species (except *pastranai*) and *My. lucida*, however, they reach segment 8 (Character 76). Longer taeniae are correlated with a laterally compressed segment 8 (see below) in the *Chetostoma* species, *My. lucida*, and *Rh. annulata*.

Segment 8. The tip of segment 8 is dorsoventrally flattened (wider than high) in most species, but in several of the outgroup species it is laterally compressed (narrower than high) (Character 71). Segment 8 is constricted at its base in several of the outgroup species (Character 70), and there is a tendency for this condition to occur in species where the tip is laterally compressed. The cloaca may be glabrous or surrounded by microtrichia, denticles, or both (Character 72; see Stoffolano and Yin [1987], figure 32).

The tip of segment 8 may bear serrations (e.g., *Strauzia* spp.), subapical points or lobes (e.g., *E. canadensis*, *R. caucasica*, *Zonosemata* spp.), or both (e.g., *G. wiedemanni*, *O. nigra*, *R. nova*). The tip is usually armed in the outgroup species, but usually bears only a single apical point in most *Rhagoletis* species (Character 73). Han (1992) used "lateral serrations toward apex" of a dorsoventrally flattened segment 8 as a synapomorphy for his Trypetina. However, these states are of questionable phylogenetic importance as both states occur in species not in Han's Trypetina (e.g., *G. wiedemanni*, *Cr. tau*, *O. nigra*). Foote et al. (1993) also used the finely serrate tip of segment 8 to

help diagnose their Trypetina. Norrbom (1994) used several attributes of the tip of segment 8 in his analysis of *Cryptodacus*, *Haywardina*, and *Rhagoletotrypeta*.

Throughout the Tephritidae, the tip of segment 8 often has points, projections, or serrations (e.g., see Hardy, 1973, 1974; Stoltzfus, 1977; White, 1988; Condon and Norrbom, 1994; Merz, 1994). Shape of the tip can vary considerably among species within higher taxa, and even within seasonal morphs of a single species (Jenkins and Turner, 1989). Selection on the shape of the tip of segment 8 may result in convergence because of its importance for placing eggs into host tissue. Evidence for convergence may be that similar shapes occur in widely divergent species. For example, shape of the tip in the dacine *Dacus deceptus* (Hardy, 1974, figure 28a) is essentially identical to that of the tephritine *Tephritis baccharis* (Jenkins and Turner, 1989, figure 13c). If tip shape is under selection, then occurrence of similar shapes in more closely related species could also be due to convergence.

The two states used here (armed and unarmed) are arbitrary and probably not very informative because of their breadth. However, accounting for all variation in shape would result in a large number of states of questionable homology. The only instance of polymorphism was in the specimens of *R. ferruginea* examined: two specimens had a single apical point and one had a pair of minute subapical points. Berlocher (1981) divided ovipositor shape into "trident shaped" tip for *E. canadensis* and "spear shaped" tip for the other species analyzed. However, Berlocher (1981) did not differentiate between the ovipositors of *O. latifrons* and *Z. electa*, which have subapical points (see Bush, 1965, figure 18; Norrbom et al., 1988, figure 6a), and species with unarmed tips.

Syntergosternum 7. Norrbom (1989, figure 6) defined the Carpomyina by the presence of a weakly sclerotized area at the apex of syntergosternum 7. The area is usually apparent in carpomyines with a darkly pigmented syntergosternum 7, but it is sometimes difficult to locate in lightly pigmented specimens. In lightly pigmented flies,

it is sometimes possible to recognize the weakly sclerotized area by using phase contrast microscopy (300x) and comparing the cuticle from areas immediately encircling the insertion of setae with areas lying between setae. The area encircling the base of a seta often forms a small sclerotized "island" that serves as a reference for comparing areas lying between setae. The weakly sclerotized area is present if the areas lying between setae are largely unsclerotized.

A weakly sclerotized area almost always occurred in species of Carpomyina examined; however, its presence was ambiguous in a number of specimens even after re-examination. Further, I was unable to identify any weakly sclerotized area in the *Zonosemata* species. Therefore the character was not included in the cladistic analysis.

Setae of syntergosternum 7 are usually unmodified, but in several species the tip has about 8-16 stout setae ventrally (Character 77).

Cladistic Analysis

> *"...in all fields of biology one needs, now and then, to ask whether current theory, however satisfying, provides a clear view of reality."* — Evans (1977)

With polymorphisms excluded from the data set, 18,691 most parsimonious reconstructions (MPRs) were generated before insufficient computer memory ended the search. These trees were 135 steps in length and, excluding uninformative characters, had a consistency index (CI) of 0.417 and retention index (RI) of 0.748. The trees are summarized by the consensus cladogram in Figure 104. When all taxa were included in the data set (Figure 105), the CI increased to 0.430 and the RI to 0.848. Reweighting the data set (Farris, 1969; Carpenter, 1988) using the rescaled consistency index (RC) of the 18,691 trees (RC = 0.322) resulted in 12,061 MPRs with a CI of 0.671 and an RI of 0.900 (Figure 106). Results from the reweighted data should be viewed with caution because iterations 2—5 of the reweighting routine could not be completed due to excessive computing time or insufficient computer memory or both. None of the 18,691 trees initially generated or the 12,061 trees from the reweighting procedure

were compatible with a user-defined constraint tree where *Rhagoletis* was placed in a monophyletic clade. A random addition search using the constraint tree produced 1,500 trees 141 steps long; with uninformative characters removed, the CI and RI of these trees were 0.399 and 0.729, respectively.

When polymorphisms were included in the data set, 13,100 MPRs (summarized in Figure 107) were found before the search was aborted because of insufficient computer memory. Length of the trees generated was 306 steps and the CI and RI were 0.281 and 0.789, respectively. None of the 13,100 trees were compatible with the constraint tree filter.

Searches with and without polymorphic characters each appear to have found a single tree island as indicated by RIs greater than 0.67 (Maddison, 1991). Although not all trees in either search were recovered, the existence of one tree island for each suggests that shorter trees will not be found with this data set.

The monophyly of *Rhagoletis* was not confirmed whether polymorphisms were included or excluded from the search, or when the data were reweighted. With polymorphisms excluded, six additional steps (135 versus 141) were needed to produce trees compatible with the constraint tree. The monophyly of *Rhagoletis* has been in question (Norrbom, 1989; Foote et al., 1991) and recent analysis of molecular data (McPheron and Han, submitted; Smith and Bush, in review) also indicates that the genus in not a natural grouping.

Intergeneric relationships have tended to be poorly resolved for tephritid flies in recent phylogenetic analyses (Norrbom, 1994; Han and McPheron, 1994; Han and McPheron, submitted; Smith and Bush, in review). In this study, carpomyines and non-carpomyines were placed in separate clades in all searches. Intergeneric relationships within each clade were largely unresolved when polymorphisms were excluded (Figure 104) and only slightly more resolved when polymorphisms were included (Figure 107) or the data were reweighted (Figure 106). In all cases, monophyly of the carpomyines

was supported by a single character: presence of an elongate subapical lobe on the distiphallus (Character 41). Interestingly, the subtribe's putative synapomorphy (Norrbom, 1989) was not included in the analysis (see discussion of female syntergosternum 7 in Character Analysis).

Reweighting the data produced clades not found in other analyses, but, as mentioned above, results from that search should be viewed with caution. In the reweigthed search, Character 65, number of spermathecal ducts, supported the monophyly of a clade containing *R. alternata*, *R. kurentsovi*, and the Neotropical species of *Rhagoletis* (Figure 106). This is of interest because Bush (1966) regarded the *R. alternata* species group and most Neotropical *Rhagoletis* to be closely related. Bush based this relationship on a "setulose" vein R_{4+5}, wing pattern, and head shape, all characters he regarded as primitive. However, as shown in Figure 98, the number of setae on R_{4+5} varies continuously; head shape and wing pattern were unspecified by Bush and therefore could not be evaluated. Even so, primitive characters are phylogenetically uninformative (Wiley, 1981).

Oedicarena and *Paraterellia*, genera regarded to be closely related to *Rhagoletis* or other carpomyines (Berlocher, 1981; Berlocher and Bush, 1982; Norrbom et al., 1988; Norrbom, 1989, 1994; Foote et al., 1993), were consistently placed as sister taxa in a clade within the basal polytomy (Figures 104—107). Monophyly of the clade was supported by shape of the epandrium (Character 39; also noted by Norrbom et al., 1988) and the divided hypoproct (Character 55). Foote et al. (1993) did not place these genera in a tribe, but results of this analysis indicate that they may belong in a group that includes the Trypetina plus *Chetostoma* and *Myoleja* species. As pointed out in the discussion of male and female genital characters (see Character Analysis), Han's (1992) Trypetini and Trypetina do not include all species possessing his synapomorphies for the tribe and subtribe. Evidently, Han (1992) was able to narrowly define the Trypetini and Trypetina by not examining many of the species

previously placed in the tribe. Based on the observations and analyses reported herein, Han's Trypetini and Trypetina and Foote et al.'s (1993) Trypetina are paraphyletic.

Myoleja and *Chetostoma* species also were consistently placed together in a clade in the basal polytomy. Monophyly of the clade was supported by the shape of the discal teeth on the eversible ovipositor sheath (Character 69, Figures 104—107). Han (1992) considered this character to be an unequivocal synapomorphy for his subtribe Chetostomina, which includes the *Chetostoma* and *Myoleja* species studied here.

A clade containing *A. cognata*, *T. inaequalis*, and the *Chetostoma*, *Euleia*, *Myoleja*, and *Strauzia* species was supported by Character 56 (extent of the hypoproct) with the data reweighted (Figure 106). This grouping corresponds to Han's (1992) Trypetina + Chetostomina and Foote et al.'s (1993) Trypetina + unplaced Trypetini. Within this larger clade, a hyaline spot in wing cell br (Character 24, Figure 106) was synapomorphic for *A. cognata* and the *Euleia* and *Strauzia* species. All three genera are placed in the Trypetina by Han (1992) and Foote et al. (1993).

A monophyletic group containing *M. pardalina* and the *Carpomya* species is supported by the dense pollenose microtrichia on the mediotergite (Character 49, Figures 104—107). The unusual short, stout, proximally directed distal setae on the surstyli of the *Carpomya* species are likely a synapomorphy for the genus (see Character Analysis).

A clade containing the *R. cingulata* and *R. suavis* species groups was supported by Character 48 with the data reweighted (Figure 106). Recent molecular studies (Ming, 1996; Smith and Bush, in review) also support this relationship (but, see Berlocher and Bush [1982] and McPheron and Han [submitted]).

Because *Rhagoletis* is very likely paraphyletic, a single outgroup will not exist for all species currently placed in the genus. The outgroup of the clade containing the *Rhagoletis* species is likewise uncertain. When polymorphisms were included in the search, a potential outgroup clade containing *Cr. tau*, the *Haywardina* and *Zonosemata*

species, and three of the four *Rhagoletotrypeta* species was found for the remaining carpomyines (Figure 107). However, this clade is weakly supported by the data. There is no synapomorphy supporting the clade, and the clade collapses in trees one step longer. Further, the fit of the characters to trees generated with polymorphic characters is decidedly worse than to trees generated with polymorphisms excluded (CIs = 0.281 and 0.430, respectively). However, the decision to accept this clade as an outgroup to the remaining carpomyines centers on the larger issue of using polymorphic characters to infer phylogenetic relationships (Nixon and Wheeler, 1990; Davis and Nixon, 1992; see also Doyle, 1992).

The essential problem of using polymorphisms for reconstructing phylogeny is one of ancestor-descendant relationships (Nixon and Wheeler, 1990; Davis and Nixon, 1992). In sexual organisms, polymorphisms that result from recombination are not hierarchic among individuals and, therefore, do not reflect historical relationships (Nixon and Wheeler, 1990; Davis and Nixon, 1992). This does not include age- and sex-specific polymorphisms that are not altered by recombination, which can be phylogenetically informative (Nixon and Wheeler, 1990; Davis and Nixon, 1992). Further, assuming that multiple states of an attribute in a terminal taxon are a result of cladogenesis is incorrect if any of the states are a result of anagenesis (Platnick et al., 1991).

Accepting polymorphisms as legitimate cladistic characters means that they can also serve as synapomorphies, and this may present serious problems. For example, Han (1992) defines his subtribe Trypetina by the "...following combination of characters: 1) dorsal sclerite of distiphallus *usually* with pattern of narrowly fusiform or oblong cells...; 2) distiphallus *usually* with median granulate sclerite...; and 3) aculeus wide and dorsoventrally flattened, *usually* with lateral serrations toward apex..." (reference to Han's figures omitted; emphasis added). By "usually" Han presumably means that a character may sometimes be lacking, and therefore polymorphic. Thus, inclusion in

Han's Trypetina is possible when none, one, two, or all three characters are absent. The grouping becomes quite meaningless. If polymorphisms are to be used at all, methods that are consistent with cladistic theory need to be developed for when they are used as synapomorphies. Qualifiers like "usually," "often," "generally," and "rarely," often used in character descriptions, can not exculpate polymorphisms because states of cladistic characters must be mutually exclusive (Pimentel and Riggins, 1987).

Polymorphisms also present problems for coding data (Pimentel and Riggins, 1987; Nixon and Davis, 1991; Platnick et al., 1991; Maddison, 1993), and computerized parsimony analysis (Platnick et al., 1991; Maddison and Maddison, 1992; Swofford, 1993). The two most common ways polymorphic characters are coded are as missing data or by assigning them the ancestral state (Nixon and Davis, 1991). However, both methods may lead to erroneous results (Pimentel and Riggins, 1987; Platnick et al., 1991). Maddison and Maddison (1992, p. 48) suggested including a third state called "polymorphic" for species possessing both states of a binary character. However, this tactic will reflect descent only if the character is truly polymorphic (i.e., every individual possesses both character states). Computer programs such as PAUP currently cannot treat polymorphic characters in a population-genetics sense (Swofford, 1993). These algorithms instead treat polymorphic terminal taxa as groups of monomorphic subtaxa and assigns their ancestor the state that minimizes tree length (Swofford, 1993).

Is it possible to accept characters that are only "slightly" polymorphic while rejecting others that are "highly" polymorphic? The arbitrariness of such divisions is apparent, but what if polymorphisms are distributed among species in such a way that a gap clearly separates characters that are polymorphic in a few species from characters that are polymorphic in many? Although this appears to give a rational basis for including polymorphisms, there is no logical reason to suppose that characters that are polymorphic within a few species are more phylogenetically informative (i.e., "more

fixed") than characters that are polymorphic in numerous species. In practice, distinctions between characters that are polymorphic in a single species and those that are polymorphic in many species may be purely arbitrary (Figure 108).

It may be argued that eliminating polymorphisms from cladistic analyses reduces the phylogenetically informative data available to systematists. An alternative viewpoint, and the one I believe to be correct, is that removing polymorphisms reduces error. Characters that do not reflect descent cannot contribute to the understanding of phylogenetic relationships. Therefore, for all of the reasons discussed above, results of the search using polymorphisms should be viewed with skepticism.

We are thus left without a definite outgroup for the clade containing the *Rhagoletis* species. Despite an extensive character analysis, few phylogenetically informative characters above the species level were found. This is similar to the findings of other recent studies (Norrbom, 1994; Han and McPheron, 1994; Han and McPheron, submitted; Smith and Bush, in review). How then should we view current classifications of the family (e.g., Hardy, 1973; Hancock, 1986; Foote et al., 1993)? Do these intuition-based arrangements present a "clear view of reality," or should we expect polytomies to be common in a "relatively recent, rapidly radiating group" (Foote et al., 1993)? These questions will only be answered by additional analysis. The character analysis reported herein, although extensive, deals only with the descriptive anatomy of the flies. Future morphological investigations will need to go beyond this preliminary phase of study to discover new characters. Identifying homologies and stabilizing terminology are areas of tephritid morphology that especially need attention. Well-reasoned character analyses are also needed. If our goal is to understand the evolution of fruit flies, then the depth of our knowledge depends on the methodology we choose.

"You don't know what you know, until you know what you don't know." — Anonymous

SUMMARY

The family Tephritidae includes over 4,200 described species (Foote et al., 1993), and contains some of humankind's most important agricultural pests (White and Elson-Harris, 1992). Fruit flies have been the focus of numerous biological studies, especially in the areas of evolution (see Bush, 1992) and behavior (see Jenkins, 1990). Despite the importance of tephritid flies to human welfare and for scientific study, classification of the family has changed little since Hering's classification was published in 1947. Current classifications are untested, intuition-based arrangements of taxa. This presents a significant problem for biologists interested in working with fruit flies because classifications, insofar as they reflect phylogeny, provide the basis for many comparative studies (Miles and Dunham, 1993).

The most widely accepted method of inferring evolutionary relationships is phylogenetic systematics (Forey et al., 1992; Kluge and Wolf, 1993). Phylogenetic systematics is a two step process consisting of separate character and cladistic analyses. Characters are identified during character analysis, the extent of their variation determined, and hypotheses about their homology tested. These characters are then used during the cladistic analysis to infer phylogenetic relationships.

In phylogenetic systematics, deductive testing can occur only during the character analysis. Cladistic analysis is an inductive method (Bryant, 1989) and, as a result, any cladogram can be explained *post hoc*. Therefore, confidence in a phylogeny depends directly on the characters used to infer it. Little, if any, attention is usually given to character analysis in phylogenetic studies of the Tephritidae. One problem is that characters useful in taxonomy are often assumed to be phylogenetically informative.

Taxonomic characters may vary continuously and yet be useful for delimiting taxa in different areas of the range of variation. However, cladistic characters must be discrete (Pimentel and Riggins, 1987). Taxonomic characters may be autapomorphous or homoplasious and still be useful taxonomically. However, autapomorphies and homoplasy are not phylogenetically informative (Wiley, 1981). Polymorphisms may be taxonomically useful when qualified by terms such as "usually." However, such qualifiers can not exculpate polymorphisms for cladistic analysis. Useful taxonomic characters, therefore, are not necessarily useful cladistic characters.

The male genitalia and wing patterns of fruit flies provide many characters that are useful in taxonomy. Problems in using these characters for phylogenetic analysis include unstable nomenclature and questionable homologies. To improve this situation, a detailed description of the male genitalia of trypetines is given in Chapter 1. The description uses current terminology and homologies for the Diptera, and should be widely applicable within the family. Internal structure of the distiphallus is as yet uncertain, but the ground plan of the phallus proposed in Chapter 1 provides a basis for homologizing distiphallic structures.

Chapter 2 presents a system of structural landmarks for identifying wing pattern elements, thereby stabilizing pattern terminology. This system helps ensure that homologous bands are recognized. A heuristic model of wing pattern evolution also was developed in Chapter 2. The model provides a basis for constructing transformation series that can be used to constrain cladistic searches. An example of a transformation series is given for several species of *Rhagoletis*.

The monophyly of *Rhagoletis* and intergeneric relationships within the Trypetini are examined in Chapter 3. Despite an extensive character analysis, most relationships among the genera remain unresolved. Results of the study indicate that *Rhagoletis* is not monophyletic; that the Trypetina is paraphyletic; that carpomyines are more derived than trypetines; and that previously unplaced genera are more closely related to

trypetines than carpomyines. These findings are contrary to current classifications (Foote et al., 1993).

To what extent, then, will it be possible to recover the evolutionary history of tephritid flies? Will our phylogeny of the family be a dichotomous "ladder" or a polytomous "bush?" We would all like it to be a ladder: ladders are more certain and inherently more informative. But will we have failed if we can resolve only a bush? Which presents the clearer view of reality?

Somewhere between essentialism and nominalism lies truth; knowing what we do and do not know is the art of science.

APPENDIX

Table 1. Specimens examined.

Species	Number of specimens[a] Males	Females	n
Acidia cognata	3(1)	2(1)	5(2)
Carpomya incompleta	3(2)	4(2)	7(4)
C. schineri	5(3)	5(3)	10(6)
C. vesuviana	1(1)	1(1)	2(2)
Chetostoma californicum	3(1)	3(1)	6(2)
Ch. curvinerve	2(1)	2(1)	4(2)
Ch. rubidium	1(1)	2(1)	3(2)
Cryptodacus tau	2(2)	4(2)	6(4)
Epochra canadensis	7(3)	7(3)	14(6)
Euleia fratria	4(1)	3(1)	7(2)
Eu. heraclei	1(1)	3(1)	4(2)
Eu. uncinata	2(1)	2(1)	4(2)
Goniglossum wiedemanni	2(1)	3(1)	5(2)
Haywardina cuculi	2(2)	2(2)	4(4)
H. cuculiformis	1(1)	2(2)	3(3)
Myiopardalis pardalina	3(2)	4(2)	7(4)
Myoleja limata	3(1)	3(1)	6(2)
My. lucida	1(1)	1(1)	2(2)
My. nigricornis	1(1)	0(0)	1(1)
Oedicarena beameri	0(0)	1(0)	1(0)
O. latifrons	5(2)	1(1)	6(3)
O. nigra	3(1)	3(1)	6(2)
O. persuasa	3(1)	1(1)	4(2)
O. tetanops	3(1)	3(3)	6(4)
Paraterellia immaculata	4(1)	3(1)	7(2)
P. superba	1(1)	5(1)	6(2)
P. varipennis	1(1)	2(1)	3(2)
P. ypsilon	2(1)	2(1)	4(2)
Rhagoletis acuticornis	2(1)	1(1)	3(2)
R. adusta	1(1)	1(1)	2(2)
R. almatensis	1(1)	1(1)	2(2)
R. alternata	12(8)	8(4)	20(12)
R. a. orientalis	1(0)	1(0)	2(0)
R. basiola	12(8)	8(4)	20(12)
R. batava	3(1)	5(2)	8(3)
R. berberidis	6(6)	9(4)	15(10)
R. berberis	13(9)	8(4)	21(13)
R. blanchardi	2(2)	4(3)	6(5)
R. boycei	10(5)	6(4)	16(9)
R. caucasica	1(1)	1(1)	2(2)
R. cerasi	13(9)	8(4)	21(13)
R. chionanthi	9(5)	9(4)	18(9)
R. cingulata	10(6)	9(5)	19(11)
R. completa	12(8)	8(4)	20(12)
R. conversa	5(3)	5(4)	10(7)
R. cornivora	12(7)	7(4)	19(11)
R. ebbettsi	0(0)	1(0)	1(0)
R. electromorpha	8(4)	8(4)	16(8)

Table 1 (cont'd).

Species	Number of specimens[a] Males	Females	n
R. emiliae	0(0)	1(1)	1(1)
R. fausta	10(6)	8(4)	18(10)
R. ferruginea	3(1)	3(3)	6(4)
R. flavicincta	3(1)	3(1)	6(2)
R. flavigenualis	3(1)	2(1)	5(2)
R. "florida"	8(4)	8(4)	16(8)
R. indifferens	12(8)	9(5)	21(13)
R. jamaicensis	2(1)	5(2)	7(3)
R. juglandis	10(6)	8(4)	18(10)
R. juniperina	14(10)	12(8)	26(18)
R. kurentsovi	3(1)	3(2)	6(3)
R. lycopersella	6(3)	9(4)	15(7)
R. macquarti	1(1)	4(2)	5(3)
R. magniterebra	4(2)	2(1)	6(3)
R. meigeni	10(6)	8(4)	18(10)
R. mendax	10(6)	9(5)	19(11)
R. metallica	0(0)	1(1)	1(1)
R. mongolica	1(1)	1(1)	2(2)
R. nova	9(5)	7(5)	16(10)
R. obsoleta	1(0)	0(0)	1(0)
R. osmanthi	8(4)	8(4)	16(8)
R. penela	1(1)	0(0)	1(1)
R. persimilis	7(4)	12(7)	19(11)
R. pomonella	15(11)	12(9)	27(20)
R. psalida	7(4)	6(3)	13(7)
R. ramosae	1(1)	1(1)	2(2)
R. reducta	0(0)	3(0)	3(0)
R. rhytida	1(1)	1(1)	2(2)
R. ribicola	12(8)	8(4)	20(12)
R. scutellata	1(0)	0(0)	1(0)
R. striatella	12(8)	9(5)	21(13)
R. suavis	15(11)	8(4)	23(15)
R. tabellaria	12(8)	7(5)	19(13)
R. nr. *tabellaria*	5(1)	7(3)	12(4)
R. tomatis	5(3)	3(2)	8(5)
R. turanica	1(1)	0(0)	1(1)
R. zephyria	12(8)	8(6)	20(14)
R. zernyi	1(1)	1(1)	2(2)
R. zoqui	6(4)	8(4)	14(8)
Rhagoletotrypeta annulata	1(1)	4(1)	5(2)
Rh. pastranai	1(1)	1(1)	2(2)
Rh. rohweri	2(1)	2(1)	4(2)
Rh. uniformis	1(1)	2(1)	3(2)
Strauzia intermedia	3(1)	3(1)	6(2)
S. longipennis	3(1)	3(1)	6(2)
S. perfecta	3(1)	3(1)	6(2)
Trypeta fractura	0(0)	1(0)	1(0)
T. inaequalis	5(2)	2(2)	7(4)

Table 1 (cont'd).

Species	Number of specimens[a] Males	Females	n
T. tortile	0(0)	1(0)	1(0)
Zonosemata electa	3(2)	3(2)	6(4)
Z. scutellata	2(1)	1(1)	3(2)
Z. vidrapennis	1(1)	1(1)	2(2)
Z. vittigera	3(2)	3(2)	6(4)
TOTAL	462(278)	417(227)	879(505)

[a]Numbers in parentheses are the number of specimens for which genitalia were examined.

Table 2. Comparison of terminology used in naming wing bands.

	Terms used herein				
	Band h	Band sc	Band r-m	Band dm-cu	Apical band
Bush (1966)	basal	medial	intercalary	subapical	apical
Steyskal (1979)	subbasal	discal	—	preapical	apical
Foote (1981)	subbasal	discal	accessory costal; discal	subapical	apical
White (1988)	subbasal	discal	—	preapical	apical
White and Elson-Harris (1992)	subbasal	discal	accessory costal; S band, in part	preapical; V band, in part	apical; S band, V band, in part
Foote et al. (1993)	subbasal	discal; costal, in part	intercalary	subapical; V band, in part	apical; S band, V band, in part
Merz (1994)	subbasal	discal	accessory	preapical	apical

Table 3. Classification of genera included in this study (after Foote et al., 1993).

- Tephritidae
  - Dacinae
    - Dacini
    - Ceratitini
  - Trypetinae
    - Euphrantini
      - *Epochra*
    - Toxotrypanini
    - Trypetini
      - Carpomyina
        - *Carpomya*
        - *Cryptodacus*
        - *Goniglossum*
        - *Haywardina*
        - *Myiopardalis*
        - *Rhagoletis*
        - *Rhagoletotrypeta*
        - *Zonosemata*
      - Trypetina
        - *Acidia*
        - *Euleia*
        - *Strauzia*
        - *Trypeta*
    - Unplaced
      - *Chetostoma*
      - *Myoleja*
      - *Oedicarena*
      - *Paraterellia*

Table 4. Distribution and larval hosts of specimens examined.

Species	Distribution	Larval host
Acidia cognata	Palearctic	*Tussilago farfara*
Carpomya incompleta	Palearctic	*Zizyphus spina*
C. schineri	Palearctic	*Rosa glutinosa*, *R. pulverulenta*
C. vesuviana	Palearctic	not given
Chetostoma californicum	Nearctic	not given
Ch. curvinerve	Palearctic	not given
Ch. rubidium	Nearctic	not given
Cryptodacus tau	Neotropical	not given
Epochra canadensis	Nearctic	not given
Euleia fratria	Nearctic	*Angelica* sp.
Eu. heracleii	Palearctic	not given
Eu. uncinata	Nearctic	not given
Goniglossum wiedemanni	Palearctic	not given
Haywardina cuculi	Neotropical	*Solanum trichoneuron*
H. cuculiformis	Neotropical	not given
Myiopardalis pardalina	Palearctic	*C.* [=*Curcubita*?] *melo* var. *nuski*, melons, gurken (cucumber)
Myoleja limata	Nearctic	*Ilex cassine*, *I. opaca*, *I. vomitoria*
My. lucidą	Palearctic	not given
My. nigricornis	Nearctic	not given
Oedicarena beameri	Nearctic	not given
O. latifrons	Nearctic	not given
O. nigra	Nearctic	not given
O. persuasa	Nearctic	not given
O. tetanops	Nearctic	not given
Paraterellia immaculata	Nearctic	*Juniperus deppiana*
P. superba	Nearctic	not given
P. varipennis	Nearctic	not given
P. ypsilon	Nearctic	not given
Rhagoletis acuticornis	Nearctic	not given
R. adusta	Neotropical	not given
R. almatensis	Palearctic	not given
R. alternata	Palearctic	*Rosa rugosa*
R. a. orientalis	Palearctic	not given
R. basiola	Nearctic	*Rosa* sp., *R. blanda*, *R. acicularis*
R. batava	Palearctic	not given
R. berberidis	Palearctic	*Berberis vulgaris*
R. berberis	Nearctic	*Berberis aquifolium*, *B. nervosa*
R. blanchardi	Neotropical	not given
R. boycei	Nearctic	*Juglans* sp.
R. caucasica	Palearctic	not given
R. cerasi	Palearctic	*Lonicera xylosteum*
R. chionanthi	Nearctic	*Chionanthus virginicus*
R. cingulata	Nearctic	*Prunus serotina*, domestic cherry
R. completa	Nearctic	*Juglans regia*, *J. hirsuta*, Persian walnut
R. conversa	Neotropical	*Solanum tomotillo*
R. cornivora	Nearctic	*Cornus amomum*, *C. a. amomum*, *C. foemina*
R. ebbettsi	Nearctic	not given
R. electromorpha	Nearctic	*Cornus foemina*, *C. racemosa*

Table 4 (cont'd).

Species	Distribution	Larval host
R. emiliae	Palearctic	not given
R. fausta	Nearctic	*Prunus emarginata*, sour cherry
R. ferruginea	Neotropical	*Solanum* sp.
R. flavicincta	Palearctic	not given
R. flavigenualis	Palearctic	not given
R. "florida"	Nearctic	*Cornus florida*
R. indifferens	Nearctic	*Prunus emarginata*, domestic cherry
R. jamaicensis	Neotropical	not given
R. juglandis	Nearctic	not given
R. juniperina	Nearctic	*Juniperus viginiana*, *Juniperus* sp.
R. kurentsovi	Palearctic	not given
R. lycopersella	Neotropical	not given
R. macquartii	Neotropical	not given
R. magniterebra	Palearctic	not given
R. meigenii	Palearctic	not given
R. mendax	Nearctic	*Vaccinium arboreum* (as *Batrodendron*), *V. corymbosum*, *V. pennsylvanicum*, *V. stamineum*, *Vaccinium* sp., huckleberry, lowbush blueberry
R. metallica	Neotropical	not given
R. mongolica	Palearctic	not given
R. nova	Neotropical	*Solanum muricatum*, *S. nigrum*
R. obsoleta	Palearctic	not given
R. osmanthi	Nearctic	*Osmanthus americanus*
R. penela	Neotropical	not given
R. persimilis	Nearctic	not given
R. pomonella	Nearctic	*Crataegus mollis*, *C. maleoides*, *C. opaca*, *Crataegus* sp., sour cherry, hawthorn, apple, wild plum
R. psalida	Neotropical	not given
R. ramosae	Nearctic	*Juglans major* var. *glabrata*
R. reducta	Palearctic	not given
R. rhytida	Neotropical	not given
R. ribicola	Nearctic	not given
R. scutellata	Palearctic	not given
R. striatella	Nearctic	*Physalis heterophylla*, *P. longifolia*
R. suavis	Nearctic	*Juglans nigra*, walnut, butternut
R. tabellaria	Nearctic	*Cornus stolonifera*, *Vaccinium parvifolium*, *V. ovalifolium*
R. nr. *tabellaria*	Nearctic	buffaloberry (? *Shepherdia* sp.)
R. tomatis	Neotropical	not given
R. turanica	Palearctic	not given
R. zephyria	Nearctic	*Crataegus douglasii*, *Symphoricarpos albus*, *S. albus* var. *laevigatus*, *S. rivularis*, *Symphoricarpos* sp., snowberry
R. zernyi	Palearctic	not given
R. zoqui	Nearctic	not given
Rhagoletotrypeta annulata	Nearctic	granjeno hausteco (=*Celtis pallida* [Norrbom 1994])

Table 4 (cont'd).

Species	Distribution	Larval host
Rh. pastranai	Neotropical	not given
Rh. rohweri	Nearctic	not given
Rh. uniformis	Nearctic	*Celtis* sp.
Strauzia intermedia	Nearctic	*Rudbekia* sp. (prob. *lanciniata*)
S. longipennis	Nearctic	*Helianthus tuberosus*
S. perfecta	Nearctic	*Ambrosia trifida*
Trypeta fractura	Nearctic	not given
T. inaequalis	Nearctic	not given
T. tortile	Nearctic	not given
Zonosemata electa	Nearctic	*Solanum carolinense*
Z. scutellata	Neotropical	not given
Z. vidrapennis	Neotropical	not given
Z. vittigera	Nearctic	*Solanum elaeagnifolium*

Table 5. Character-state matrix used in cladistic analysis.

	Characters[a]											
	0	0	0	0	0	0	0	0	0	1	1	1
Species[b,c]	1	2	3	4	5	6	7	8	9	0	1	2
Acidia cognata	0	0	0	0	0	0	0	0	0	0	0	0
Carpomya incompleta	1	0	0	1	1	1	1	0	0	0	0	0
C. schineri	1	0	0	1	1	1	1	0	0	0	0	1
C. vesuviana	1	0	0	1	1	1	1	0	0	0	0	1
Chetostoma californicum	0	0	0	0	0,1	0	0	0	1	0	0	0
Ch. rubidium	0	0	0	0	0,1	0	0	0	1	0	0	0
Ch. curvinerve	0	0	0	0	0,1	0	0	0	1	0	0	0
Cryptodacus tau	0	0	0	0	1	0	0	0	0	0	1	2
Epochra canadensis	0	0	0	0	0	0	0	1	0	0	0	0
Eulela fratria	1	1	1	0,1	0,1	0,1	0,1	0	0	0	0	0
Eu. heraclei	0,1	1	1	0,1	0,1	0,1	0,1	0	0	0	0,1	0
Eu. uncinata	0,1	1	1	0,1	0,1	0	0	0	0	0	0	0
Goniglossum wiedemanni	0,1	0	0	0,1	1	0,1	0	0	0	0	0	1
Haywardina cuculi	0,1	0	0	1	1	0	0	0,1	0	0	0	2
H. cuculiformis	0	0	0	1	1	0	0	0	0	0	0	2
Myiopardalis pardalina	1	0	0	1	1	1	1	0	0	0	0	1
Myoleja · limata	0	0	0	0	0	0	0	0	0	0	0	0
My. lucida	0	0	0	0	0,1	0	0	0	0	0	0	0
Oedicarena latifrons	0	0	0	0	0	0	0	0	0	0	0,1	0
O. nigra	0	0	0	0	0,1	0,1	0,1	0	0	0	1	0
O. persuasa	0	0	0	0	0	0	0	0	0	0	0	0
O. tetanops	0	0	0	0	0,1	0	0,1	0	0	0	0	0
Paraterellia immaculata	0	0	0	1	1	0	0	0	0	0	0	2
P. varipennis	0	0	0	1	1	0	0	0	0	0	0	2
P. superba	0	0	0	0,1	0,1	0	0	0	0	0	0	0
P. ypsilon	0	0	0	1	1	0	0	0	0	0	0	2
Rhagoletis acuticornis	1	0	0	1	1	0	0	0	0	0	1	0
R. alternata	0,1	0	0	0,1	1	0,1	0,1	0	0	0	0	0
R. juniperina	1	0	0	0,1	1	1	0	0	0	0	1	0
R. berberidis	1	0	0	0	0,1	0	0	0	0	0	1	0
R. berberis	1	0	0	0,1	1	0,1	0	0	0	0	1	0
R. cerasi	1	0	0	0	0,1	0	0	0	0	0	1	0
R. almatensis	1	0	0	0	1	0	0	0	0	0	1	0
R. cingulata	1	0	0	1	1	1	0,1	0	0	0	1	0
R. chionanthi	1	0	0	1	1	1	0,1	0	0	0	1	0
R. indifferens	1	0	0	1	1	1	0,1	0	0	0	1	0
R. osmanthi	1	0	0	1	1	1	0	0,1	0	0	1	0
R. completa	1	0	0	0,1	1	1	1	0,1	0	0	0,1	0
R. boycei	0,1	0	0	0	1	1	0,1	0	0	0	1	0
R. ramosae	1	0	0	0,1	1	1	0	0	0	0	0	0
R. zoqui	1	0	0	0	1	1	0	0	0	0	0	0
R. conversa	1	1	0	0	1	0,1	0	0	0	0	1	0
R. lycopersella	0,1	1	0	0	0	0	0	0	0	0	1	0
R. nova	1	1	0	1	1	1	0,1	0	0	0	1	0
R. tomatis	0,1	1	0	0	0,1	0	0	0	0	0	1	0
R. cornivora	1	0	0	1	1	1	0	0	0	0	1	0
R. fausta	0,1	0	0	0,1	1	1	0	0	0	0	1	0

Table 5 (cont'd).

Species[b,c]	Characters[a]											
	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2
R. caucasica	0	0	0	0,1	1	1	0	0	0	0	0	0
R. ferruginea	1	1	0	0,1	1	0,1	0	0	0	0	0	0
R. adusta	1	1	0	0	1	1	0	0	0	0	1	0
R. blanchardi	1	1	0	0	1	0	0	0	0	0	0,1	0
R. flavicincta	1	0	0	0,1	1	1	1	0	0	0	1	0
R. kurentsovi	0	0	0	0,1	1	1	0,1	0	0	0	0	0
R. macquarti	0,1	1	0	1	1	1	0	0	0	0	1	0
R. jamaicensis	0,1	1	0	1	1	1	0	0	0	0	1	0
R. magniterebra	1	0	0	1	1	1	0,1	0	0	0	1	0
R. melgeni	0,1	0	0	1	1	1	1	0,1	0	0	0	0
R. mongolica	1	0	0	0,1	1	1	0	0	0	0	1	0
R. basiola	1	0	0	1	1	0,1	0,1	0	0	0	0	0
R. batava	1	0	0	0,1	1	1	0,1	0	0	0	1	0
R. pomonella	0,1	0	0	1	1	1	0	0	0	0	1	0
R. "florida"	0,1	0	0	1	1	1	0	0	0	0	1	0
R. mendax	1	0	0	1	1	1	0,1	0	0	0	1	0
R. zephyria	1	0	0	0,1	1	1	0	0	0	0	1	0
R. persimilis	1	0	0	0,1	1	1	0	0	0	0	1	0
R. nr. *tabellaria*	1	0	0	1	1	1	0,1	0	0	0	1	0
R. psalida	0,1	1	0	1	1	0	0	0	0	0	1	0
R. rhytida	1	1	0	0	0,1	0	0	0	0	0	1	0
R. ribicola	0,1	0	0	1	1	1	0,1	0	0	0	1	0
R. striatella	1	0	0	0,1	1	0,1	0	0	0	0	1	0
R. suavis	1	0	0	1	1	1	1	0	0	0	0	0
R. juglandis	1	0	0	1	1	1	1	0	0	0	0	0
R. tabellaria	0,1	0	0	0,1	1	1	0	0	0	0	1	0
R. electromorpha	1	0	0	0,1	1	1	0	0	0	0	1	0
R. zernyi	1	0	0	1	1	1	0	0	0	0	1	0
R. flavigenualis	1	0	0	1	1	1	0,1	0	0	0	1	0
Rhagoletotrypeta annulata	0	0	0	0	0,1	0	0	0	0	0	1	2
Rh. pastranal	0	1	0	0	0,1	0	0	0	0	0	1	2
Rh. rohweri	0	0	0	0	0,1	0	0	0	0	0	1	2
Rh. uniformis	0	0	0	0	0,1	0	0	0	0	0	1	2
Strauzia intermedia	0	0	0	0	0	0	0	1	0	1	0	0
S. longipennis	0	0	0	0	0,1	0	0	1	0	1	0	0
S. perfecta	0	0	0	0	0,1	0	0	1	0	1	0	0
Trypeta inaequalis	0	0	0	0	0,1	0	0	0	0	0	0	0
Zonosemata electa	1	0	0	0,1	1	1	0	0	0	0	0	2
Z. scutellata	1	0	0	1	1	1	0	0	0	0	0	2
Z. vidrapennis	1	0	0	0,1	1	0	0	0	0	0	0	2
Z. vittigera	1	0	0	0,1	1	0,1	0	0	0	0	0	2

Table 5 (cont'd).

Species[b,c]	Characters[a]											
	13	14	15	16	17	18	19	20	21	22	23	24
Acidia cognata	1	0	0	0	0	0	0	0	0	0	0,1	1
Carpomya incompleta	0	0	0	1	0	1	1	0	1	1	1	0
C. schineri	0	0	1	1	0	1	1	0	1	1	1	0
C. vesuviana	0	0	1	1	0	1	1	0	1	1	1	0
Chetostoma californicum	0	0	0	0	0	0	1	0	0	0	0	0
Ch. rubidium	0	0	0	0	0	0	1	0	0	0	0	0
Ch. curvinerve	0	0	0	0	0	0	1	0	0	1	0	0
Cryptodacus tau	0	1	0	0	0	0,1	0,1	0	1	1	0	0
Epochra canadensis	0	0	0	0	0	0	1	0	0	0	0	0
Euleia fratria	1	0	0	0	0	0,1	1	0	0	0	0,1	1
Eu. heraclei	1	0	0	0	0	0	0,1	0	0	0	0	1
Eu. uncinata	1	0	0	0	0	0	1	0	0	0	0	1
Goniglossum wiedemanni	0	0	1	0	0	0,1	0,1	0	1	1	1	0
Haywardina cuculi	0	1	0	0	0	0	1	0	1	1	0	0
H. cuculiformis	1	0	0	0	0	0	1	0	1	1	0	0
Myiopardalis pardalina	0	0	1	1	0	1	1	0	1	1	1	0
Myoleja . limata	0	0	0	0	0	0,1	0,1	0	0	0	0	0
My. lucida	0	0	0	0	0	0	0	0	0	0	0	0
Oedicarena latifrons	0	0	0	0	0	0	0	1	0	1	0	0
O. nigra	0	0	0	0	1	0,1	0,1	1	0	1	1	0
O. persuasa	0	0	0	0	0	0	0	1	0	1	0,1	0
O. tetanops	0	0	0	0	0	0	0	1	0	1	0,1	0
Paraterellia immaculata	0	0	0	0	0	0	1	0	0	0	0	0
P. varipennis	0	0	0	0	0	0	1	0	0	0	0	0
P. superba	0	0	0	0	0	0,1	0,1	0	0	0	0	0
P. ypsilon	0	0	0	0	0	0,1	1	0	0	0	0	0
Rhagoletis acuticornis	0	0	0	0	0	0	1	0	1	1	1	0
R. alternata	0	0	0	0	0	0,1	0,1	0	0	1	0	0
R. juniperina	0	0	0	0	0	0,1	1	0	1	1	1	0
R. berberidis	0	0	0	0	0	0,1	0,1	0	0	1	1	0
R. berberis	0	0	0	0	0	0,1	0,1	0	1	1	1	0
R. cerasi	0	0	0	0	0	0	0,1	0	0	1	1	0
R. almatensis	0	0	0	0	0	0,1	1	0	0	1	1	0
R. cingulata	0	0	0	0	0	1	1	0	1	1	1	0
R. chionanthi	0	0	0	0	0	1	1	0	1	1	1	0
R. indifferens	0	0	0	0	0	1	1	0	1	1	1	0
R. osmanthi	0	0	0	0	0	1	1	0	1	1	1	0
R. completa	0	0	0	0	0	1	1	0	1	1	1	0
R. boycei	0	0	0	0	0	1	1	0	1	1	1	0
R. ramosae	0	0	0	0	0	1	1	0	1	1	1	0
R. zoqui	0	0	0	0	0	1	1	0	1	1	0	0
R. conversa	0	0	0	0	0	0	1	0	0	1	0,1	0
R. lycopersella	0	0	0	0	0	0	0	0	0	1	1	0
R. nova	0	0	0	0	0	0,1	1	0	0	1	0	0
R. tomatis	0	1	0	0	0	0	0	0	0	1	0,1	0
R. cornivora	0	1	0	0	1	1	1	0	1	1	1	0
R. fausta	0	0	0	0	0	0,1	1	0	1	1	1	0

Table 5 (cont'd).

	Characters[a]											
	1	1	1	1	1	1	1	2	2	2	2	2
Species[b,c]	3	4	5	6	7	8	9	0	1	2	3	4
R. caucasica	0	0	0	0	0	1	1	0	0	1	1	0
R. ferruginea	0	0	0	0	0	0	1	0	0	1	0	0
R. adusta	0	0	0	0	0	0	1	0	0	1	0,1	0
R. blanchardi	0	0	0	0	0	0	1	0	0	1	0	0
R. flavicincta	0	0	0	0	0	1	1	0	1	1	1	0
R. kurentsovi	0	0	0	0	0	1	1	0	0	1	1	0
R. macquarti	0	1	0	0	0	0	1	0	1	1	1	0
R. jamaicensis	0	1	0	0	0	0,1	1	0	1	1	1	0
R. magniterebra	0	0	0	0	0	1	1	0	0	1	1	0
R. meigeni	0	0	0	0	0	1	1	0	0	1	1	0
R. mongolica	0	0	0	0	0	0	1	0	1	1	1	0
R. basiola	0	0	0	0	0	0,1	1	0	0	1	0	0
R. batava	0	0	0	0	0	0,1	1	0	1	1	0,1	0
R. pomonella	0	0,1	0	0	1	1	1	0	1	1	1	0
R. "florida"	0	1	0	0	1	1	1	0	1	1	1	0
R. mendax	0	1	0	0	1	1	1	0	1	1	1	0
R. zephyria	0	1	0	0	1	1	1	0	1	1	1	0
R. persimilis	0	0	0	0	0	0	1	0	1	1	1	0
R. nr. *tabellaria*	0	0	0	0	0	1	1	0	1	1	1	0
R. psalida	1	0	1	0	0	0	1	0	0	1	1	0
R. rhytida	1	0	1	0	0	0	0,1	0	0	1	1	0
R. ribicola	0	0	0	0	0	1	1	0	1	1	1	0
R. striatella	0	1	0	0	0	0	1	0	1	1	1	0
R. suavis	0	0	0	0	0	1	1	0	1	1	0,1	0
R. juglandis	0	0	0	0	0	1	1	0	1	1	1	0
R. tabellaria	0	0	0	0	0	0,1	1	0	1	1	1	0
R. electromorpha	0	0	0	0	0	0	1	0	1	1	1	0
R. zernyi	0	0	0	0	0	1	1	0	1	1	1	0
R. flavigenualis	0	0	0	0	0	1	1	0	1	1	1	0
Rhagoletotrypeta annulata	0	1	0	0	0	0	0,1	0	0	1	0	0
Rh. pastranai	0	1	0	0	0	0	0	0	0	1	1	0
Rh. rohweri	0	1	0	0	0	0	0,1	0	0,1	1	0	0
Rh. uniformis	0	1	0	0	0	0	0,1	0	0,1	1	0,1	0
Strauzia intermedia	0	0	0	0	0	0	0	0	0	0	0	1
S. longipennis	0	0	0	0	0	0	0	0	0	0	0	1
S. perfecta	0	0	0	0	0	0	0	0	0	0	0	1
Trypeta inaequalis	0	0	0	0	0	0	0,1	0	1	1	0	0
Zonosemata electa	1	1	0	0	0	0,1	1	0	0	1	0	0
Z. scutellata	1	1	0	0	0	1	1	0	0	1	0	0
Z. vidrapennis	1	0	0	0	0	1	1	0	0	1	0	0
Z. vittigera	1	0,1	0	0	0	0	1	0	0	1	0	0

Table 5 (cont'd).

Species[b,c]	Characters[a]											
	25	26	27	28	29	30	31	32	33	34	35	36
Acidia cognata	0	0	0	0	1	0	0,1	0	0	0	0	0
Carpomya incompleta	0	0	0	0	0	0	0	0	0	0	0	0
C. schineri	0	0	0	0	0	0	0	0	0	0	0	0
C. vesuviana	0	0	0	0	0	0	0	0	0	0	0	0
Chetostoma californicum	0	0	0	0	1	0	0	0	0	0	0	0
Ch. rubidium	0	0	0	0	1	0	0	0	0	0	0	0
Ch. curvinerve	0	0	0	0	1	0	0	0	0	0	0	0
Cryptodacus tau	0	0	1	0	0	0	0	0	0	0	0	0
Epochra canadensis	0	0	0	0	0	0	0	0	0	0	0	0
Eulela fratria	0	0	0	0	1	0	0	0	0	0	0	0
Eu. heraclei	0	0	0	0	1	0	0	0	0	0,1	0	0
Eu. uncinata	0	0	0	0	1	0	0	0	0	0	0	0
Goniglossum wiedemanni	0	0	0	0	1	0	0	0	0	0	1	0
Haywardina cuculi	0	0	0	0	0	0	0	0	0	0	0	0
H. cuculiformis	0	0	0	0	0	0	0	0	0	0	0	?
Mylopardalis pardalina	0	0	0	0	0	0	0	0	0	0	0	0
Myoleja . limata	0	0	0	0	1	1	0	0	0	0	0	0
My. lucida	0	0	0	0	1	0	0	1	0	0	0	0
Oedicarena latifrons	0	0	1	0	1	0	1	0	0	1	0	0
O. nigra	0	0	1	0	1	0	1	0	0	1	0	0
O. persuasa	0	0	0	0	1	0	1	0	0	0	0	0
O. tetanops	0	0	0	0	1	0	1	0	0	0	0	0
Paraterellia immaculata	0	0	0	0,1	1	0	0,1	0	0	0	0	0
P. varipennis	0	0	0	0	1	0	0,1	0	0	0	0	0
P. superba	0	0	0	0	1	0	0,1	0	0	0,1	0	0
P. ypsilon	0	0	0	0	1	0	0	0	0	0	0	0
Rhagoletis acuticornis	0	0	1	0	1	0	0	0	0,1	1	0	0
R. alternata	0	0	0	0	0	0	0	0	0	0	0	0,1
R. juniperina	0	0	1	0,1	0	0	0	0	0	1	0,1	0
R. berberidis	0	0	1	0	1	0	0	0	0	1	0	0
R. berberis	0	0	1	0	0	0	0	0	0	1	1	0
R. cerasi	0	0	1	0	1	0	0	0	0	1	0	1
R. almatensis	0	0	1	0	1	0	0	0	0	1	0	0
R. cingulata	0	1	0,1	0,1	0	0	0	0	0	0,1	1	0
R. chionanthi	0	1	0	0,1	0	0	0	0	0	1	1	0,1
R. indifferens	0	1	1	0	0	0	0	0	0	1	1	0,1
R. osmanthi	0	1	0,1	0,1	0	0	0	0	0	0,1	1	0
R. completa	0	0	0,1	1	0	0	0	0	0	0,1	1	0
R. boycei	0	0	1	0,1	0	0	0	0	0	1	1	0
R. ramosae	0	0	1	1	0	0	0	0	0	0	1	0
R. zoqui	0	0	0,1	1	0	0	0	0	0	0	1	0
R. conversa	0	0	1	0,1	0	0	0	0	0	1	1	0
R. lycopersella	0	0	1	0,1	0	0	0	0	1	1	1	0
R. nova	0	0	1	0	0	0	0	0	0	1	1	0
R. tomatis	0	0	1	1	0	0	0	0	1	1	1	0
R. cornivora	1	0	1	1	0	0	0	0	0	1	1	0
R. fausta	0	0	1	0	1	0	0	0	0	1	0	0

Table 5 (cont'd).

	Characters[a]											
	2	2	2	2	2	3	3	3	3	3	3	3
Species[b,c]	5	6	7	8	9	0	1	2	3	4	5	6
R. caucasica	0	0	0	0	1	0	0	0	0	0	1	0
R. ferruginea	0	0	0	0	0	0	0	1	0	0	1	0
R. adusta	0	0	0	0	0	0	0	1	0	1	1	0
R. blanchardi	0	0	0	0,1	0	0	0	1	0	1	1	?
R. flavicincta	0	0	1	0	0	0	0	0	0	0,1	0,1	0
R. kurentsovi	0	0	0	0	0	0	0	0	0	0	0	0
R. macquarti	0	0	1	0	0	0	0	0	0	1	1	0
R. jamaicensis	0	0	1	0,1	0	0	0	0	0	1	1	0
R. magniterebra	0	0	0	0	0	0	0	0	0	1	1	0
R. melgeni	0	0	0	0,1	1	0	0	0	0	0	0	0
R. mongolica	0	0	1	0	0	0	0	0	0	1	1	0
R. basiola	0	0	0	0	0	0	0	0	0	0	0	0
R. batava	0	0	1	0	0	0	0	0	0	1	1	0
R. pomonella	1	0	1	0,1	0	0	0	0	0	1	1	0
R. "florida"	1	0	1	1	0	0	0	0	0	1	1	0
R. mendax	1	0	1	0,1	0	0	0	0	0	1	1	0
R. zephyria	1	0	1	1	0	0	0	0	0	1	1	0
R. persimilis	0	0	1	1	1	0	0	0	0	1	1	0
R. nr. *tabellaria*	0	0	1	0	1	0	0	0	0	1	1	0
R. psalida	0	0	1	1	0	0	0	0	0	1	1	0
R. rhytida	0	0	1	1	0	0	0	0	0	1	1	0
R. ribicola	0	0	0,1	0	1	0	0	0	0	1	1	0
R. striatella	0	0	1	1	0	0	0	0	0	1	1	0
R. suavis	0	0	1	0	0	0	0	0	0	0,1	0	0
R. juglandis	0	0	0	0,1	0	0	0	0	0	0	1	0
R. tabellaria	0	0	1	0	1	0	0	0	0	1	1	0,1
R. electromorpha	0	0	1	0	1	0	0	0	0	1	1	0
R. zernyi	0	0	1	1	0	0	0	0	0	1	1	0
R. flavigenualis	0	0	0,1	0	0	0	0	0	0	1	1	0
Rhagoletotrypeta annulata	0	0	1	0,1	0	0	0	0	0	1	1	0
Rh. pastranai	0	0	1	1	0	0	0	0	0	1	1	0
Rh. rohweri	0	0	1	0,1	0	0	0	0	0	1	1	0
Rh. uniformis	0	0	0	0,1	0	0	0	0	0	0,1	1	0
Strauzia intermedia	0	0	0	1	1	1	0	0	0	0	0	0
S. longipennis	0	0	0	0	1	0,1	0	0	0	0	0	0
S. perfecta	0	0	0	0	1	0,1	0	0	0	0	0	0
Trypeta inaequalis	0	0	0	0	1	1	0	0	0	0	0	0
Zonosemata electa	0	0	0	0	0	0	0	0	0	0	0,1	0
Z. scutellata	0	0	0	0	0	0	0	0	0	0	0	0
Z. vidrapennis	0	0	0	0	0	0	0	0	0	0	0	0
Z. vittigera	0	0	0	0	0	0	0	0	0	0	0,1	0

Table 5 (cont'd).

Species[b,c]	Characters[a]											
	37	38	39	40	41	42	43	44	45	46	47	48
Acidia cognata	0	0	0	0	0	0	1	0	0	0	0	0
Carpomya incompleta	0	0,1	0	0	1	0	0	1	0	0	1	0
C. schineri	0	0,1	0	0	1	0	0	1	0	0	1	0
C. vesuviana	0	1	0	0	1	0	0	1	0	0	1	0
Chetostoma californicum	0	0	0	0	2	0	0	0	0	1	1	0
Ch. rubidium	0	0	0	0	2	0	0	0	0	1	1	0
Ch. curvinerve	0	0	0	0	0	0	0	1	0	1	1	0
Cryptodacus tau	0	0	0	0	1	0	0	0	0	0	1	0
Epochra canadensis	0	0	0	0	0	0	0	0	0	0	0	0
Euleia fratria	1	1	0	0	0	0	0	0	0	1	1	0
Eu. heraclei	1	0	0	0	0	0	0	0	0	1	1	0
Eu. uncinata	1	0	0	0	0	0	0	0	0	1	1	0
Goniglossum wiedemanni	0	0	0	0	1	0	0	1	0	0	1	0
Haywardina cuculi	0	0	0	0	1	0	0	1	0	0	1	0
H. cuculiformis	0	0	0	0	1	0	0	1	0	0	1	0
Myiopardalis pardalina	0	0	0	0	1	0	0	1	0	0	1	0
Myoleja · limata	0	0	0	0	0	0	0	1	0	1	0	0
My. lucida	0	0	0	0	0	0	0	1	0	1	0	0
Oedicarena latifrons	1	0	1	0	0	0	0	1	0	0	1	0
O. nigra	1	0	1	0	0	0	0	1	0	0	0	0
O. persuasa	0	0	1	0	0	0	0	1	0	0	0	0
O. tetanops	0	0	1	0	0	0	0	1	0	0	0	0
Paraterellia immaculata	1	0	1	0	0	0	1	1	0	0	0	0
P. varipennis	1	0	1	0	0	0	1	1	0	0	0	0
P. superba	1	0	1	0	0	0	1	1	0	0	0	0
P. ypsilon	1	0	1	0	0	0	1	1	0	0	1	0
Rhagoletis acuticornis	0	0	0	0	1	1	0	1	0	0	1	0
R. alternata	0	0,1	0	0	1	1	0	1	0	0	1	0
R. juniperina	0	0	0	0	1	1	0,1	1	0	0	1	0
R. berberidis	0	0	0	0	1	0	0	1	0	0	1	0
R. berberis	0	0	0	0	1	1	0,1	1	0	0,1	1	0
R. cerasi	0	0	0	0	1	0	0	1	0	0,1	1	0
R. almatensis	0	0	0	0	1	0	0	1	0	1	1	0
R. cingulata	0	0	0	0	1	1	0,1	1	1	0	1	1
R. chionanthi	0	0	0	0	1	1	0,1	1	1	0	1	1
R. indifferens	0	0	0	0	1	1	0,1	1	1	0	1	1
R. osmanthi	0	0	0	0	1	1	0	1	1	0	1	1
R. completa	0	0	0	1	1	1	0	1	1	0	1	1
R. boycei	0	0	0	1	1	1	0	1	1	0	1	1
R. ramosae	0	0	0	1	1	1	1	1	1	0	1	1
R. zoqui	0	0	0	1	1	1	1	1	1	0	1	1
R. conversa	0	0	0	0	1	0	0,1	1	0	0	1	0
R. lycopersella	0	0	0	0	1	0	1	1	0	0	1	0
R. nova	0	0	0	0	1	0	0	1	0	0	1	0
R. tomatis	0	0	0	0	1	0	0,1	1	0	0	1	0
R. cornivora	0	0	0	0	1	1	0,1	1	0	0	1	0
R. fausta	0	0	0	0	1	0	1	1	1	0	1	0

Table 5 (cont'd).

	Characters[a]											
	3	3	3	4	4	4	4	4	4	4	4	4
Species[b,c]	7	8	9	0	1	2	3	4	5	6	7	8
R. caucasica	0	0	0	0	1	0	1	1	1	0	1	0
R. ferruginea	0	1	0	0	1	0	1	1	0	0	0	0
R. adusta	0	1	0	0	1	0	0	1	0	0	0	0
R. blanchardi	0	0	0	0	1	0	0	1	0	?	0	0
R. flavicincta	0	0	0	0	1	0	1	1	0	1	1	0
R. kurentsovi	0	0	0	0	1	1	1	1	1	0	1	0
R. macquarti	0	0	0	0	1	0	0	1	0	0	1	0
R. jamaicensis	0	0	0	0	1	0	0	1	0	0	1	0
R. magniterebra	0	0	0	0	1	1	0	1	1	0	1	0
R. meigeni	0	0	0	0	1	1	0,1	1	1	0	1	0
R. mongolica	0	0	0	0	1	1	0	1	0	0	1	0
R. basiola	0	0	0	0	1	1	0	1	1	0	1	0
R. batava	0	0	0	0	1	1	0	1	0	0	1	0
R. pomonella	0	0	0	0	1	0	1	1	1	0	1	0
R. "florida"	0	0	0	0	1	0	0,1	1	1	0	1	0
R. mendax	0	0	0	0	1	0	0,1	1	1	0	1	0
R. zephyria	0	0	0	0	1	0	0,1	1	0,1	0	1	0
R. persimilis	0	0	0	0	1	1	1	1	1	0	1	0
R. nr. *tabellaria*	0	0	0	0	1	1	1	1	1	0	1	0
R. psalida	0	0	0	0	1	0	0	1	0	0	1	0
R. rhytida	0	0	0	0	1	0	0	1	0	0	1	0
R. ribicola	1	1	0	0	1	1	1	1	0	0	1	0
R. striatella	0	0,1	0	0	1	0	0,1	1	0	0	1	0
R. suavis	0	0	0	1	1	1	1	1	0,1	0	1	1
R. juglandis	0	0	0	1	1	1	0,1	1	1	0	1	1
R. tabellaria	1	0	0	0	1	1	0,1	1	1	1	1	0
R. electromorpha	1	0	0	0	1	1	1	1	1	1	1	0
R. zernyi	0	0	0	0	1	1	0	1	0	0	1	0
R. flavigenualis	0	0	0	0	1	1	1	1	0	0	1	0
Rhagoletotrypeta annulata	0	0	0	0	1	0	0	1	0	0	1	0
Rh. pastranai	0	0	0	0	1	0	1	1	1	0	1	0
Rh. rohweri	0	0	0	0	1	0	1	1	1	0	1	0
Rh. uniformis	0	0	0	0	1	0	0	1	0	0	1	0
Strauzia intermedia	0	0	0	0	0	0	0	0	0	1	0	0
S. longipennis	0	0	0	0	0	0	0	0	0	0	0	0
S. perfecta	0	0	0	0	0	0	0	0	0	1	0	0
Trypeta inaequalis	0	0	0	0	0	0	0	0	0	1	0	0
Zonosemata electa	0	0	0	0	1	0	0	1	0	0	1	0
Z. scutellata	0	0	0	0	1	0	0	1	0	1	1	0
Z. vidrapennis	0	0	0	0	1	0	0	1	0	0	1	0
Z. vittigera	0	0	0	0	1	0	0	1	0	0	1	0

Table 5 (cont'd).

Species[b,c]	Characters[a]											
	4 9	5 0	5 1	5 2	5 3	5 4	5 5	5 6	5 7	5 8	5 9	6 0
Acidia cognata	0	0	2	0	0	1	0	1	0	0	1	0
Carpomya incompleta	1	1	1	0	1	0	0	0	0	0	1	0
C. schineri	1	1	1	0	1	0	0	0	0	0	1	0
C. vesuviana	1	1	1	0	1	0	0	0	0	0	1	0
Chetostoma californicum	0	0	1	1	0	0	0	1	0	0	1	0
Ch. rubidium	0	0	1	1	0	0	0	1	0	0	1	0
Ch. curvinerve	0	0	1	1	0	0	0	1	0	0	1	0
Cryptodacus tau	0	1	1	0	1	0	0	0	0	0	1	1
Epochra canadensis	0	0	0	0	0	0	0	0	0	0	0	0
Eulela fratria	0	0	1	0	0	0	0	1	0	0	1	0
Eu. heraclei	0	0	1	0	0	0	0	1	0	0	1	0
Eu. uncinata	0	0	1	0	0	0	0	1	0	0	1	0
Goniglossum wiedemanni	0	1	1	0	1	0	0	0	0	0	1	0
Haywardina cuculi	0	1	1	0	0	0	0	0	0	0	1	1
H. cuculiformis	0	1	1	0	0	0	0	0	0	0	1	0
Myiopardalis pardalina	0	1	1	0	1	0	0	0	0	0	1	0
Myoleja limata	0	0	1	0	0	0	0	1	1	0	1	0
My. lucida	0	1	1	0	0	0	0	1	1	0	1	0
Oedicarena latifrons	0	0	1	0	0	0	1	0	1	1	0	0
O. nigra	0	0	1	0	0	0	1	0	1	1	1	1
O. persuasa	0	0	1	0	0	0	1	0	1	1	1	1
O. tetanops	0	0	1	0	0	0	1	0	1	1	1	1
Paraterellia immaculata	0	0	1	0	0	0	1	0	1	1	1	1
P. varipennis	0	0	1	0	0	0	1	0	1	1	1	1
P. superba	0	0	1	0	0	0	1	0	1	1	0	1
P. ypsilon	0	0	1	0	0	0	1	0	1	1	1	1
Rhagoletis acuticornis	0	1	1	0	1	0	0	0	0	0	1	0
R. alternata	0	1	1	0	1	0	0	0	0	0	1	0
R. juniperina	0	1	1	0	1	0	0	0	0	0	1	0
R. berberidis	0	1	1	0	1	0	0	0	0	0	1	0
R. berberis	0	1	1	0	1	0	0	0	0	0	1	0
R. cerasi	0	1	1	0	1	0	0	0	0	0	1	0
R. almatensis	0	1	1	0	1	0	0	0	0	0	1	0
R. cingulata	0	1	1	0	1	0	0	0	0	0	1	0
R. chionanthi	0	1	1	0	1	0	0	0	0	0	1	0
R. indifferens	0	1	1	0	1	0	0	0	0	0	1	0
R. osmanthi	0	1	1	0	1	0	0	0	0	0	1	0
R. completa	0	1	1	0	1	0	0	0	0	0	1	0
R. boycei	0	1	1	0	1	0	0	0	0	0	1	0
R. ramosae	0	1	1	0	1	0	0	0	0	0	1	0
R. zoqui	0	1	1	0	1	0	0	0	0	0	1	0
R. conversa	0	1	1	0	1	0	0	0	0	0	1	0
R. lycopersella	0	1	1	0	1	0	0	0	0	0	1	0
R. nova	0	1	1	0	1	0	0	0	0	0	1	0
R. tomatis	0	1	1	0	1	0	0	0	0	0	1	0
R. cornivora	0	1	1	0	1	0	0	0	0	0	1	0
R. fausta	0	1	1	0	1	0	0	0	0	0	1	0

Table 5 (cont'd).

Species[b,c]	Characters[a] 49	50	51	52	53	54	55	56	57	58	59	60
R. caucasica	0	1	1	0	1	0	0	0	0	0	1	0
R. ferruginea	0	1	1	0	1	0	0	0	0	0	1	0
R. adusta	0	1	1	0	1	0	0	0	0	0	1	0
R. blanchardi	0	1	1	0	1	0	0	0	0	0	1	0
R. flavicincta	0	1	1	0	1	0	0	0	0	0	1	0
R. kurentsovi	0	1	1	0	1	0	0	0	2	0	1	0
R. macquarti	0	1	1	0	1	0	0	0	0	0	1	0
R. jamaicensis	0	1	1	0	1	0	0	0	0	0	1	0
R. magniterebra	0	1	1	0	1	0	0	0	0	0	1	0
R. meigeni	0	1	1	0	1	0	0	0	2	0	1	0
R. mongolica	0	1	1	0	1	0	0	0	0	0	1	0
R. basiola	0	1	1	0	1	0	0	0	0	0	1	0
R. batava	0	1	1	0	1	0	0	0	0	0	1	0
R. pomonella	0	1	1	0	1	0	0	0	0	0	1	0
R. "florida"	0	1	1	0	1	0	0	0	0	0	1	0
R. mendax	0	1	1	0	1	0	0	0	0	0	1	0
R. zephyria	0	1	1	0	1	0	0	0	0	0	1	0
R. persimilis	0	1	1	0	1	0	0	0	0	0	1	0
R. nr. *tabellaria*	0	1	1	0	1	0	0	0	0	0	1	0
R. psalida	0	1	1	0	1	0	0	0	0	0	1	0
R. rhytida	0	1	1	0	1	0	0	0	0	0	1	0
R. ribicola	0	1	1	0	1	0	0	0	0	0	1	0
R. striatella	0	1	1	0	1	0	0	0	0	0	1	0
R. suavis	0	1	1	0	1	0	0	0	0	0	1	0
R. juglandis	0	1	1	0	1	0	0	0	0	0	1	0
R. tabellaria	0	1	1	0	1	0	0	0	0	0	1	0
R. electromorpha	0	1	1	0	1	0	0	0	0	0	1	0
R. zernyi	0	1	1	0	1	0	0	0	0	0	1	0
R. flavigenualis	0	1	1	0	1	0	0	0	0	0	1	0
Rhagoletotrypeta annulata	0	1	1	0	1	0	0	0	2	0	1	0
Rh. pastranai	0	1	1	0	1	0	0	0	0	0	1	0
Rh. rohweri	0	1	1	0	1	0	0	0	2	0	1	0
Rh. uniformis	0	1	1	0	1	0	0	0	2	0	1	0
Strauzia intermedia	0	1	1	0	0	0	0	1	0	1	1	0
S. longipennis	0	1	1	0	0	0	0	1	0	1	1	0
S. perfecta	0	1	1	0	0	0	0	1	0	1	1	0
Trypeta inaequalis	0	1	2	0	0	1	0	1	1	0	1	0
Zonosemata electa	0	1	0	0	0	0	0	0	0	0	1	0
Z. scutellata	0	1	0	0	0	0	0	0	0	0	1	0
Z. vidrapennis	0	1	0	0	0	0	0	0	0	0	1	0
Z. vittigera	0	1	0	0	0	0	0	0	0	0	1	0

Table 5 (cont'd).

Species[b,c]	Characters[a]											
	6 1	6 2	6 3	6 4	6 5	6 6	6 7	6 8	6 9	7 0	7 1	7 2
Acidia cognata	0	0	0	1	0	1	0	0	0	0	0	0
Carpomya incompleta	0	0	1	1	1	1	1	1	0	0	0	0
C. schineri	0	0	1	1	1	1	1	1	0	0	0	0
C. vesuviana	0	0	1	1	1	1	1	1	0	0	0	0
Chetostoma californicum	0	0	0	1	0	1	1	1	1	1	1	1
Ch. rubidium	0	0	0	1	0	1	1	1	1	1	1	1
Ch. curvinerve	0	0	0	1	0	1	1	1	1	1	1	1
Cryptodacus tau	0	0	1	1	1	1	0	1	0	1	0	0
Epochra canadensis	0	0	0	0	0	0	0	0	0	0	0	0
Euleia fratria	0	0	0	1	0	1	0	0	0	0	0	1
Eu. heraclei	0	0	0	1	0	1	0	0	0	0	0	1
Eu. uncinata	0	0	0	1	0	1	0	0	0	0	0	0
Goniglossum wiedemanni	0	0	0	1	0	1	1	0	0	0	0	0
Haywardina cuculi	0	0	1	1	1	1	0	1	0	0	0	0
H. cuculiformis	0	0	1	1	1	1	0	1	0	0	0	0
Mylopardalis pardalina	0	0	0	1	0	1	1	1	0	0	0	0
Myoleja . limata	0	0	0	1	0	1	0	1	1	1	0	0
My. lucida	0	0	0	1	0	1	0	1	1	1	1	0
Oedicarena latifrons	0	0	2	1	0	1	0	1	0	0	0	0
O. nigra	0	0	2	1	0	1	0	1	0	0	0	0
O. persuasa	0	0	2	1	2	0	1	1	0	0	0	1
O. tetanops	0	0	2	1	2	0	1	1	0	0	0	1
Paraterellia immaculata	0	0	0	1	0	1	0	1	0	0	0	1
P. varipennis	0	0	0	1	0	1	0	1	0	0	0	1
P. superba	0	1	0	1	0	1	0	1	0	0	0	1
P. ypsilon	0	1	0	1	0	1	0	1	0	0	0	1
Rhagoletis acuticornis	0	0	0	1	0	1	0	1	0	0	0	0
R. alternata	0	0	1	1	1	1	0	1	0	0	0	0
R. juniperina	0	0	1	1	1	1	0	0,1	0	0	0	0
R. . berberidis	0	0	0	1	0	1	0	1	0	0	0	0
R. berberis	0	2	1	0	0	1	0	0	0	0	0	0
R. cerasi	0	4	0	0	0	1	0	1	0	0	0	0
R. almatensis	0	4	0	0	0	1	0	1	0	0	0	0
R. cingulata	0	3	1	0	0	1	0	0,1	0	0	0	0
R. chionanthi	0	3	1	0	0	1	0	0,1	0	0	0	0
R. indifferens	0	3	1	0	0	1	0	0	0	0	0	0
R. osmanthi	0	3	1	0	0	1	0	1	0	0	0	0
R. completa	0	3	0	0	0	1	0	1	0	0	0	0
R. boycei	0	3	0	0	0	1	0	1	0	0	0	0
R. ramosae	0	3	0	0	0	1	0	1	0	0	0	0
R. zoqui	0	3	0	0	0	1	0	1	0	0	0	0
R. conversa	0	2	1	0	1	1	0	1	0	0	0	0
R. lycopersella	0	2	1	0	1	1	0	1	0	0	0	0
R. nova	0	2	1	0	1	1	0	1	0	0	0	0
R. tomatis	0	2	1	0	1	1	0	1	0	0	0	0
R. cornivora	0	2	1	0	0	1	0	0	0	0	0	0
R. fausta	0	0	1	1	0	1	0	0	0	0	0	0

Table 5 (cont'd).

	Characters[a]											
	6	6	6	6	6	6	6	6	6	7	7	7
Species[b,c]	1	2	3	4	5	6	7	8	9	0	1	2
R. caucasica	0	0	1	0	0	1	0	1	0	0	0	0
R. ferruginea	0	0	1	1	1	1	0	1	0	0	0	0
R. adusta	0	0	1	1	1	1	0	1	0	0	0	0
R. blanchardi	0	0	1	1	1	1	0	1	0	0	0	0
R. flavicincta	0	0	0	1	0	1	0	1	0	0	0	0
R. kurentsovi	0	0	1	1	1	1	0	1	0	0	0	0
R. macquarti	0	0	1	1	1	1	0	1	0	0	0	0
R. jamaicensis	0	0	1	1	1	1	0	1	0	0	0	0
R. magniterebra	0	0	1	0	0	1	1	1	0	0	0	0
R. meigeni	0	0	1	1	0	1	0	1	0	0	0	0
R. mongolica	0	0	1	1	0	1	0	1	0	0	0	0
R. basiola	0	0	1	1	0	1	0	1	0	0	0	0
R. batava	0	0	1	1	0	1	0	0,1	0	0	0	0
R. pomonella	0	2	0	0	0	1	0	1	0	0	0	0
R. "florida"	0	2	0	0	0	1	0	1	0	0	0	0
R. mendax	0	2	0	0	0	1	0	1	0	0	0	0
R. zephyria	0	2	0	0	0	1	0	1	0	0	0	0
R. persimilis	0	0	0	1	0	1	0	0,1	0	0	0	0
R. nr. *tabellaria*	0	0	0	1	0	1	0	0	0	0	0	0
R. psalida	0	2	1	0	1	1	0	1	0	0	0	0
R. rhytida	0	2	1	0	1	1	0	1	0	0	0	0
R. ribicola	0	2	0	0	0	1	0	1	0	0	0	0
R. striatella	0	0	1	1	1	1	0	0	0	0	0	0
R. suavis	0	2	0	0	0	1	0	1	0	0	0	0
R. juglandis	0	2	0	0	0	1	0	0,1	0	0	0	0
R. tabellaria	0	0	1	0,1	0	1	0	0	0	0	0	0
R. electromorpha	0	0	1	1	0	1	0	0	0	0	0	0
R. zernyi	0	0	1	1	0	1	0	0	0	0	0	0
R. flavigenualis	0	0	1	1	0	1	0	0	0	0	0	0
Rhagoletotrypeta annulata	0	0	1	1	1	1	0	0	0	1	1	0
Rh. pastranai	0	2	0	1	0	1	0	1	0	0	0	0
Rh. rohweri	0	0	1	1	1	1	0	0	0	1	0	1
Rh. uniformis	0	0	1	1	1	1	0	0	0	1	0	1
Strauzia intermedia	0	0	0	1	0	1	0	1	0	0	0	0
S. longipennis	0	0	0	1	0	1	0	1	0	0	0	1
S. perfecta	0	0	0	1	0	1	0	1	0	0	0	1
Trypeta inaequalis	0	0	0	1	0	1	0	0	0	0	0	1
Zonosemata electa	1	2	1	0	1	1	1	1	0	0	0	0
Z. scutellata	1	2	1	0	1	1	1	1	0	0	0	0
Z. vidrapennis	1	2	1	0	1	1	1	1	0	0	0	0
Z. vittigera	1	2	1	0	1	1	1	1	0	0	0	0

Table 5 (cont'd).

Species[b,c]	Characters[a] 7 3	7 4	7 5	7 6	7 7
Acidia cognata	0	0	0	0	0
Carpomya incompleta	1	0	0	0	1
C. schineri	1	0	0	0	1
C. vesuviana	1	0	0	0	1
Chetostoma californicum	0	0	0	1	0
Ch. rubidium	0	0	0	1	0
Ch. curvinerve	0	0	0	1	0
Cryptodacus tau	0	0	0	0	0
Epochra canadensis	0	0	0	0	0
Euleia fratria	0	0	0	0	0
Eu. heraclei	0	0	0	0	0
Eu. uncinata	0	0	0	0	0
Goniglossum wiedemanni	0	0	0	0	0
Haywardina cuculi	0	0	0	0	0
H. cuculiformis	0	0	0	0	0
Myiopardalis pardalina	1	0	0	0	0
Myoleja limata	1	0	0	0	0
My. lucida	0	0	0	1	0
Oedicarena latifrons	0	0	0	0	0
O. nigra	0	0	0	0	0
O. persuasa	1	0	0	0	0
O. tetanops	1	0	0	0	0
Paraterellia immaculata	0	1	0	0	1
P. varipennis	0	1	0	0	1
P. superba	0	1	0	0	1
P. ypsilon	0	1	0	0	1
Rhagoletis acuticornis	1	0	?	0	0
R. alternata	1	0	0	0	0
R. juniperina	1	0	0	0	0
R. berberidis	1	1	0	0	1
R. berberis	1	0	0	0	0
R. cerasi	1	0	0	0	0
R. almatensis	1	0	0	0	0
R. cingulata	1	0	0	0	0
R. chionanthi	1	0	0	0	0
R. indifferens	1	0	0	0	0
R. osmanthi	1	0	0	0	0
R. completa	1	1	0	0	0
R. boycei	1	1	0	0	0
R. ramosae	1	1	0	0	0
R. zoqui	1	1	0	0	0
R. conversa	0	0	0	0	0
R. lycopersella	1	0	0	0	0
R. nova	0	0	0	0	0
R. tomatis	1	0	0	0	0
R. cornivora	1	0	0	0	0
R. fausta	1	0	0	0	0

Table 5 (cont'd).

Species[b,c]	Characters[a] 7 3	7 4	7 5	7 6	7 7
R. caucasica	0	0	0	0	0
R. ferruginea	0,1	0	0	0	0
R. adusta	1	?	0	0	0
R. blanchardi	0	0	0	0	0
R. flavicincta	1	1	0	0	0
R. kurentsovi	1	0	0	0	1
R. macquarti	1	0	0	0	0
R. jamaicensis	1	0	0	0	0
R. magniterebra	0	0	0	0	1
R. meigeni	1	0	0	0	1
R. mongolica	1	0	0	0	0
R. basiola	1	0	0	0	0
R. batava	1	0	0	0	0
R. pomonella	1	0,1	0	0	0
R. "florida"	1	0,1	0	0	0
R. mendax	1	0	0	0	0
R. zephyria	1	0,1	0	0	0
R. persimilis	1	1	0	0	0
R. nr. *tabellaria*	1	0,1	0	0	0
R. psalida	1	0	0	0	0
R. rhytida	1	?	0	0	0
R. ribicola	1	0	0	0	0
R. striatella	1	0	0	0	0
R. suavis	1	0,1	0	0	0
R. juglandis	1	0,1	0	0	0
R. tabellaria	1	0	0	0	0
R. electromorpha	1	0	0	0	0
R. zernyi	1	0	0	0	1
R. flavigenualis	1	0	0	0	1
Rhagoletotrypeta annulata	0	0	0	1	0
Rh. pastranai	0	0	0	0	0
Rh. rohweri	1	0	0	1	0
Rh. uniformis	1	0	0	1	0
Strauzia intermedia	0	0	0	0	0
S. longipennis	0	0	0	0	0
S. perfecta	0	0	0	0	0
Trypeta inaequalis	0	1	0	0	0
Zonosemata electa	0	0	1	0	0
Z. scutellata	0	0	1	0	0
Z. vidrapennis	0	0	1	0	0
Z. vittigera	0	0	1	0	0

[a]Monomorphic characters and their states appear in bold typeface, and polymorphic characters and their states appear in plain typeface.

[b]A species in plain typeface is redundant in monomorphic characters with the species in bold typeface immediately preceding it.

[c]*Ch. rubidium* is redundant with *Ch. californicum* for all characters.

Table 6. Characters occurring in single species.

Head

Median occipital sclerite with a shelf-like protuberance: *Chetostoma curvinerve*

Proboscis geniculate: *Goniglossum wiedemanni*

Labellum with capitate setae: *Paraterellia ypsilon*

Face with a pair of dark spots: *Cryptodacus tau*

Flagellum with an apical fringe of black setae: *Cryptodacus tau*

Thorax

Anatergite with long, fine, erect hairs: *Epochra canadensis*

Presutural supra-alar seta absent: *Epochra canadensis*

Postsutural acrostichal seta absent: *Oedicarena nigra*

Katepisternal seta absent: *Acidia cognata*

Wing

Whitish spot at apex of cell r_{4+5}: *Epochra canadensis*

Abdomen

Invaginated sac-like structure in pleura between segments 4 and 5: *Myoleja limata*

Tergal setae of female grading from relatively long medial ones to shorter lateral ones: *Epochra canadensis*

Male Genitalia

Basiphallus with a pair of small tubercles ventrally at its base: *Paraterellia immaculata*

Table 7. Characters used in cladistic analysis.

1. Flagellum rounded or angular dorsoapically and without a detectable point (0); or flagellum more or less angular dorsoapically and with at least a small dorsoapical point (1).

2. Distal half of arista bare or with a few scattered microtrichia (1); or arista uniformly microtrichiose (0).

3. Facial ridge about as wide as or narrower than parafacial (0); or facial ridge decidedly wider than parafacial (1).

4. Genal seta concolorous (0) or not concolorous (1) to principle head setae (excluding gular, postocellar, and postocular).

5. Gular seta concolorous (0) or not concolorous (1) to principle head setae (excluding genal, postocellar, and postocular).

6. Postocellar seta concolorous (0) or not concolorous (1) to principle head setae (excluding genal, gular and postocular).

7. Postocular seta concolorous (0) or not concolorous (1) to principle head setae (excluding genal, gular and postocellar).

8. Upper orbital seta absent (1) or present (0).

9. Genal setae enlarged, numerous, or both (1); or genal setae not enlarged or unusually numerous (0).

10. Male with frontal setae pointed and similar in size to the frontal setae of female (0); or frontal setae of male blunt and larger than frontal setae of female (1).

11. Ground color of scutum yellowish (0); or ground color black or brownish (1).

12. Integument of scutum with a Carpomya-like pattern (1); with a whitish or yellowish medial stripe or prescutellar spot (2); or more or less uniformly pigmented or with an intraspecifically variable pattern (0).

13. Disc of scutum with microtrichia (0); or disc lacking microtrichia, scutum with peripheral microtrichia only (1).

14. Disc of scutum with setulae of uniform color (0); or disc of scutum with a mixture of light and dark setulae (1).

15. Supra-alar area with unmodified microtrichia (0); or supra-alar area with black, velvety microtrichia (1).

16. Mediotergite with simple microtrichia (0); or mediotergite with pollenose microtrichia (1).

Table 7 (cont'd).

17. Halter wholly yellowish or brownish (0); or halter with the stem yellowish and the knob dark brown or black (1).

18. Outer scapular seta concolorous (0) or not concolorous (1) to principle thoracic setae (excluding presutural acrostichal, and proepisternal setae).

19. Proepisternal setae concolorous (0) or not concolorous (1) to principle thoracic setae (excluding outer scapular, and presutural acrostichal setae).

20. Bare spots at the inner ends of the transverse suture and base of postsutural dorsocentral seta (1); or transverse suture and base of postsutural dorsocentral seta without bare spots (0).

21. Band r-m present (0) or band r-m absent (1).

22. Band sc not crossing vein r-m (0) or band sc crossing vein r-m (1).

23. At least proximal hairs of fringe of upper calypter dark brownish or black (0); or all hairs of upper calyptral fringe whitish (1).

24. Cell br within band sc with a hyaline spot (1); or cell br within band sc entirely pigmented or part of a larger hyaline area (0).

25. Wing pattern with bands sc, r-m, and dm-cu fused anteriorly, and bands h and sc fused posteriorly (1); or wing pattern with one or more of these bands not fused as described (0).

26. Wing pattern with bands h, sc, and dm-cu free posteriorly, band r-m absent, and the apical band with the posterodistal corner of the anterior arm well ahead of vein M (1); or wing pattern otherwise (0).

27. Hind femur wholly yellowish (0) or infuscated (1).

28. Tarsomere 4 or 5 or both same color as rest of tarsus (usually yellowish) (0); or darker than basal segments (1).

29. Mid tibia with a distinct posterodorsal row of setae (0); or mid tibia without a distinct posterodorsal row of setae (1).

30. Hind tibia with a distinct anterodorsal row of setae (0); or hind tibia without a distinct anterodorsal row of setae (1).

31. Mid femur or hind femur or both with enlarged setae ventrally (1); or both femora with setae not enlarged (0).

32. Males with anteroventral row of setae on fore femur enlarged (1); or anteroventral row with setae on fore femur normal, not enlarged (0).

Table 7 (cont'd).

33. Fifth tarsomere relatively small, cylindrical, about twice as long as maximum diameter (1); or fifth tarsomere larger, flattened, less than twice as long as maximum diameter (0).

34. Ground color of terga yellowish (0) or brownish to black (1).

35. Excluding tergite 1, one or more terga with bands of light and dark colored setae (1); or setal color of terga uniform (0).

36. Sternum 7 of male with polygonal sculpturing (1); or sternum 7 of male without sculpturing (0).

37. Basiphallic vesica present (1) or basiphallic vesica absent (0).

38. Ejaculatory apodeme with distal edge flared (1); or ejaculatory apodeme with edge coplanar with blade of apodeme (0).

39. Dorsal portion of epandrium produced posteriorly well beyond base of surstyli, the angle formed by posterior edge of epandrium below proctiger and long axis of surstyli decidedly less than 90° (1); or dorsal portion of epandrium not markedly produced posteriorly, the angle formed by posterior edge of epandrium below proctiger and long axis of surstyli about 90° or more (0).

40. Hypandrial sac lined with numerous heavily sclerotized denticles (1); or hypandrial sac not lined with denticles, or intrahypandrial membrane not forming a sac (0).

41. Sub apical distiphallic lobe trumpet-shaped (0); an elongate lobe or flap (1); or with a pair of large apical hooks (2).

42. Bacilliform sclerites with a dorsal keel, at least distally (1); or bacilliform sclerites rounded dorsally and without a keel (0).

43. Microtrichia present on base of surstyli anteriorly (1); or base of surstyli bare anteriorly (0).

44. Membrane connecting bacilliform sclerites to surstylus with microtrichia present (0); or membrane connecting bacilliform sclerites to surstylus bare (1).

45. Epandrium with numerous, evenly distributed microtrichia (1); or epandrium without microtrichia or at most with a few patchy ones (0).

46. Syntergosternum$_{7+8}$ with one or more macrochaetae (0); or syntergosternum$_{7+8}$ with only microtrichia or bare (1).

47. Parameral sheath of distiphallus with polygonal sculpturing (0); or parameral sheath of distiphallus without polygonal sculpturing (1).

Table 7 (cont'd).

48. Tips of surstyli with a cluster of long setae (1); or tips of outer surstyli with setae shorter and not forming a cluster (0).

49. Surstyli with Carpomya-like setae distally (1); or surstyli with normal setae (0)

50. Hypandrial apodeme present (0); hypandrial apodeme absent (1).

51. Surstyli with anterior lobe only (0); surstyli with anterior and posterior lobes (1); or surstyli with anterior, medial, and posterior lobes (2).

52. Right pregonite deflected ventrally (0); or right and left pregonites even (1).

53. Acrophallus present (1); or acrophallus absent (0).

54. Inner prensiseta on a large tubercle that places it decidedly distal of the outer prensiseta (1); or inner and outer prensisetae at about the same level (0).

55. Hypoproct entire (0); or hypoproct divided (1).

56. Hypoproct extending dorsally for most or all of the height of the proctiger (1); or hypoproct extending dorsally for less than half the height of the proctiger, if at all (0).

57. Inner and outer prensisetae similar in size (0); inner prensisetae larger than outer prensisetae (1); or inner prensisetae smaller than outer prensisetae (2).

58. Anterolateral corner of bacilliform sclerites forming lobes (0); or anterolateral corner of bacilliform sclerites not forming lobes (1).

59. Apex of aedeagus enclosed by parameral sheath (1); or distal portion aedeagus not enclosed by parameral sheath (0).

60. Basiphallus with membranous ventral keels (1); or basiphallus without membranous ventral keels (0).

61. Vesica contiguous with phallotheca (1); or vesica free distally (0).

62. Subapical distiphallic lobe bare (0); with numerous sclerotized denticles (1); microtrichiose (2); fimbriate without supernumerary lobe (3); or fimbriate with supernumerary lobe (4).

63. Total number of spermathecae three (0); total number of spermathecae two (1); or total number of spermathecae four (2).

64. Spermathecae cylindrical (0); or spermathecae globular (1).

65. Number of spermathecal ducts: 3 (0); 2 (1); or 4 (2).

Table 7 (cont'd).

66. Eversible ovipositor sheath about as long as segment 8 (1); or eversible ovipositor sheath distinctly longer than segment 8 (0).

67. Eversible ovipositor sheath with microtrichia proximally (1); or eversible ovipositor sheath without microtrichia (0).

68. Denticles on eversible ovipositor sheath near segment 8 with single point (0); or teeth near segment 8 with multiple points (1).

69. Large discal denticles on ventral surface of eversible ovipositor sheath triangular and with a single point (0); or large discal denticles on ventral surface of eversible ovipositor sheath squarish and irregular apically (1).

70. Segment 8 constricted at base (1); or segment 8 not constricted basally (0).

71. Segment 8 with tip laterally flattened (1); or segment 8 with tip dorsoventrally flattened (0).

72. Segment 8 with microtrichia or denticles or both around cloaca (0); or cloaca glabrous (1).

73. Tip of segment 8 with subapical points, projections or serrations (0); or tip of segment 8 with single, apical point (1).

74. One spermatheca definitely smaller than other(s) (1); or spermathecae nearly the same size (0).

75. Spermathecal ducts definitely annulated and radiator hose-like (1); or spermathecal ducts smooth (0).

76. Dorsal taeniae extend to segment 8 (1); or dorsal taeniae not reaching segment 8 (0).

77. Ventrally, tip of syntergosternum 7 with about 8-16 stout setae (1); or setae at tip of syntergosternum 7 with setae of normal size (0).

Table 8. Characters not included in the cladistic analysis.

Character	Variation
Head	
shape of flagellum	continuous
color of principle setae	ambiguous
color of genal and gular setae	ambiguous
color of postocellar seta	ambiguous
size of ocellar setae	continuous
size of postocular setae	continuous
shape of median occipital sclerite	discrete
size of paravertical seta	continuous
position of inner vertical seta	continuous
width of palps	continuous
size of genal and gular setae	continuous
size of head setae	continuous
coloration of gena	ambiguous
shape of arista	ambiguous
number of frontal setae	continuous
number of orbital setae	ambiguous
attitude of upper orbital seta	discrete
Thorax	
color of principle setae	ambiguous
color of scapular setae	ambiguous
size of scapular setae	ambiguous
coloration of scutum	ambiguous
color of katepisternum	ambiguous
color of postpronotal lobe	ambiguous
color of setulae on postpronotal lobe	ambiguous
presence of microtrichiose stripes on scutum	discrete
coloration of scutellum	ambiguous
presence of velvety microtrichia on scutum	ambiguous
coloration of mediotergite	ambiguous
position of dorsocentral seta	continuous
presence of dark flecks in cuticle	ambiguous
size of proepisternal setae	continuous
number of anepisternal setae	continuous
number of katepisternal setae	discrete
color of inner scapular seta	ambiguous
color of outer scapular seta	ambiguous
color of katepisternal seta	discrete
presence of pleural stripe	ambiguous
presence of minute setae on halter	ambiguous
Wing	
extent of band r-m	ambiguous
position of band sc	ambiguous
number of apical bands	ambiguous
coloration of bands	ambiguous
number of setae on R_{4+5}	continuous
presence of spurious vein or bullule in cell r_1	ambiguous
position of vein r-m	continuous

Table 8 (cont'd).

Character	Variation
Wing (cont'd.)	
shape of lower calypter	continuous
extent of microtrichia on wing membrane	ambiguous
apex of wing hyaline or infuscate	discrete
coloration of wing base	ambiguous
prominence of proximal and distal subcostal bands	ambiguous
number of setae at tip of vein R_1 ventrally	ambiguous
Legs	
coloration of legs	ambiguous
Abdomen	
color of tergal setae	ambiguous
presence of tergal microtrichia	ambiguous
tergal coloration	ambiguous
color of setae on tergite 1	ambiguous
Male Genitalia	
bleb present between sterna 6 and 7	ambiguous
size of sterna 6 and 7	invariable
shape of sternum 5	ambiguous
shape of sternum 7	ambiguous
length of microtrichia in membrane between sterna 6 and 7	invariable
position of mechanoreceptors on sterna 6 and 7	ambiguous
shape of phallapodeme	ambiguous
length of distiphallus	continuous
coloration of ejaculatory apodeme	ambiguous
shape of epandrial phragma	continuous
shape of surstylus	continuous
shape of hypandrium	continuous
size of proctiger	continuous
shape of hypoproct	continuous
appressed flap of distiphallus with distal microtrichia	invariable
size of denticles on subepandrial membrane at base of phallus	continuous
presence of subapical distiphallic lobe	invariable
basiphallus with sculpturing	ambiguous
shape of dorsal keel of bacilliform sclerite	continuous
shape of prensisetae	continuous
extent of denticles on anterior surstylar lobe	continuous
bacilliform sclerite with anteroventral lobe	ambiguous
vestiture of surstylus	ambiguous
vestiture of epandrium	continuous
size of apical distiphallic lobe	continuous
vestiture of apical distiphallic lobe	ambiguous
position of prensisetae	ambiguous
sclerotization of subapical distiphallic lobe	ambiguous
sculpturing of parameral sheath of distiphallus	ambiguous
coloration of epandrium	ambiguous
location of denticles on surstylus	continuous
number of sensilla on anterior surstylar lobe	continuous
position of anterior surstylar lobe	continuous

Table 8 (cont'd).

Character	Variation
Male Genitalia (cont'd.)	
number of gonopores	ambiguous
shape of apical distiphallic lobe	continuous
absence of epiphallic sclerite	invariable
shape of anterior bridge of bacilliform sclerite	ambiguous
shape of rectal lining	ambiguous
presence of free sclerite on basiphallus distally	ambiguous
attachment of subepandrial sclerite to bacilliform sclerites	ambiguous
position of subepandrial sclerite	ambiguous
fusion of bacilliform sclerites to surstyli	invariable
presence of muscle between bacilliform sclerite and epandrium	invariable
shape of sclerotized portion of parameral sheath of distiphallus	ambiguous
presence of sensilla on distiphallus	ambiguous
Female Genitalia	
number of spermathecae per side	ambiguous
color of spermathecae	continuous
shape of spermathecae	continuous
ornamentation of spermathecae	continuous
orientation of spermathecal ornamentation	ambiguous
length of spermathecal ducts	continuous
sclerotization of syntergosternum 7	ambiguous
shape of small denticles on eversible ovipositor sheath	continuous
shape of large denticles on eversible ovipositor sheath	invariable
presence of denticles on segment 8	ambiguous
presence of sac-like structure within base of segment 8	ambiguous
presence of lateral groove in tip of segment 8	invariable
number of sensilla in lateral groove of segment 8	continuous
shape of tip of segment 8	ambiguous
spermathecae with atrium	ambiguous
spermathecae with minute capitate structures	invariable
sterna 10 visible within eversible ovipositor sheath	ambiguous
segment 8 twisted	ambiguous

Table 9. Leg coloration by segment, excluding tarsi.

Species	Fore Leg				Mid Leg				Hind Leg			
	cx[a]	tr	fm	tb	cx	tr	fm	tb	cx	tr	fm	tb
Acidia cognata	-	-	-	-	-	-	-	-	-	-	-	-
Carpomya incompleta	-	-	-	-	-	-	-	-	-	-	-	-
C. schineri	-	-	-	-	-	-	-	-	-	-	-	-
C. vesuviana	-	-	-	-	-	-	-	-	-	-	-	-
Chetostoma californicum	-	-	-	-	-	-	-	-	-	-	-	-
Ch. curvinerve	-	-	-	-	-	-	-	-	-	-	-	-
Ch. rubidium	-	-	-	-	-	-	-	-	-	-	-	-
Cryptodacus tau	+	-	-	-	+	-	+	-	+	-	+	+
Epochra canadensis	-	-	-	-	-	-	-	-	-	-	-	-
Euleia fratria	-	-	-	-	-	-	-	-	-	-	-	-
Eu. heraclei	-	-	-	-	-	-	-	-	-	-	-	-
Eu. uncinata	-	-	-	-	-	-	-	-	-	-	-	-
Goniglossum wiedemanni	-	-	-	-	-	-	-	-	-	-	-	-
Haywardina cuculi	-	-	-	-	-	-	-	-	-	-	-	-
H. cuculiformis	-	-	-	-	-	-	-	-	-	-	-	-
Myiopardalis pardalina	-	-	-	-	-	-	-	-	-	-	-	-
Myoleja limata	-	-	-	-	-	-	-	-	-	-	-	-
My. lucida	-	-	-	-	-	-	-	-	-	-	-	-
My. nigricornis	-	-	-	-	-	-	-	-	-	-	-	-
Oedicarena beameri	-	-	-	-	-	-	-	-	-	-	-	-
O. latifrons	-	-	+	-	-	-	+	-	±	-	+	-
O. nigra	±	-	+	-	±	-	+	-	±	-	+	±
O. persuasa	-	-	-	-	-	-	-	-	-	-	-	-
O. tetanops	-	-	-	-	-	-	-	-	-	-	-	-
Paraterellia immaculata	-	-	-	-	-	-	-	-	-	-	-	-
P. superba	-	-	-	-	-	-	-	-	-	-	-	-
P. varipennis	-	-	-	-	-	-	-	-	-	-	-	-
P. ypsilon	-	-	-	-	-	-	-	-	-	-	-	-
Rhagoletis acuticornis	-	-	-	-	+	-	-	-	+	±	+	±
R. adusta	-	-	-	-	-	-	-	-	-	-	-	+
R. almatensis	+	-	+	-	+	-	+	-	+	-	+	-
R. alternata	-	-	-	-	-	-	-	-	-	-	-	-
R. a. orientalis	-	-	-	-	-	-	-	-	-	-	-	-
R. basiola	-	-	-	-	-	-	-	-	-	-	-	-
R. batava	±	-	±	-	+	-	+	-	+	-	+	-
R. berberidis	+	±	+	-	+	±	+	-	+	±	+	±
R. berberis	+	+	+	-	+	+	+	-	+	+	+	+
R. blanchardi	-	-	-	-	-	-	-	-	-	-	-	+
R. boycei	+	-	+	±	+	-	+	±	+	-	+	+
R. caucasica	-	-	-	-	-	-	-	-	-	-	-	-
R. cerasi	+	-	+	-	+	±	+	-	+	+	+	±
R. chionanthi	-	-	-	-	-	-	-	-	-	-	-	-
R. cingulata	-	-	-	-	±	-	±	-	±	-	±	-
R. completa	±	±	±	-	±	-	±	-	±	±	±	±
R. conversa	+	±	+	±	+	±	+	±	+	+	+	+
R. cornivora	+	-	±	-	+	-	+	-	+	-	+	-
R. ebbettsi	+	?	?	?	+	?	?	?	+	?	?	?
R. electromorpha	+	±	+	-	+	±	+	±	+	+	+	±

Table 9 (cont'd).

Species	Fore Leg				Mid Leg				Hind Leg			
	cx[a]	tr	fm	tb	cx	tr	fm	tb	cx	tr	fm	tb
R. emiliae	-	-	-	-	-	-	-	-	-	-	-	-
R. fausta	+	-	+	-	+	-	+	±	+	-	+	±
R. ferruginea	-	-	-	-	-	-	-	-	-	-	-	+
R. flavicincta	-	-	-	-	+	-	±	-	+	±	+	-
R. flavigenualis	-	-	-	-	+	-	±	-	+	-	±	-
R. "florida"	±	-	±	-	+	-	+	-	+	-	+	-
R. indifferens	±	-	+	-	+	-	+	±	+	-	+	+
R. jamaicensis	±	-	-	-	+	-	+	-	+	-	+	±
R. juglandis	-	-	-	-	-	-	-	-	-	-	-	-
R. juniperina	+	-	+	-	+	±	+	-	+	±	+	±
R. kurentsovi	-	-	-	-	-	-	-	-	-	-	-	-
R. lycopersella	+	-	+	+	+	±	+	±	+	+	+	+
R. macquarti	+	-	+	-	+	-	+	-	+	-	+	-
R. magniterebra	-	-	-	-	-	-	-	-	±	-	-	-
R. *meigeni*	-	-	-	-	-	-	-	-	-	-	-	-
R. mendax	±	-	±	-	+	-	+	-	+	-	+	-
R. metallica	+	+	+	+	+	+	+	+	+	+	+	+
R. mongolica	+	-	+	-	+	-	+	-	+	+	+	-
R. nova	±	-	±	-	±	-	±	-	+	±	+	±
R. obsoleta	+	-	+	-	+	-	+	-	+	+	+	+
R. osmanthi	-	-	-	-	±	-	±	-	±	-	±	-
R. penela	+	-	+	-	+	-	+	-	+	+	+	+
R. persimilis	+	-	+	-	+	-	+	-	+	+	+	±
R. pomonella	±	-	±	-	+	-	+	-	+	±	+	-
R. psalida	+	±	+	-	+	±	+	-	+	+	+	+
R. ramosae	±	-	+	-	+	-	+	-	+	-	+	+
R. reducta	+	-	+	-	+	-	+	-	+	-	+	-
R. rhytida	+	+	+	-	+	+	+	-	+	+	+	+
R. ribicola	±	-	±	-	±	-	±	-	+	±	±	-
R. scutellata	?	?	?	?	+	?	?	?	+	-	+	-
R. striatella	+	-	+	-	+	-	+	-	+	±	+	±
R. suavis	-	-	-	-	-	-	-	-	-	-	-	-
R. tabellaria	+	-	+	-	+	-	+	±	+	±	+	±
R. nr. *tabellaria*	+	-	+	-	+	-	+	-	+	±	+	-
R. tomatis	+	-	+	±	+	-	+	-	+	+	+	+
R. turanica	-	-	-	-	-	-	-	-	-	-	-	-
R. zephyria	+	-	+	-	+	-	+	±	+	±	+	±
R. zernyi	-	-	-	-	+	-	-	-	+	-	-	-
R. zoqui	±	-	±	±	±	-	±	-	-	±	±	+
Rhagoletotrypeta annulata	+	-	+	+	+	-	+	+	+	-	+	+
Rh. pastranai	-	-	+	+	-	-	+	+	±	-	+	+
Rh. rohweri	±	-	±	±	±	-	+	±	±	-	+	+
Rh. uniformis	-	-	-	-	-	-	-	-	-	-	-	+
Strauzia intermedia	-	-	-	-	-	-	-	-	-	-	-	-
S. longipennis	-	-	-	-	-	-	-	-	-	-	-	-
S. perfecta	-	-	-	-	-	-	-	-	-	-	-	-
Trypeta fractura	-	-	-	-	-	-	-	-	-	-	-	-
T. inaequalis	-	-	-	-	-	-	-	-	-	-	-	-

Table 9 (cont'd).

Species	Fore Leg				Mid Leg				Hind Leg			
	cx[a]	tr	fm	tb	cx	tr	fm	tb	cx	tr	fm	tb
T. tortile	-	-	-	-	-	-	-	-	-	-	-	-
Zonosemata electa	-	-	-	±	-	-	-	±	-	-	-	+
Z. scutellata	-	-	-	-	-	-	-	-	-	-	-	±
Z. vidrapennis	-	-	-	-	-	-	-	-	-	-	-	+
Z. vittigera	-	-	-	-	-	-	-	-	-	-	-	+

[a]Abbreviations: cx, coxa; tr, trochanter; fm, femur; tb, tibia; -, wholly yellowish; +, infuscate; ±, polymorphic; ?, segment missing.

Table 10. Species with tergal patterns matching the medial pattern system[a].

Species	Subfamily	Reference[b]
Abebaiodacus fuscatus (Wiedemann)	Dacinae	Munro 1984, fig. 98
Acanodacus botianus Munro	Dacinae	Munro 1984, fig. 105
Acanodacus brevis (Coquillett)	Dacinae	Munro 1984, fig. 73
Acanodacus ceropegiae Munro	Dacinae	Munro 1984, fig. 100
Acanodacus cuspidatus Munro	Dacinae	Munro 1984, figs. 73, 101
Acanodacus serratus Munro	Dacinae	Munro 1984, figs. 73, 103
Acanodacus viator (Munro)	Dacinae	Munro 1984, fig. 99
Ancylodacus collarti (Munro)	Dacinae	Munro 1984, fig. 64
Ancylodacus flavicrus (Graham)	Dacinae	Munro 1984, fig. 64
Bactrocera albistrigata (deMeijere)	Dacinae	White & Elson-Harris 1992, fig. 177
Bactrocera caudata (Fabricius)	Dacinae	White & Elson-Harris 1992, fig. 205
Bactrocera correcta (Bezzi)	Dacinae	White & Elson-Harris 1992, fig. 179
Bactrocera cucurbitae (Coquillett)	Dacinae	White & Elson-Harris 1992, fig. 206
Bactrocera depressa (Shiraki)	Dacinae	White & Elson-Harris 1992, fig. 201
Bactrocera distincta (Malloch)	Dacinae	White & Elson-Harris 1992, fig. 181
Bactrocera dorsalis (Hendel)	Dacinae	White & Elson-Harris 1992, fig. 182
Bactrocera facialis (Coquillett)	Dacinae	White & Elson-Harris 1992, fig. 183
Bactrocera frauenfeldi (Schineri)	Dacinae	White & Elson-Harris 1992, fig. 184
Bactrocera jarvisi (Tryon)	Dacinae	White & Elson-Harris 1992, fig. 175
Bactrocera kirki (Froggatt)	Dacinae	White & Elson-Harris 1992, fig. 185
Bactrocera minax (Enderlein)	Dacinae	White & Elson-Harris 1992, fig. 203
Bactrocera musae (Tryon)	Dacinae	White & Elson-Harris 1992, fig. 188
Bactrocera tau (Walker)	Dacinae	White & Elson-Harris 1992, fig. 207
Bactrocera tryoni (Froggatt)	Dacinae	White & Elson-Harris 1992, fig. 193
Bactrocera tsuneonis (Miyake)	Dacinae	White & Elson-Harris 1992, fig. 204
Bactrocera zonata (Saunders)	Dacinae	White & Elson-Harris 1992, fig. 196
Callantra apicalis (Shiraki)	Dacinae	Shiraki 1933, pl. XIV fig. 5
Callantra ihai Shiraki	Dacinae	Shiraki 1968, fig. 9,10
Callantra indecora Hardy	Dacinae	Hardy 1974, fig. 2a
Callantra nummularia (Bezzi)	Dacinae	Hardy 1974, fig. 2b
Callantra pedunculata (Bezzi)	Dacinae	Hardy 1974, fig. 3b
Callantra subsessilis (Bezzi)	Dacinae	Hardy 1974, fig. 5b

Table 10 (cont'd).

Species	Subfamily	Reference[b]
Callantra vittata Hardy	Dacinae	Hardy 1974, fig. 6c
Ceratitis punctata (Wiedemann)	Dacinae	White & Elson-Harris 1992, fig. 216; specimens examined
Dacus abbreviatus Hardy	Dacinae	Hardy 1974, fig. 26c
Dacus abdoangustus Drew	Dacinae	Hardy 1982, fig. 8a
Dacus absconditus Drew & Hancock	Dacinae	Drew et al. 1981, fig. 3
Dacus adustus Wang & Zhao	Dacinae	Wang & Zhao 1989, fig. 1b
Dacus aeroginosus Drew & Hancock	Dacinae	Drew et al. 1981, fig. 4
Dacus aethribasis Hardy	Dacinae	Hardy 1973, fig. 10e
Dacus affinidorsallis Hardy	Dacinae	Hardy 1982, fig. 16a
Dacus antigone Drew & Hancock	Dacinae	Drew et al. 1981, fig. 5
Dacus ascitus Hardy	Dacinae	Hardy 1983, fig. 9
Dacus aurantiacus Drew & Hancock	Dacinae	Drew et al. 1981, fig. 6
Dacus bangaloriensis Agarwal & Kapoor	Dacinae	Agarwal & Kapoor 1983, fig. 1e
Dacus beckerae Hardy	Dacinae	Hardy 1982, fig. 17
Dacus bogorensis Hardy	Dacinae	Hardy 1983, fig. 10
Dacus connexus Hardy	Dacinae	Hardy 1982, fig. 10
Dacus costalis (Shiraki)	Dacinae	Shiraki 1933, pl. II, fig. 1
Dacus dianensis Wang & Zhao	Dacinae	Wang & Zhao 1989, fig. 4b
Dacus disjunctus (Bezzi)	Dacinae	Munro 1984, fig. 41
Dacus diastatus Munro	Dacinae	Munro 1984, fig. 49
Dacus dispar Hardy	Dacinae	Hardy 1982, fig. 20a
Dacus drewi Hardy	Dacinae	Hardy 1983, fig. 8
Dacus dubiosus Hardy	Dacinae	Hardy 1982, fig. 11
Dacus durbanensis Munro	Dacinae	Munro 1984, fig. 46
Dacus elegantulus Hardy	Dacinae	Hardy 1974, fig. 17c
Dacus emittens Walker	Dacinae	Hardy 1982, fig. 12
Dacus erubescentis Drew & Hancock	Dacinae	Drew et al. 1982, fig. 7
Dacus flavipilosus Hardy	Dacinae	Hardy 1982, fig. 13
Dacus fuliginus Drew & Hancock	Dacinae	Drew et al. 1983, fig. 8
Dacus hyalinus (Shiraki)	Dacinae	Shiraki 1933, pl. I, fig. 6
Dacus involutus Hardy	Dacinae	Hardy 1982, fig. 23
Dacus isolatus Hardy	Dacinae	Hardy 1973, fig. 26a
Dacus limbifer rufulus (Bezzi) Hardy	Dacinae	Hardy 1982, fig. 24
Dacus longistyla Wiedemann	Dacinae	Hardy 1955, fig. 12
Dacus maculatus (Perkins)	Dacinae	Hardy 1973, fig. 27c
Dacus matsumurai (Shiraki)	Dacinae	Shiraki 1933, pl. III, fig. 3
Dacus melanopsis Hardy	Dacinae	Hardy 1982, fig. 3
Dacus montanus Hardy	Dacinae	Hardy 1983, fig. 7
Dacus momordicae (Bezzi)	Dacinae	Munro 1984, fig. 55
Dacus okunii (Shiraki)	Dacinae	Shiraki 1933, pl. III, fig. 2
Dacus ortholomatus Hardy	Dacinae	Hardy 1982, fig. 4
Dacus perkinsi Drew & Hancock	Dacinae	Drew et al. 1983, fig. 11
Dacus personatus Hardy	Dacinae	Hardy 1983, fig. 11
Dacus petersoni Hardy	Dacinae	Hardy 1974, fig. 23b
Dacus platamus Hardy	Dacinae	Hardy 1973, fig. 28c
Dacus propinquus Hardy & Adachi	Dacinae	Hardy 1955, fig. 15
Dacus punctatifrons Karsch	Dacinae	Munro 1984, fig. 41
Dacus pusillus Hardy	Dacinae	Hardy 1983, fig. 4

Table 10 (cont'd).

Species	Subfamily	Reference[b]
Dacus romigae Drew & Hancock	Dacinae	Drew et al. 1983, fig. 12
Dacus rubiginus Wang & Zhao	Dacinae	Wang & Zhao 1989, fig. 1b
Dacus rufofusculus Drew & Hancock	Dacinae	Drew et al. 1983, fig. 13
Dacus silvaticus Hardy	Dacinae	Hardy 1983, fig. 5
Dacus stenomus Wang & Zhao	Dacinae	Wang & Zhao 1989, fig. 3b
Dacus sumatranus Hardy	Dacinae	Hardy 1983, fig. 6
Dacus tappanus (Shiraki)	Dacinae	Shiraki 1933, pl. II, fig. 2
Dacus theophrastus Hering	Dacinae	Munro 1984, fig. 50
Dacus transversus Hardy	Dacinae	Hardy 1982, fig. 6a
Dacus trifasciatus Hardy	Dacinae	Hardy 1982, fig. 28a
Dacus ubiquitus Hardy	Dacinae	Hardy 1974, fig. 37a
Dacus vargus Hardy	Dacinae	Hardy 1982, fig. 15a
Dacus vertebratus Bezzi	Dacinae	White & Elson-Harris 1992, fig. 229
Dacus yangambinus Munro	Dacinae	Munro 1984, fig. 41
Dixoodacus amphoratus Munro	Dacinae	Munro 1984, fig. 79
Dixoodacus binotatus (Loew)	Dacinae	Munro 1984, fig. 81
Dixoodacus ficicola (Bezzi)	Dacinae	Munro 1984, fig. 86
Dixoodacus opinatus (Munro)	Dacinae	Munro 1984, fig. 85
Dixoodacus umbeluzinus Munro	Dacinae	Munro 1984, fig. 84
Ectopodacus fasciolatus (Collart)	Dacinae	Munro 1984, fig. 69
Ectopodacus vansomereni (Munro)	Dacinae	Munro 1984, fig. 71
Epochra canadensis (Loew)	Trypetinae	specimens examined
Gymnodacus amplexus Munro	Dacinae	Munro 1984, fig. 35
Gymnodacus calophylli Perkins & May	Dacinae	Munro 1984, fig. 36
Gymnodacus kuniyoshii Shiraki	Dacinae	Shiraki 1968, fig. 8
Gymnodacus mesomelas (Bezzi)	Dacinae	Munro 1984, fig. 35
Lactodacus adenionis Munro	Dacinae	Munro 1984, fig. 90
Metidacus delicatus Munro	Dacinae	Munro 1984, fig. 67
Mictodacus opacatus (Munro)	Dacinae	Munro 1984, fig. 94
Mictodacus pallidilatus (Munro)	Dacinae	Munro 1984, fig. 94
Myrmecodacus mirificus Munro	Dacinae	Munro 1984, fig. 107
Paratridacus expandens (Walker)	Dacinae	Shiraki 1968, fig. 12
Psilodacus annulatus (Becker)	Dacinae	Munro 1984, fig. 111
Pycnodacus purpurifrons (Bezzi)	Dacinae	Munro 1984, fig. 119
Strumeta asatoi Shiraki	Dacinae	Shiraki 1968, fig. 9
Tomoplagia fiebrigi Hendel	Tephritinae	Aczél 1955b, fig. 102j-k
Zeugodacus ishigakiensis Shiraki	Dacinae	Shiraki 1968, fig. 7,15
Zeugodacus scutellatus (Hendel)	Dacinae	Shiraki 1968, fig. 7

[a]A tergal pattern was judged to match the medial pattern system if one or more terga distal to syntergum 1+2 had a medial dark mark. The ceromae of dacines (see Munro 1984, p. 8) were ignored.

[b]Munro (1984) considers dacines to constitute a separate family, the Dacidae. This view has not been adopted by other taxonomists.

Table 11. Species with tergal patterns matching the sublateral pattern system[a].

Species	Subfamily	Reference
Acanthoneura amamioshimaensis Shiraki	Trypetinae	Shiraki 1968, fig. 9
Acidogona melanura (Loew)	Tephritinae	Benjamin 1934, fig. 24L
Acidoxantha balabacensis Hardy	Trypetinae	Hardy 1974, fig. 105c
Acidoxantha totoflava Hardy	Trypetinae	Hardy 1973, fig. 101b
Acroceratitis bimacula Hardy	Trypetinae	Hardy 1973, fig. 105b
Bactrocera oleae (Gmelin)	Dacinae	White & Elson-Harris 1992, fig. 197; specimens examined
Campiglossa producta (Loew)	Tephritinae	Merz 1994, fig. 4g; specimens examined
Chaetorellia acrolophi White & Marcquart	Tephritinae	specimens examined
Chaetorellia conjuncta (Becker)	Tephritinae	specimens examined
Chaetorellia loricata (Rondani)	Tephritinae	specimens examined
Chaetorellia succinea (O. Costa)	Tephritinae	specimens examined
Chaetostomella cylindrica Robineau-Desvoidy	Tephritinae	specimens examined
Chaetostomella nigripunctata Shiraki	Tephritinae	Shiraki 1933, pl. XI, fig. 3
Chaetostomella onotrophes Loew	Tephritinae	specimens examined
Chaetostomella undosa (Coquillett)	Tephritinae	specimens examined
Cryptodacus tau (Foote)	Trypetinae	specimens examined
Cycasia flava Hardy	Trypetinae	Hardy 1973, fig. 78b
Dioxyna bidentis (Robineau-Desvoidy)	Tephritinae	specimens examined
Dioxyna brachybasis Hardy	Tephritinae	Hardy 1988, fig. 7c
Dioxyna sororcula (Wiedemann)	Tephritinae	Shiraki 1968, fig. 7,8 (as *Ensina*); specimens examined
Dioxyna (as *Paroxyna*) *picciola* (Bigot)	Tephritinae	Benjamin 1934, fig. 30M; specimens examined
Elaphromyia incompleta Shiraki	Tephritinae	Shiraki 1933, pl. XI, fig. 6
Elaphromyia incompleta punctata Shriaki	Tephritinae	Shiraki 1968, fig. 9,10
Elaphromyia multisetosa Shiraki	Tephritinae	Shiraki 1933, pl. XI, fig. 5
Elaphromyia pterocallaeformis (Bezzi)	Tephritinae	Hardy 1974, fig. 136b
Euaresta bella (Loew)	Tephritinae	specimens examined
Euaresta punctata Shiraki	Tephritinae	Shiraki 1968, fig. 7,8
Euaresta stigmatica Coquillett	Tephritinae	specimens examined
Eurosta solidaginis (Fitch)	Tephritinae	specimens examined
Eutreta novaeboracenis (Fitch)	Tephritinae	specimens examined
Haywardina cuculi (Hendel)	Trypetinae	Aczél 1951, fig. 9, 11; specimens examined
Haywardina cuculiformis (Aczél)	Trypetinae	Aczél 1951, fig. 21, 23; specimens examined
Jamesomyia geminata (Loew)	Tephritinae	specimens examined
Laksyetsa trinotata Foote	Tephritinae	specimens examined

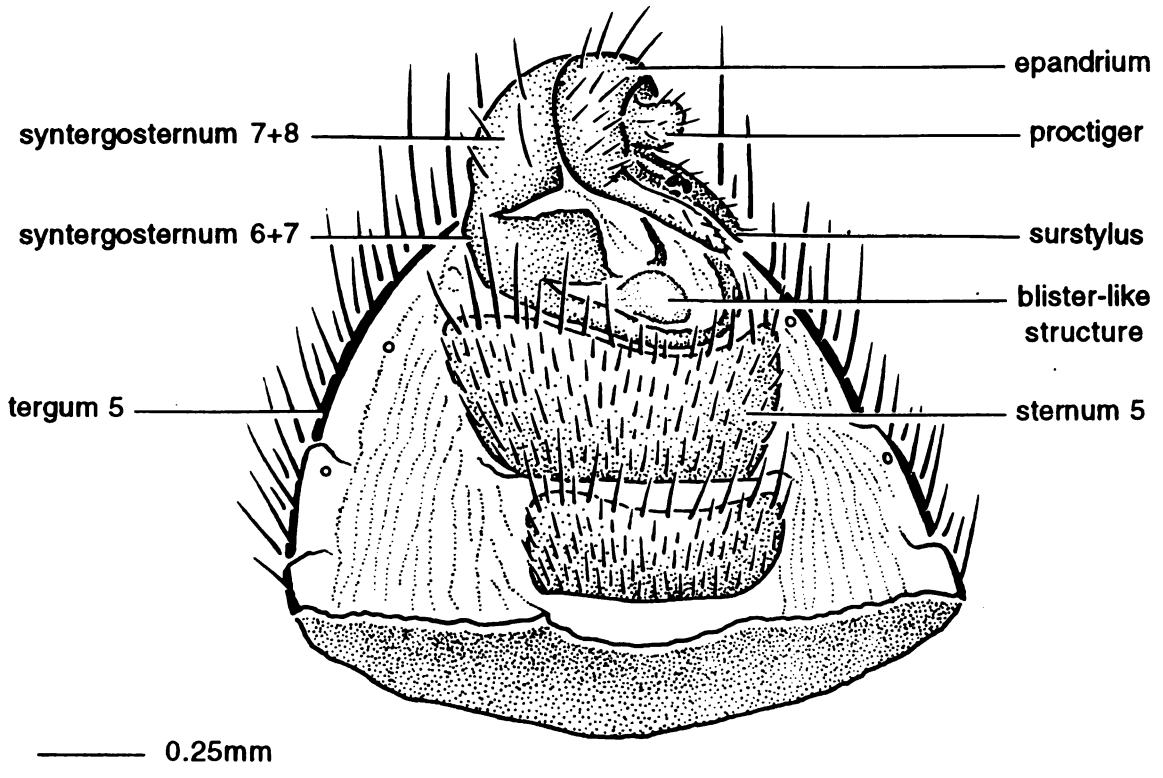
Table 11 (cont'd).

Species	Subfamily	Reference
Myopites apicatus Freidberg	Tephritinae	specimens examined
Myopites inulaedyssentericae Blot	Tephritinae	specimens examined
Noeta pupillata (Fallen)	Tephritinae	specimens examined
Orellia falcata (Scopoli)	Tephritinae	specimens examined
Orellia occindentalis (Snow)	Tephritinae	specimens examined
Orellia palposa (Loew)	Tephritinae	specimens examined
Oxyna utahensis Quisenberry	Tephritinae	specimens examined
Paracantha gentilis Hering	Tephritinae	specimens examined
Paramyiolia takeuchii Shiraki	Trypetinae	Shiraki 1933, pl. VIII, fig. 3
Paraterellia immaculata Blanc	Trypetinae	specimens examined
Paraterellia superba Foote	Trypetinae	specimens examined
Paraterellia varipennis (Coquillett)	Trypetinae	specimens examined
Paraterellia ypsilon Foote	Trypetinae	specimens examined
Paroxyna absinthii (Fabricius)	Tephritinae	specimens examined
Paroxyna albiceps (Loew)	Tephritinae	specimens examined; Jenkins 1985, fig. 124
Paroxyna clathrata (Loew)	Tephritinae	specimens examined
Paroxyna difficilis Hendel	Tephritinae	specimens examined
Paroxyna loewiana Hendel	Tephritinae	specimens examined
Paroxyna matsumotoi Shiraki	Tephritinae	Shiraki 1968, fig. 9
Paroxyna misella (Loew)	Tephritinae	specimens examined
Paroxyna punctata Shiraki	Tephritinae	Shiraki 1933, pl. XII, fig. 5
Paroxyna variabilis (Doane)	Tephritinae	specimens examined
Phaeospilodes fritilla Hardy	Trypetinae	Hardy 1973, fig. 93b
Rhagoletis cingulata (Loew)	Trypetinae	Bush 1966, fig. 50; specimens examined
Rhagoletis completa Cresson	Trypetinae	Bush 1966, fig. 63, 64; specimens examined
Rhagoletis osmanthi Bush	Trypetinae	Bush 1966, fig. 53; specimens examined
Rhagoletis zoqui Bush	Trypetinae	Bush 1966, fig. 61; specimens examined
Rhagoletotrypeta pastranai Aczél	Trypetinae	Aczél 1954, fig. 7, 10
Rhagoletotrypeta xanthogastra Aczél	Trypetinae	Aczél 1950, fig. 3d
Sophria cociinna Walker	Trypetinae	Hardy 1980, fig. 13c
Sophria limbata borneensis Hering	Trypetinae	Hardy 1980, fig. 4b
Terellia longicauda (Meigen)	Tephritinae	specimens examined
Terellia lappae (Cederhjelm)	Tephritinae	specimens examined
Terellia ruficauda (Fabricius)	Tephritinae	specimens examined
Terellia tussilaginis (Fabricius)	Tephritinae	specimens examined
Terellia virens (Loew)	Tephritinae	specimens examined
Tetramyiolia sapporensis Shiraki	Trypetinae	Shiraki 1933, pl. X, fig. 1
Tritaeniopteron elachispilotum Hardy	Trypetinae	Hardy 1973, fig. 49a
Tritaeniopteron tetraspilotum Hardy	Trypetinae	Hardy 1973, fig. 50e
Xanthomyia platyptera (Loew)	Tephritinae	specimens examined

Table 11 (cont'd).

Species	Subfamily	Reference
Xenochaeta aurantiaca (Doane)	Tephritinae	specimens examined
Xyphosia punctigera Coquillett	Tephritinae	Shiraki 1933, pl. XIV, fig. 2
Zonosemata minuta Bush	Trypetinae	Bush 1965, fig. 15-16

[a]A tergal pattern was judged to match the sublateral pattern system if one or more terga distal to syntergum 1+2 had a pair of sublateral dark marks that were closer to the midline than the lateral edges of the tergum. The ceromae of dacines (see Munro 1984, p. 8) were not counted.



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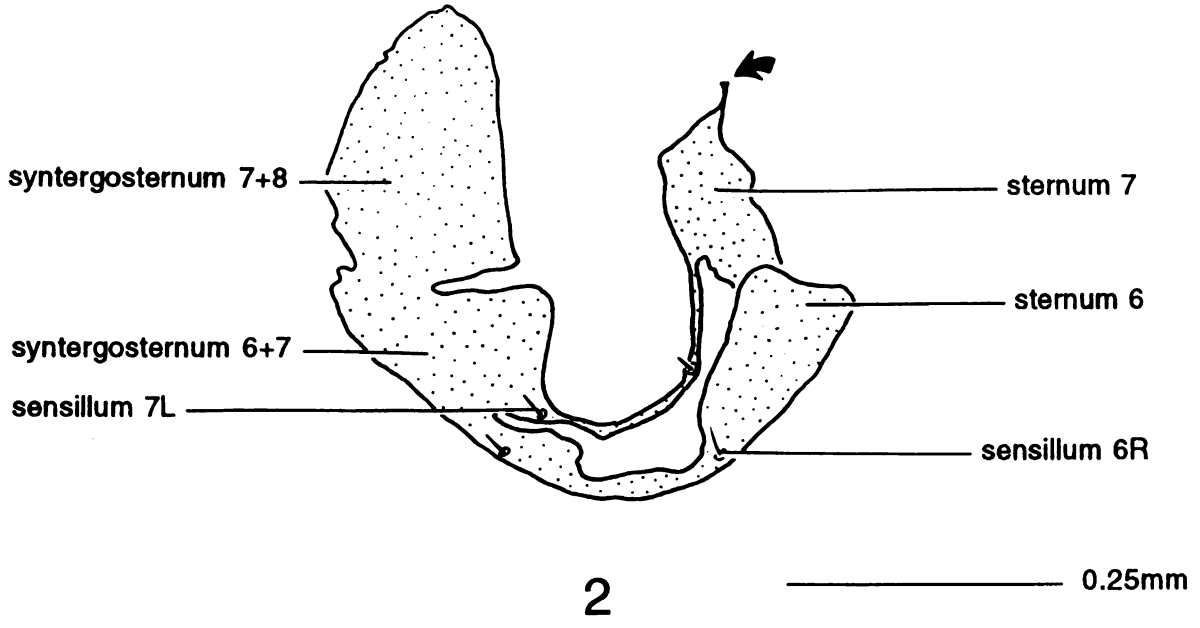


2

Figures 1—2. Distal abdominal structures of *Rhagoletis pomonella*. 1, Segments 4—8 and genitalia, ventral view. 2, Postabdominal sterna and syntergosterna, ventral view; arrow indicates point of attachment to hypandrium.

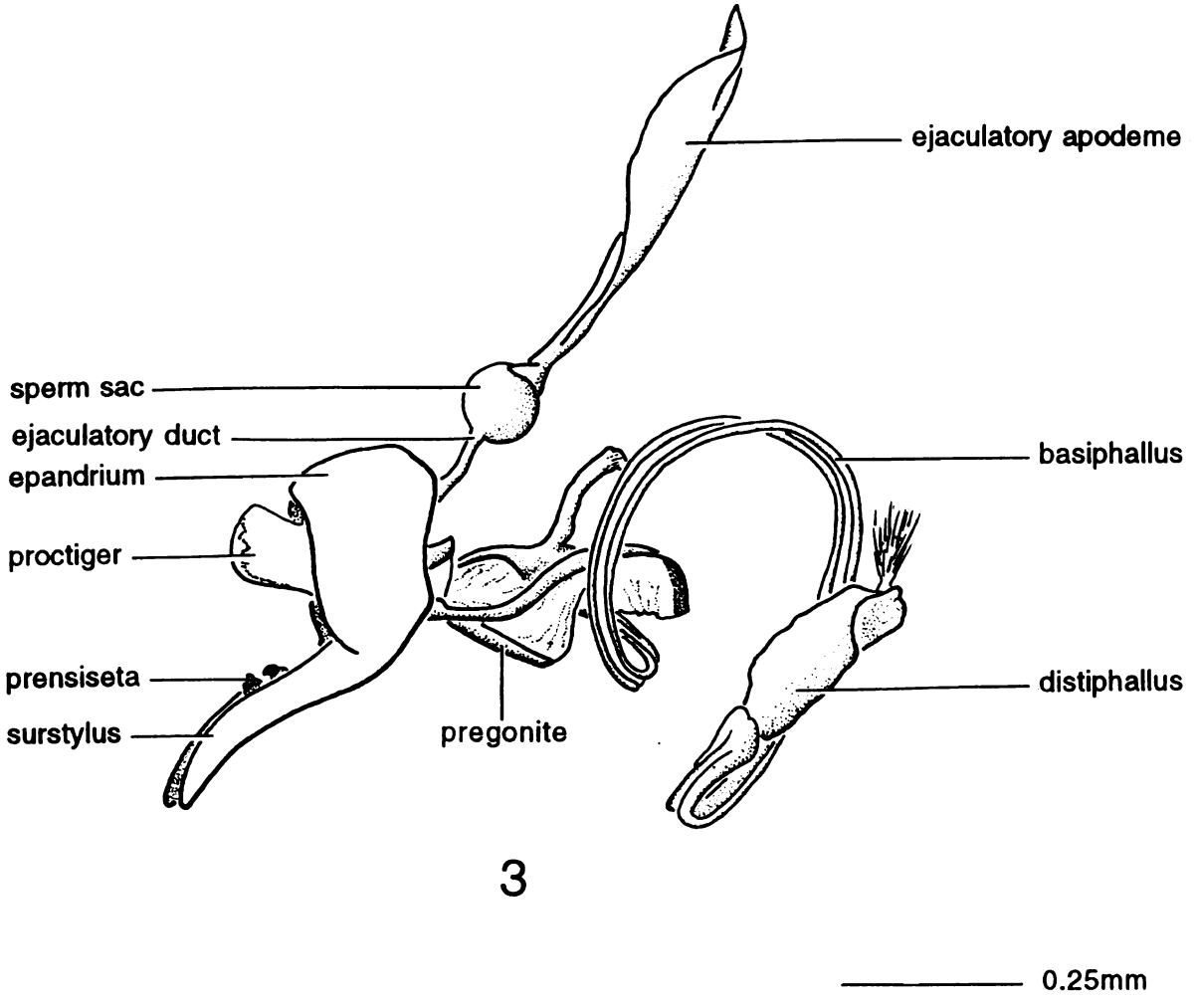
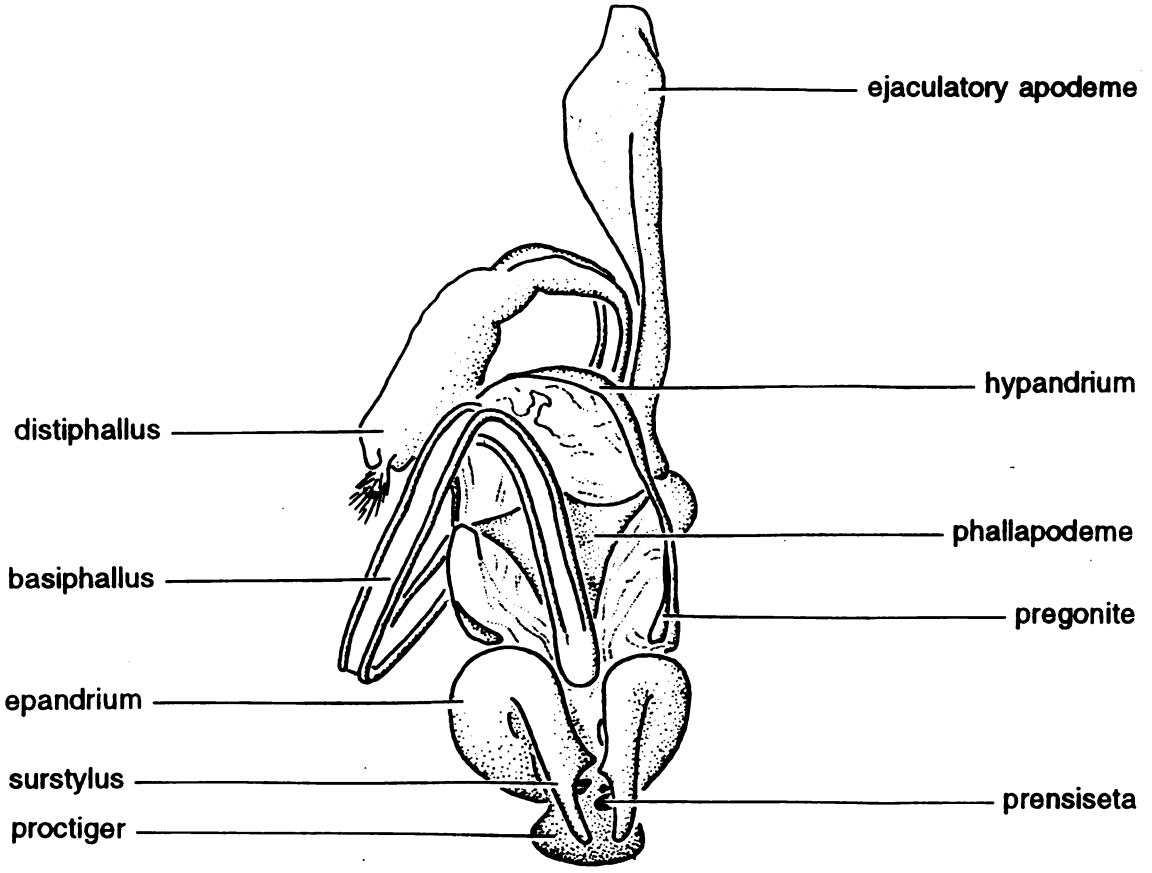


Figure 3. Genitalia of *Rhagoletis pomonella*, right lateral view.



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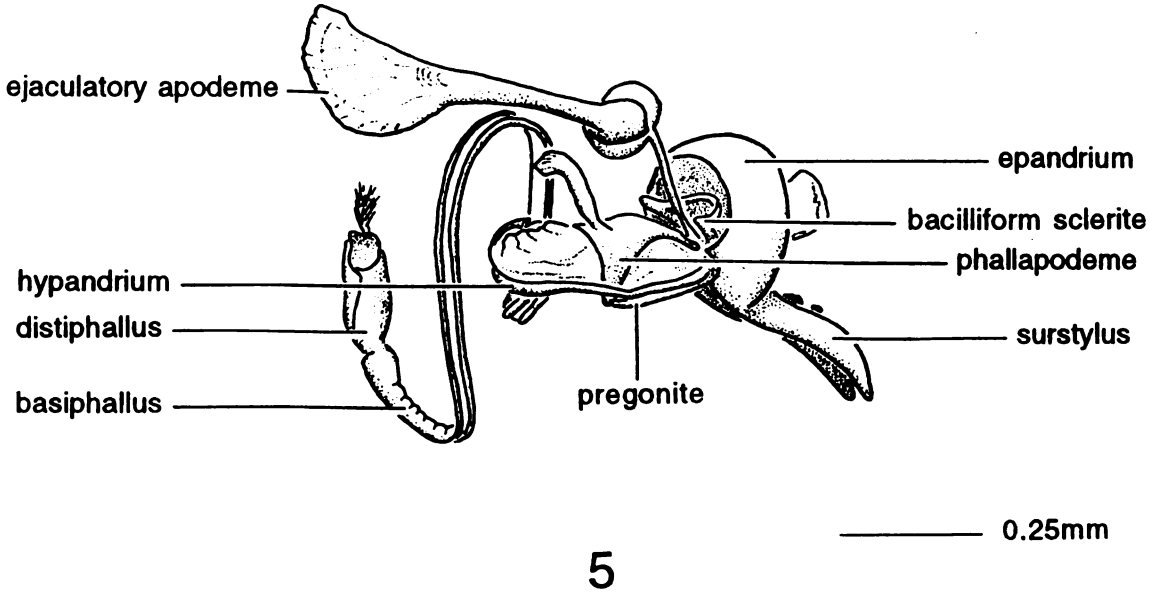

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Figures 4—5. Genitalia of *Rhagoletis pomonella*. 4, Ventral view. 5, Left oblique view.

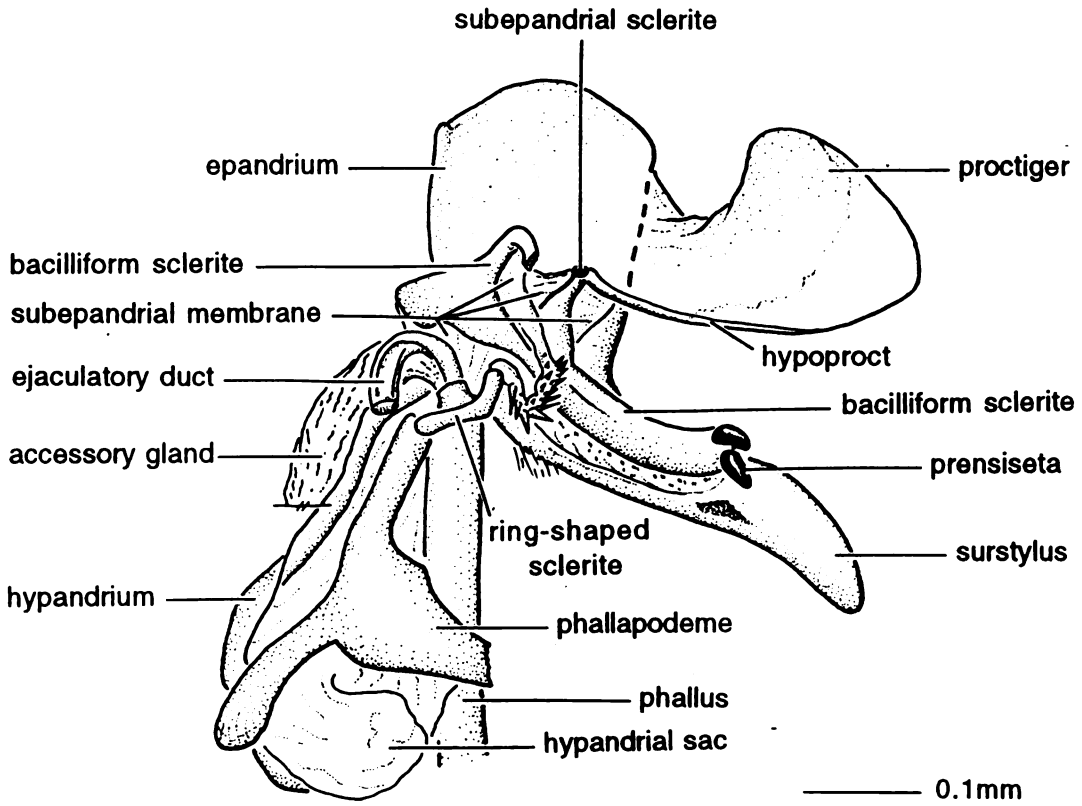

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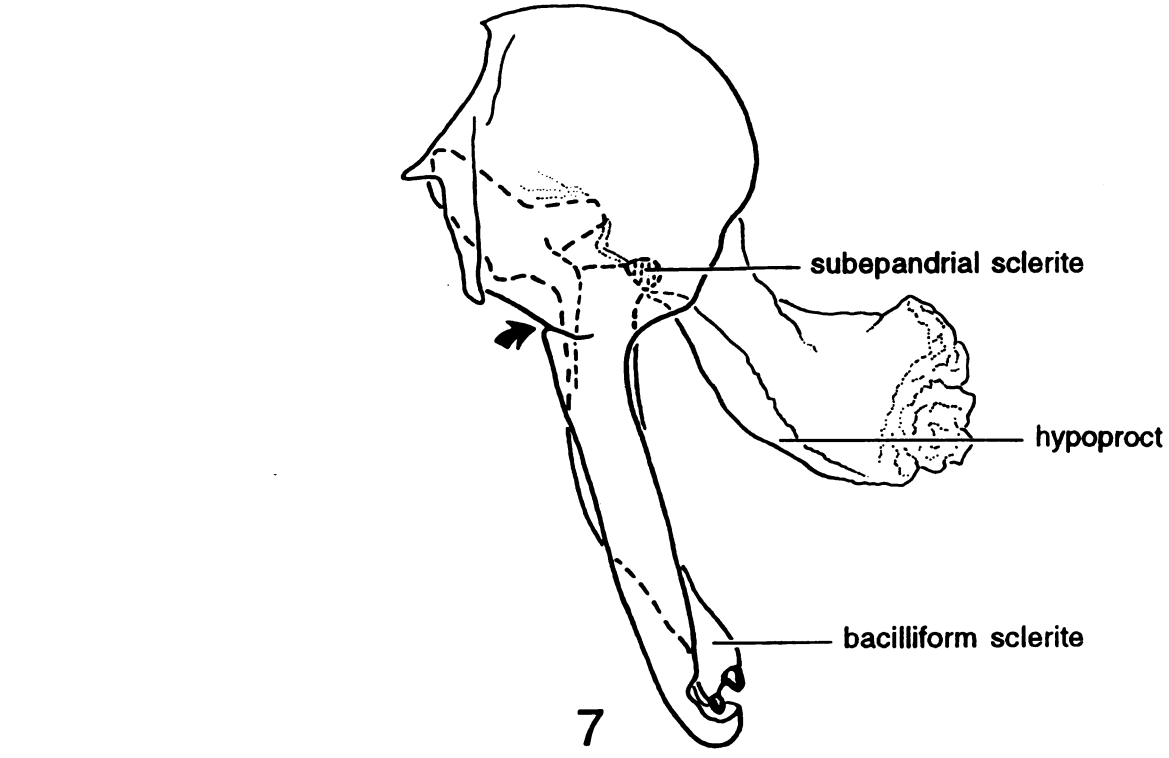
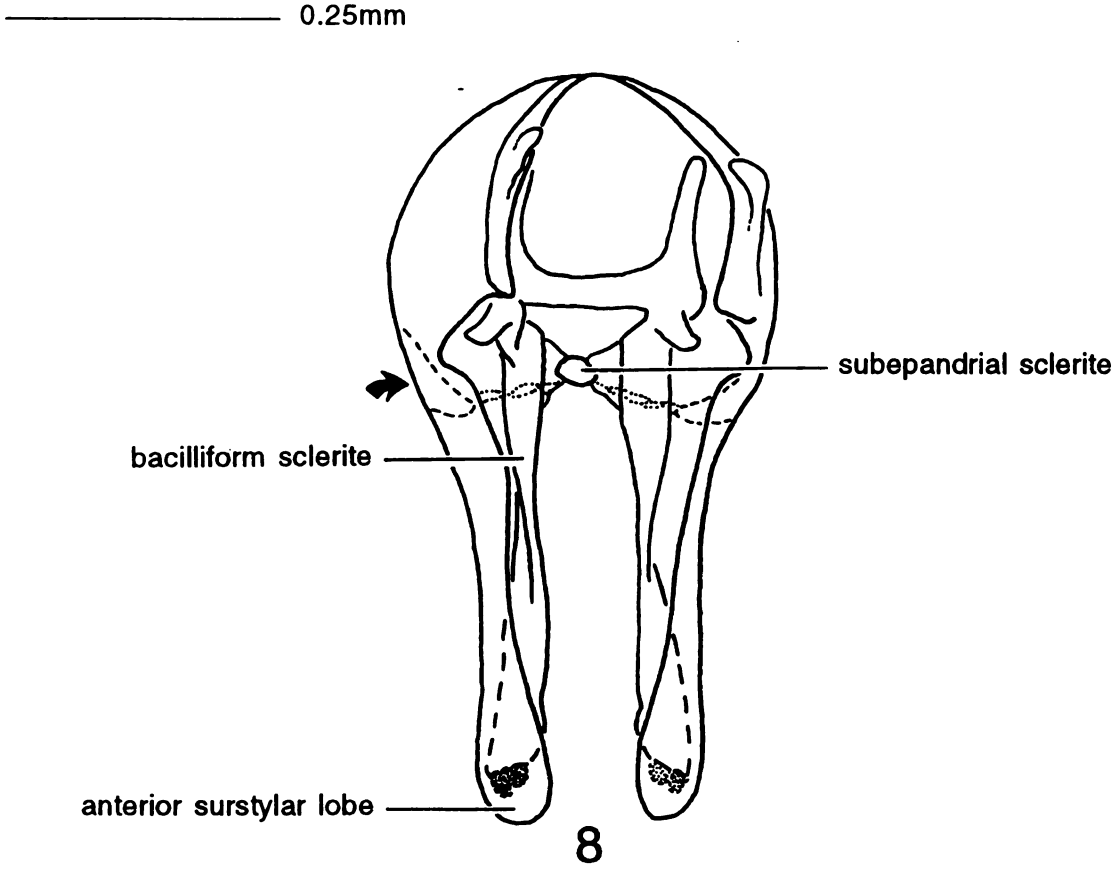
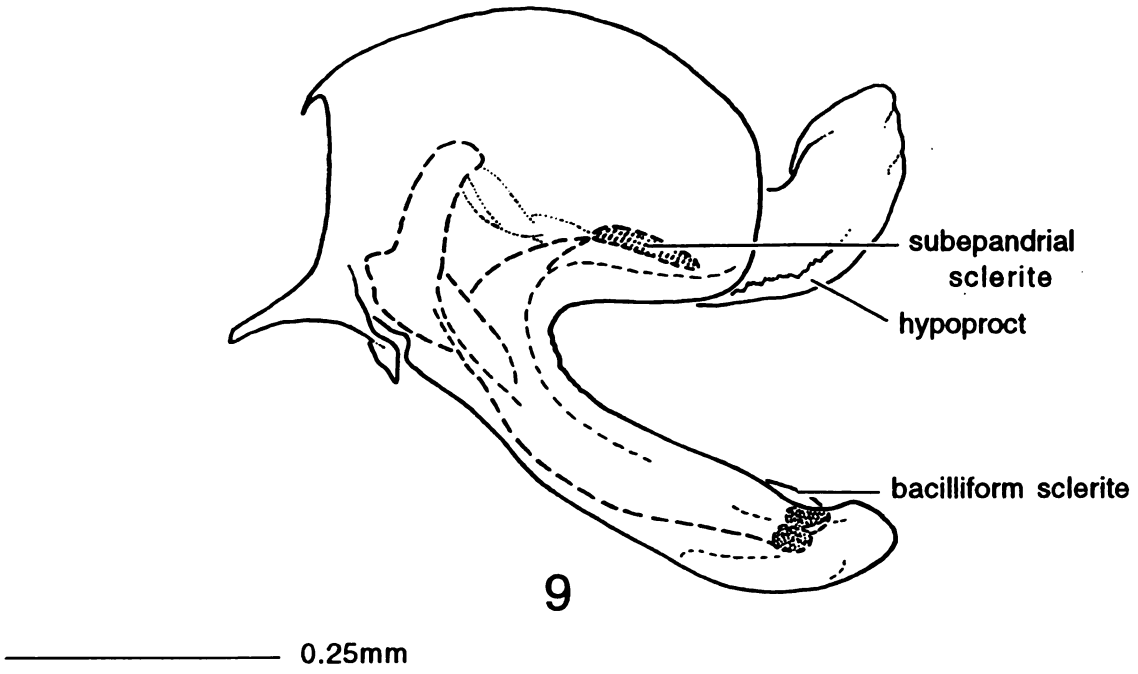
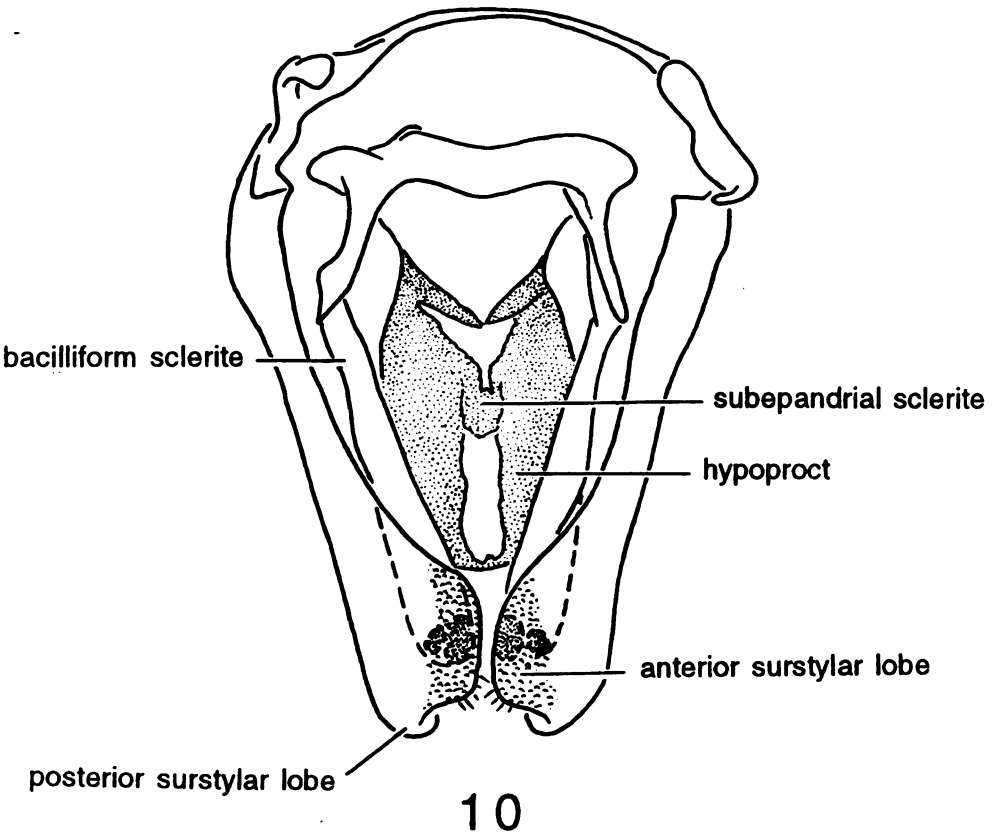
Figure 6. Genitalia of *Rhagoletis pomonella*. Sagittal section through epandrium, left lateral view.



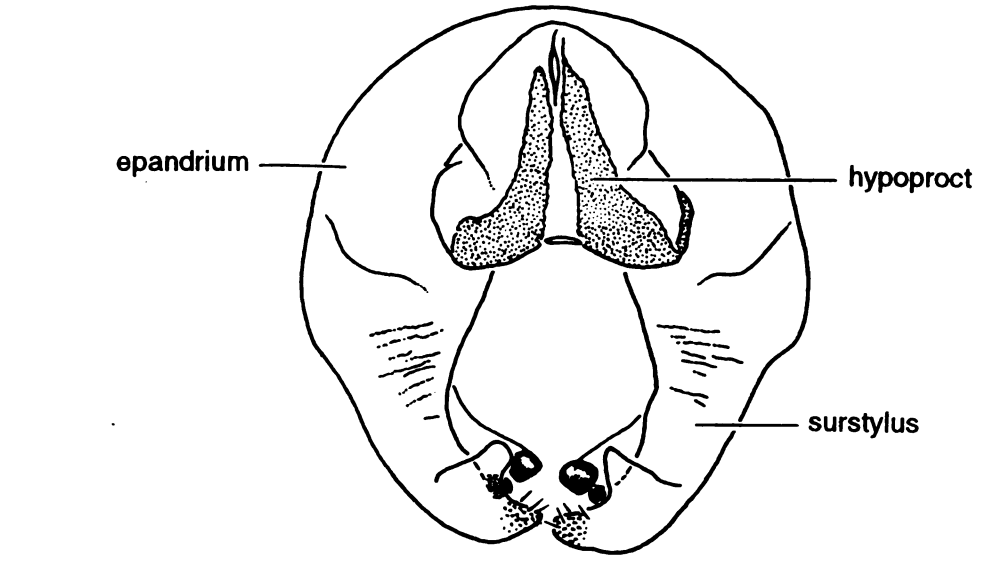


Figures 7—8. Epandrium and associated structures of *Epochra canadensis*. 7, Left lateral view. 8, Anterior view (proctiger omitted). Arrows indicate external sulcus (Figure 7) and internal apodeme (Figure 8).





Figures 9—10. Epandrium and associated structures of *Oedicarena latifrons*. 9, Left lateral view. 10, Anterior view.



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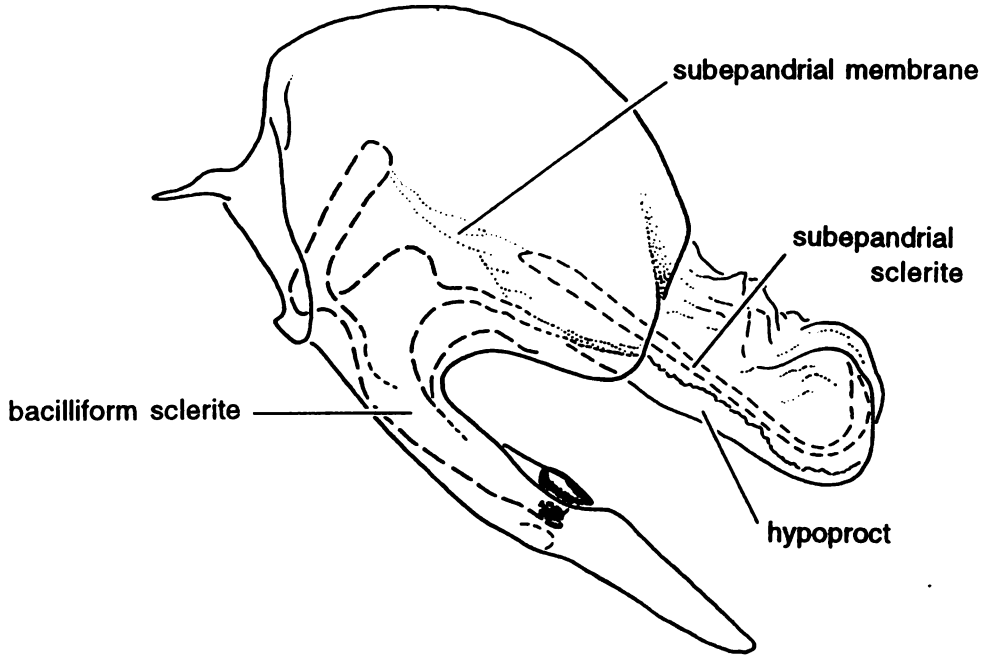

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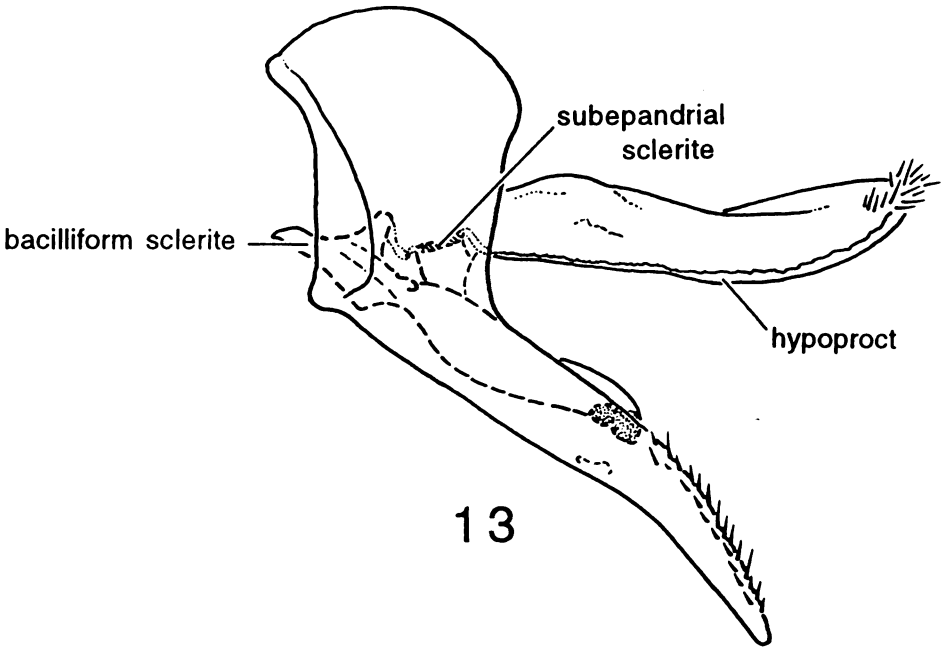
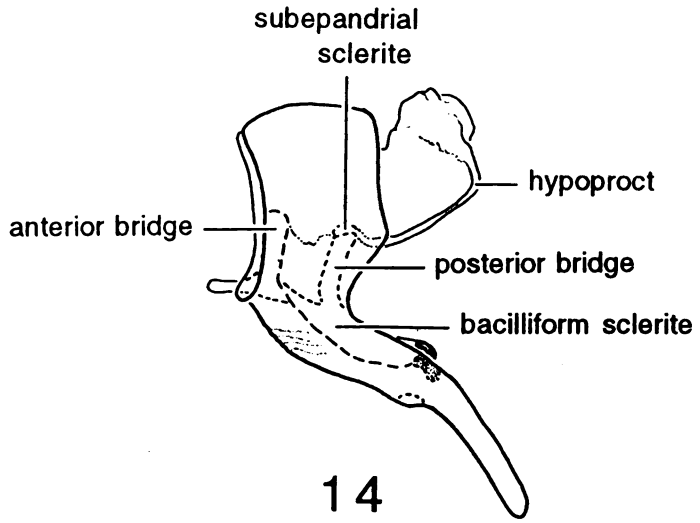
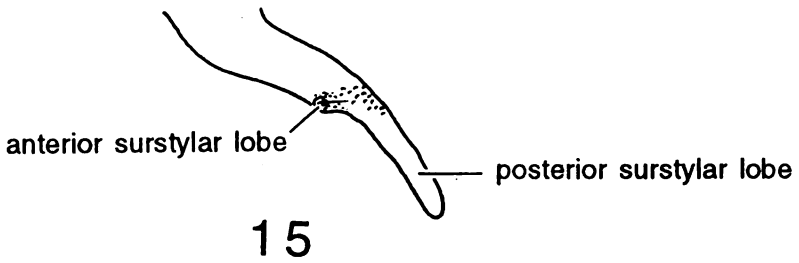
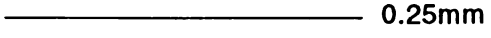
Figures 11—12. Epandrium and associated structures. 11, *Oedicarena latifrons*, posterior view. 12, *Parateralia immaculata*, left lateral view.

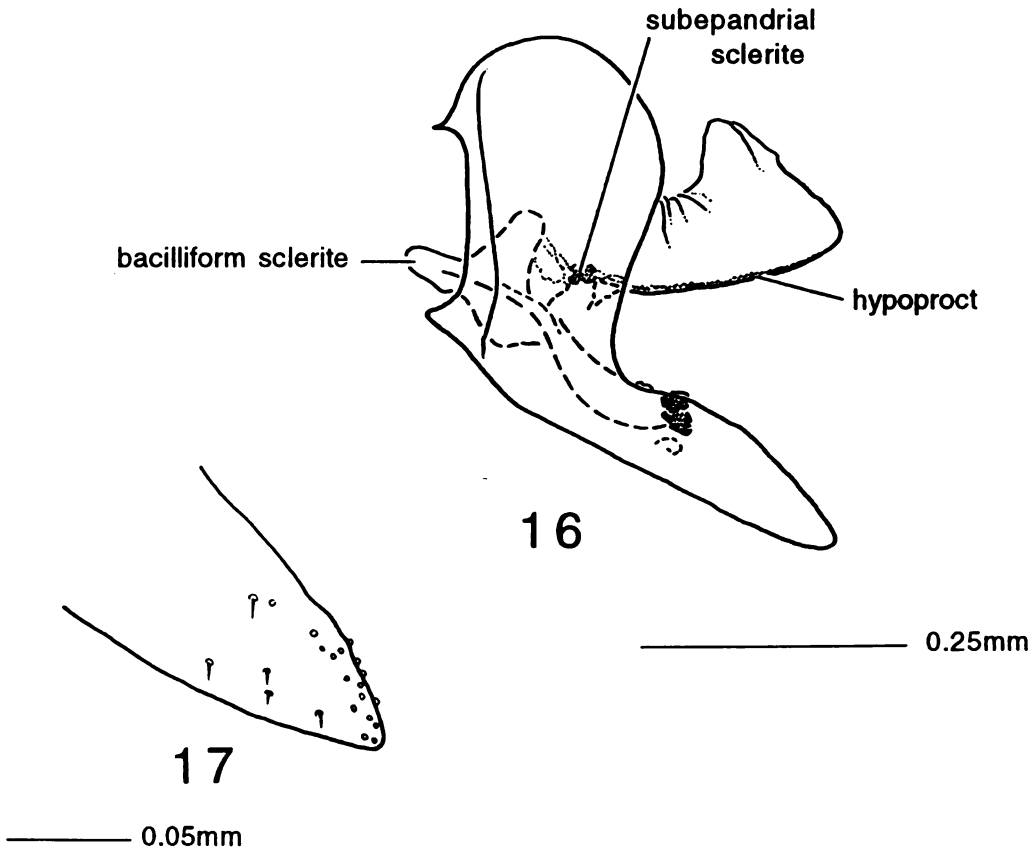


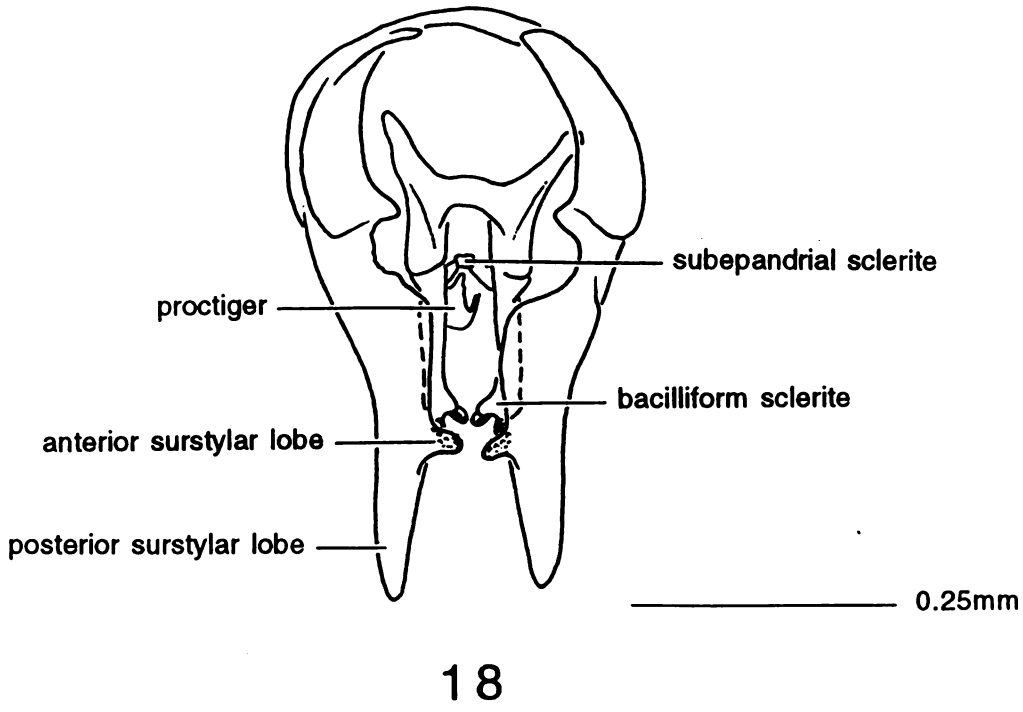




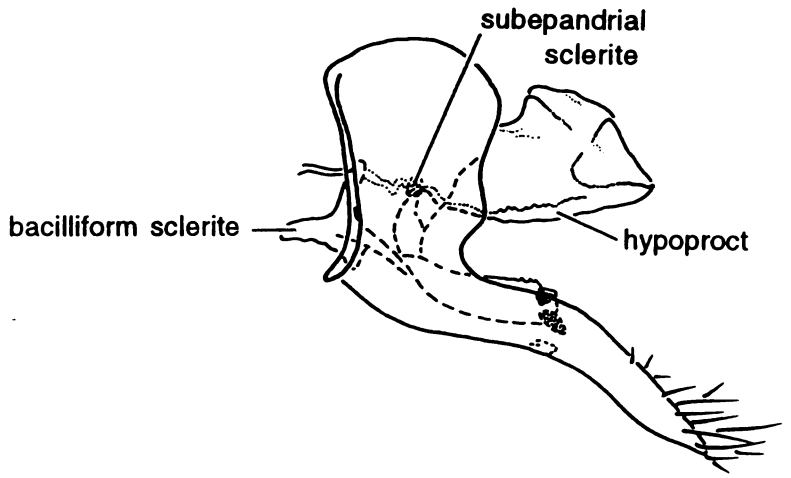


Figures 13—15. Epandrium and associated structures. 13, *Carpomya schineri* and 14, *Rhagoletis cerasi*, left lateral view. 15, *Rhagoletis cerasi*, right surstylus, medial view.





Figures 16—18. Epandrium and associated structures of *Rhagoletis berberidis*. 16, Left lateral view. 17, Tip of left surstylus, lateral view. 18, Anterior view.



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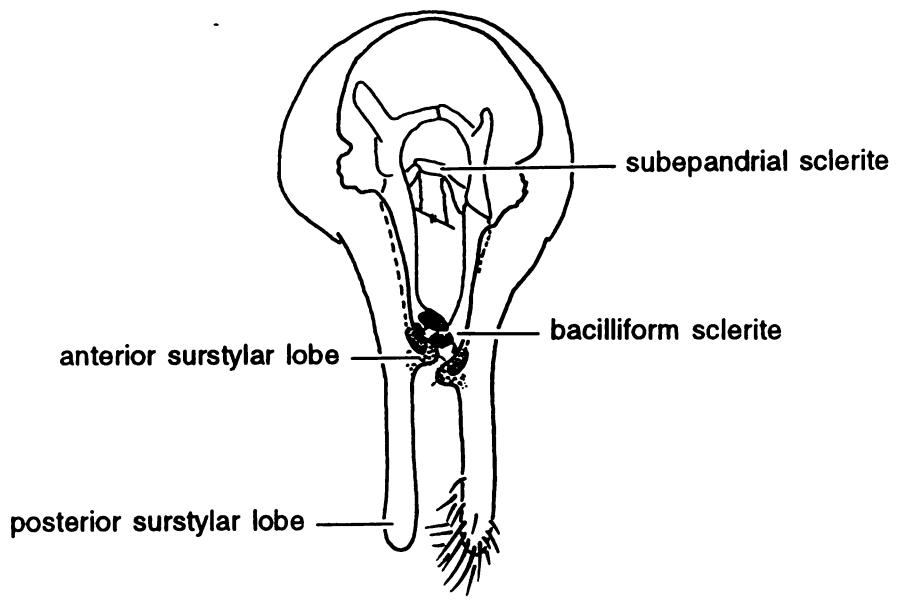

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Figures 19—20. Epandrium and associated structures of *Rhagoletis cingulata*. 19, Left lateral view. 20, Anterior view (proctiger and setae on right surstylus omitted).

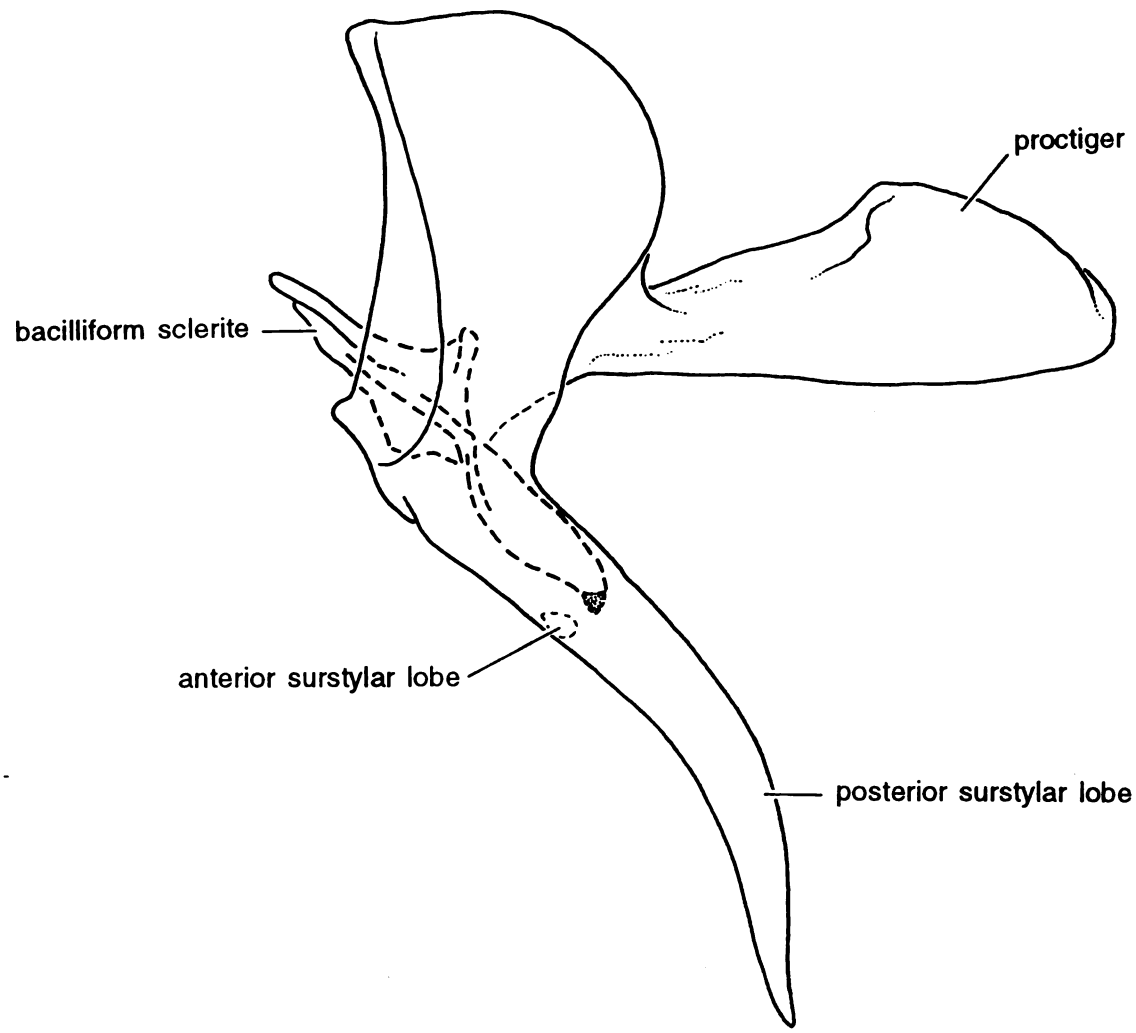


Figure 21. Epandrium and associated structures of *Rhagoletis magniterebra*, left lateral view.

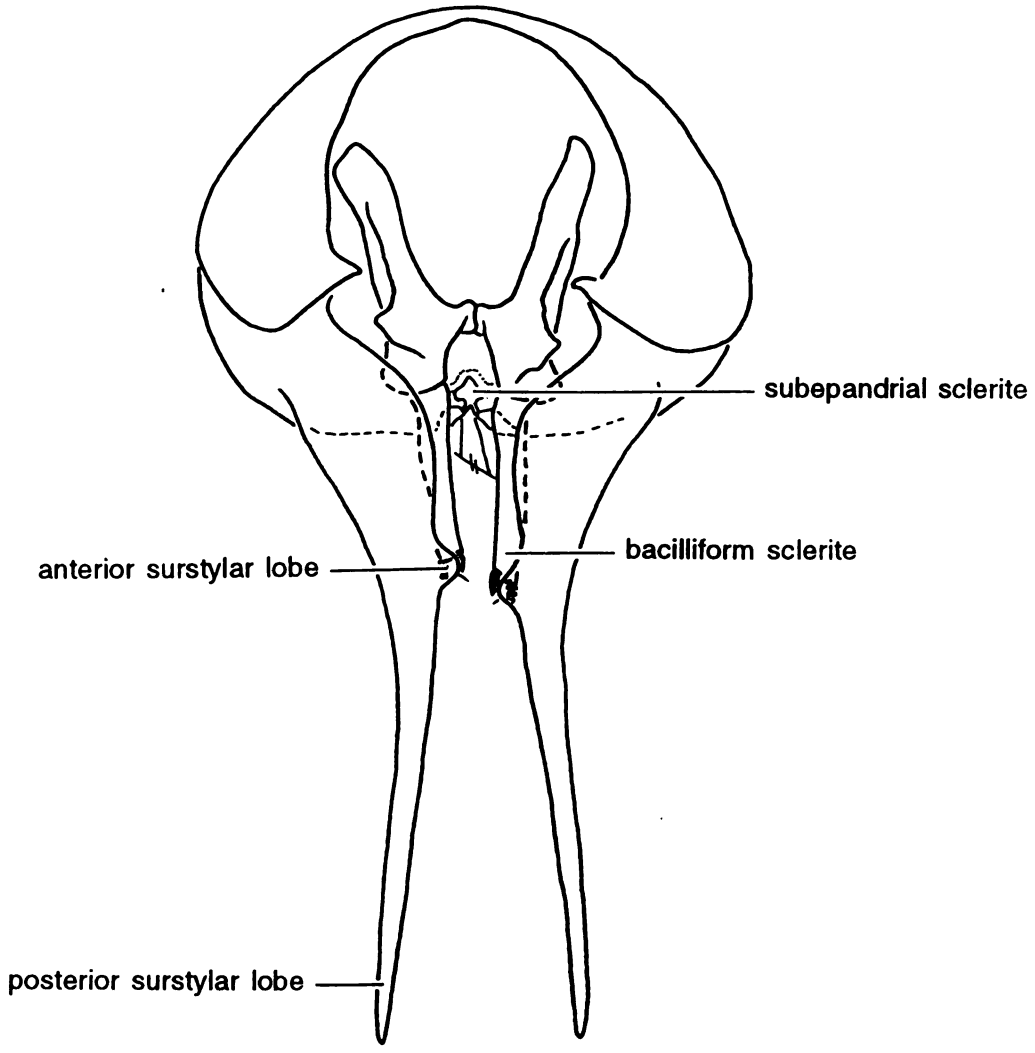
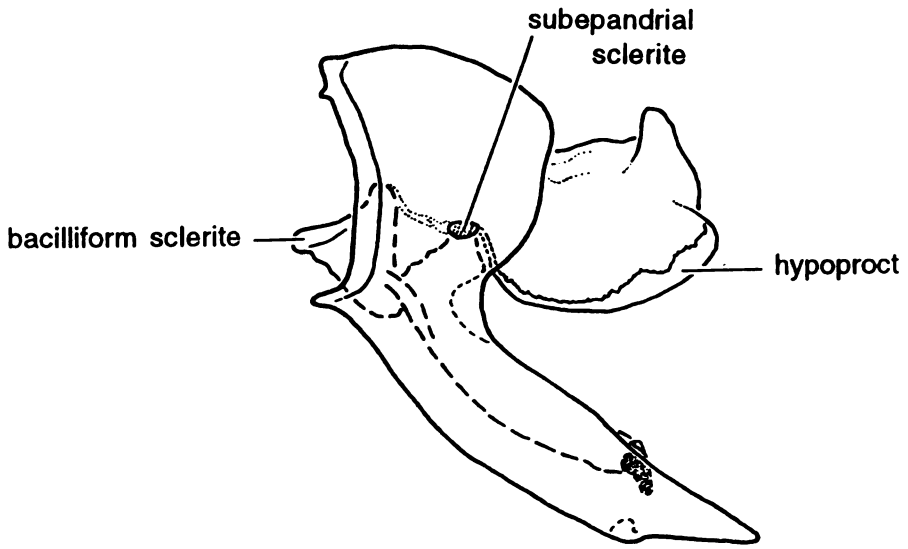


Figure 22. Epandrium and associated structures of *Rhagoletis magniterebra*, anterior view (proctiger omitted).



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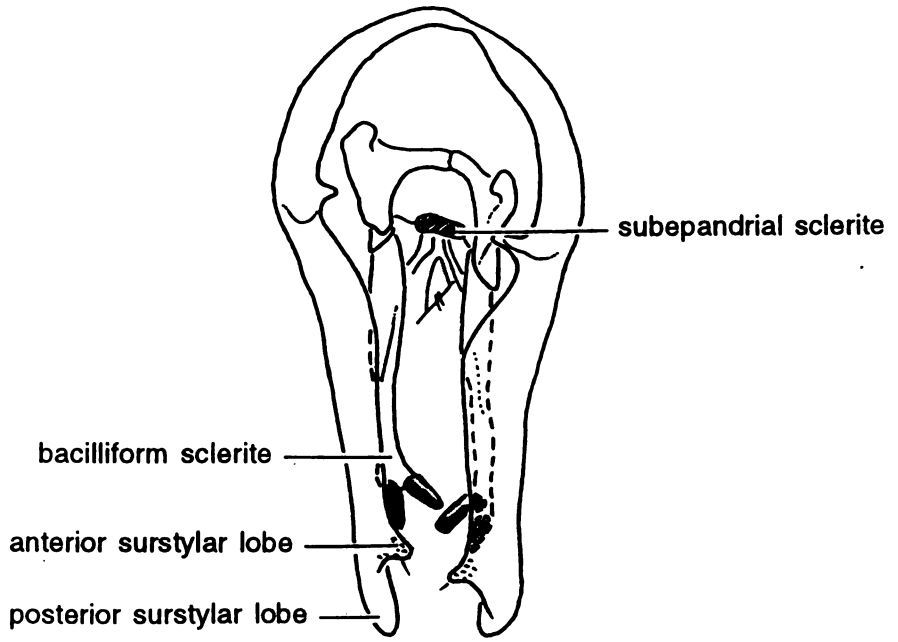

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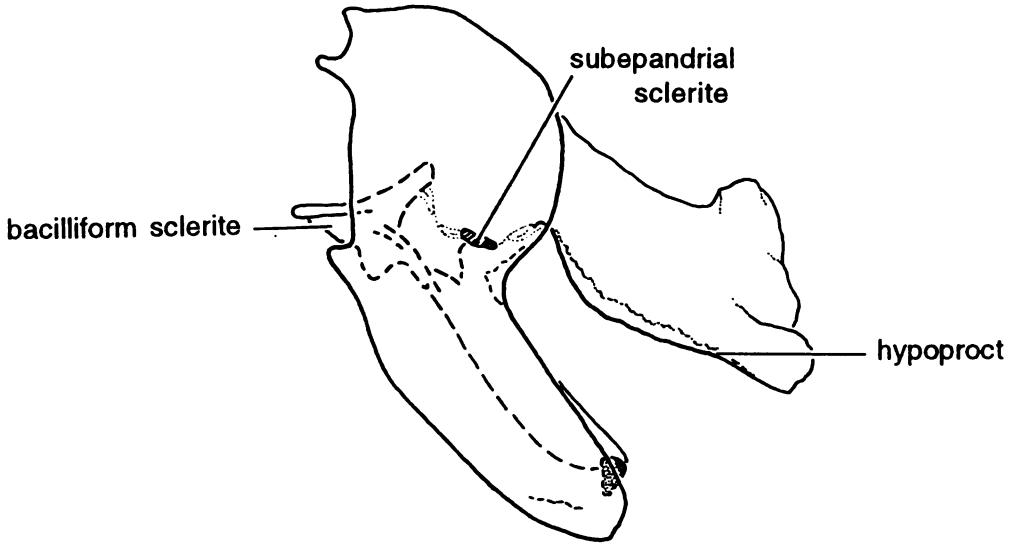
Figures 23—24. Epandrium and associated structures of *Rhagoletis psalida*. 23, Left lateral view. 24, Anterior view (proctiger omitted).



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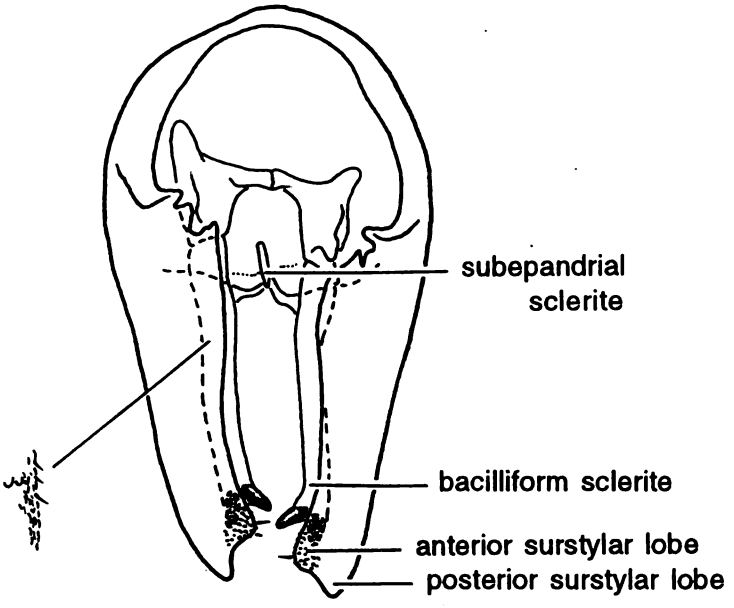

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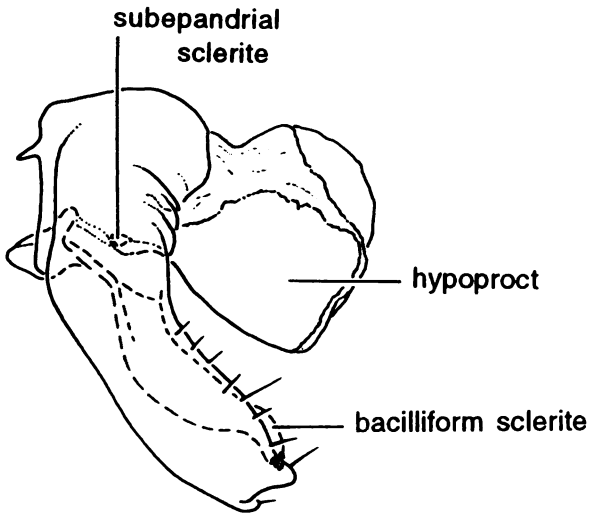
Figures 25—26. Epandrium and associated structures of *Rhagoletis striatella*. 25, Left lateral view. 26, Anterior view (proctiger omitted).



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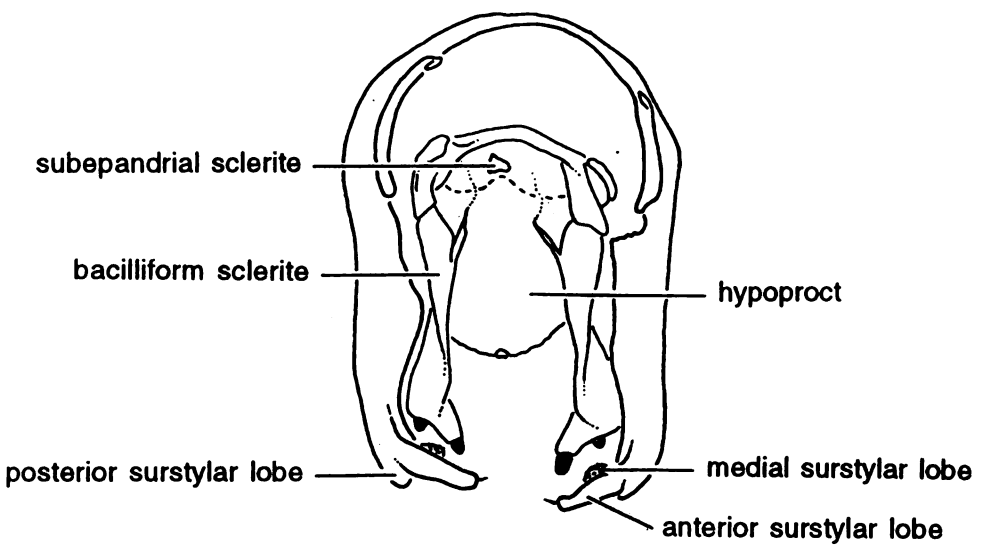

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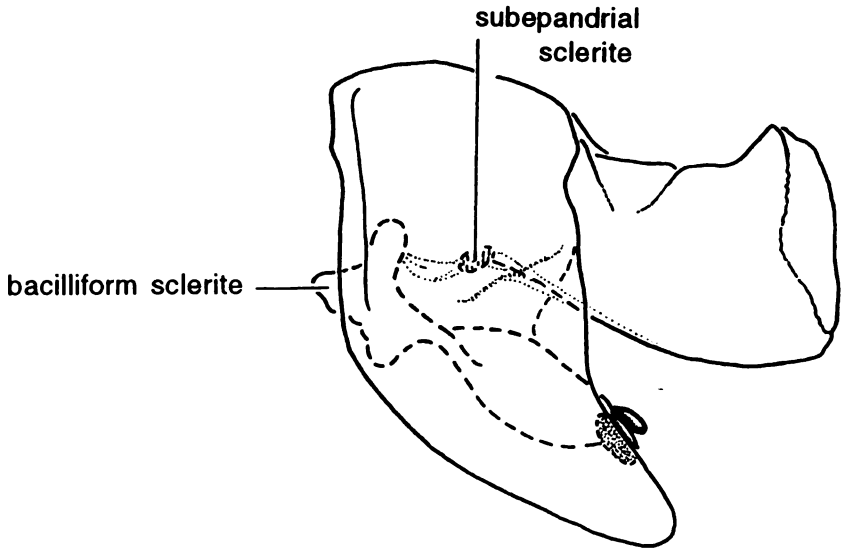
Figures 27—28. Epandrium and associated structures of *Trypeta inaequalis*. 27, Left lateral view. 28, Anterior view.



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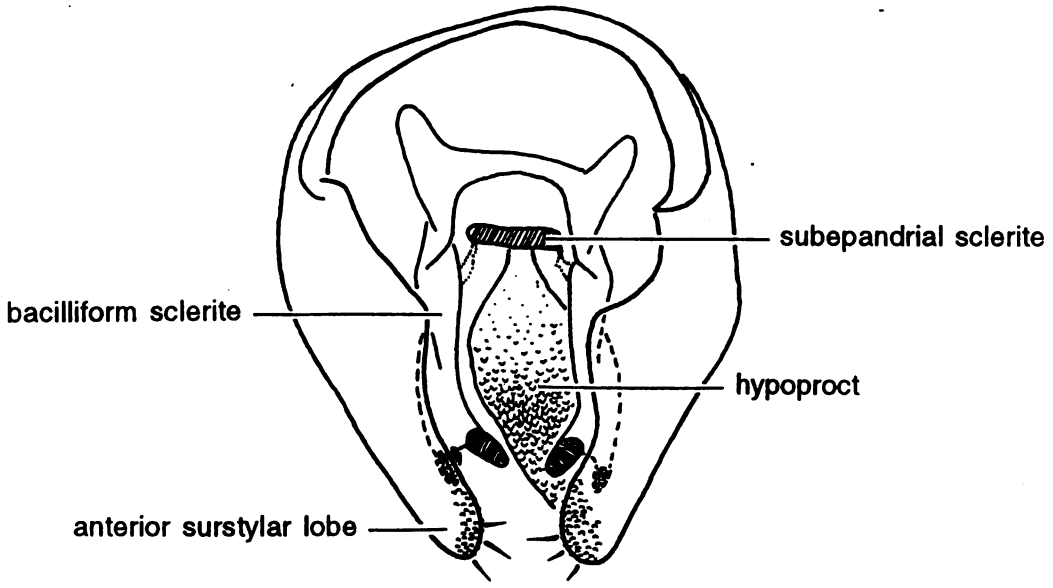

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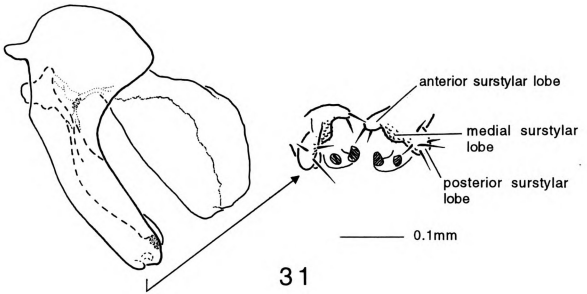
Figures 29—30. Epandrium and associated structures of *Zonosemata electa*. 29, Left lateral view. 30, Anterior view.



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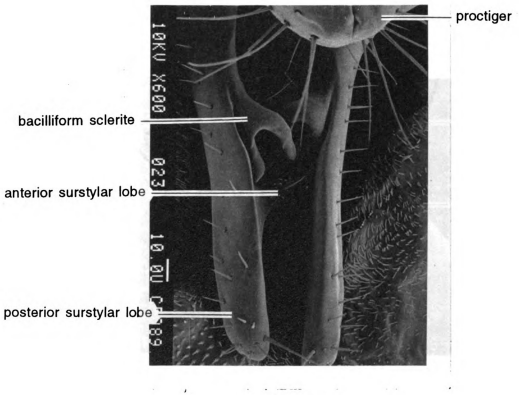

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Figures 31—32. 31, Tips of surstyli, *Acidia cognata*, ventral view. 32, Micrograph, surstyli, *Rhagoletis pomonella*, posterior view.

33 0.1mm 34

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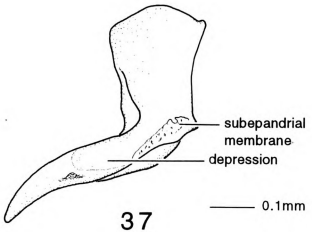

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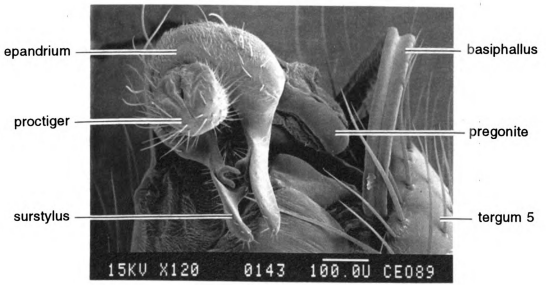
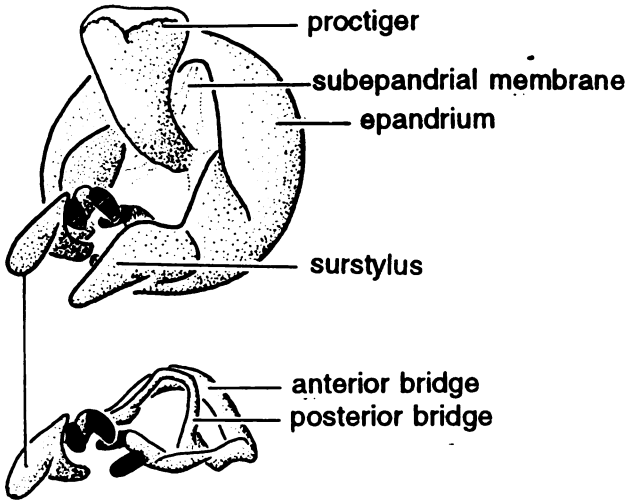


38

Figures 33—38. 33—34, Left bacilliform sclerite, *Rhagoletis pomonella*. 33, Lateral view. 34, Medial view. 35—36, Prensisetae, posterior view. 35, *Rhagoletis alternata*. 36, *Acidia cognata*. 37, Left half epandrium and surstylus, *Rhagoletis pomonella*, medial view. 38, Micrograph, genitalia, *Rhagoletis pomonella*, posterior view.



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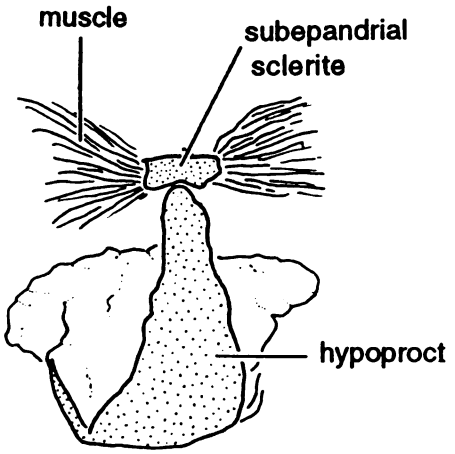

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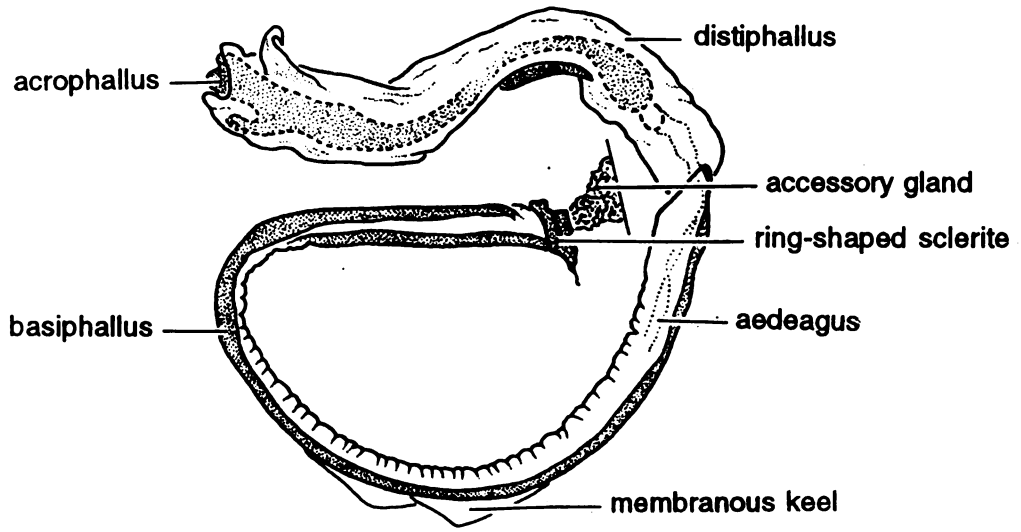

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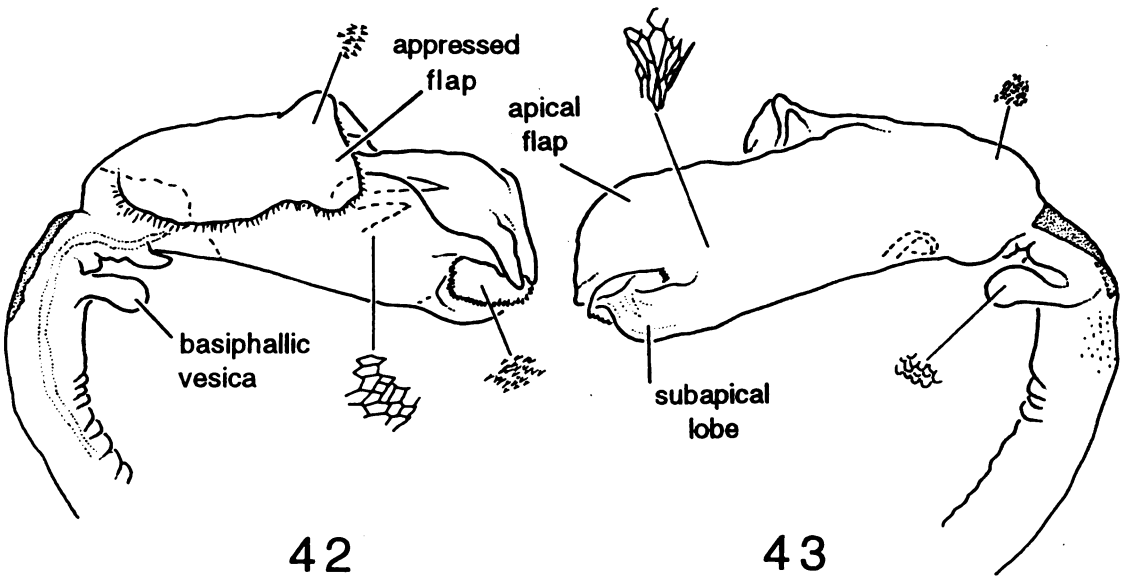
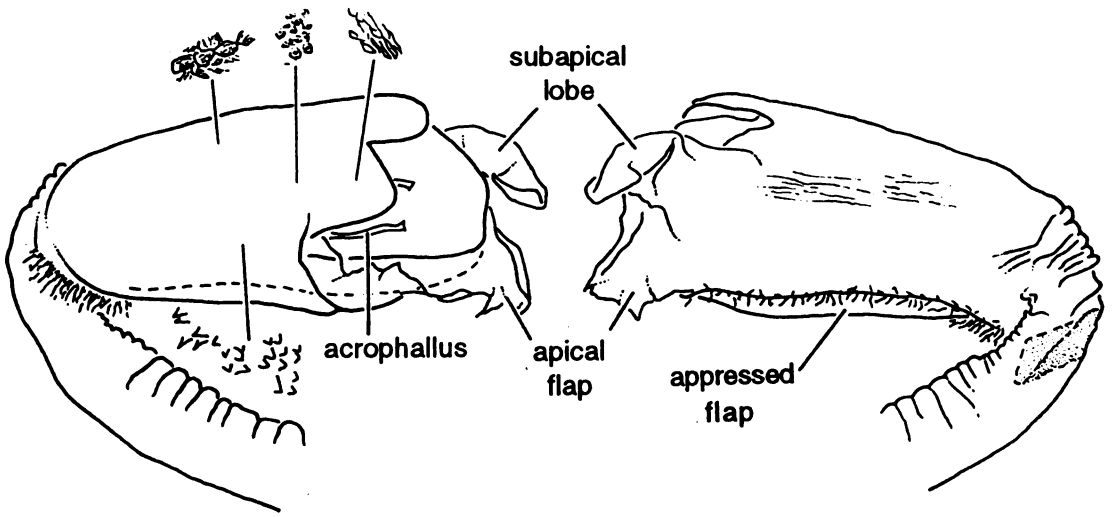
Figures 39—41, Genital structures and proctiger. 39, Bacilliform sclerites (diagrammatic), *Rhagoletis pomonella*, posterolateral view. 40, Proctiger (slide-mounted), *Rhagoletis pomonella*, ventral view. 41, Phallus, *Cryptodacus tau*, left lateral view.



42 43



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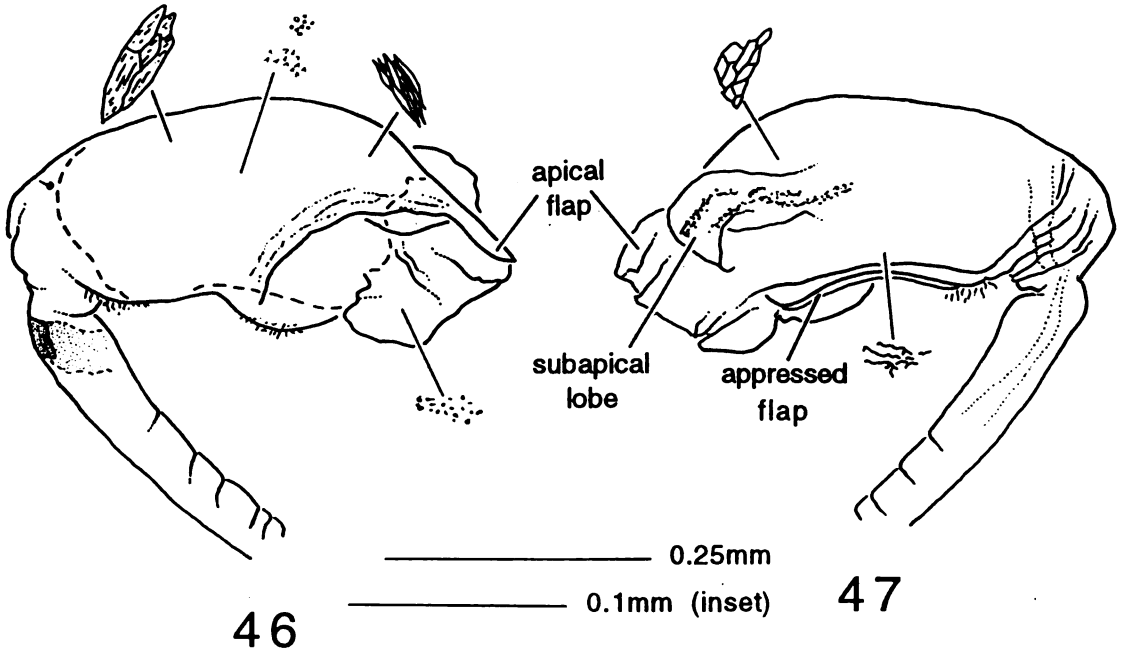
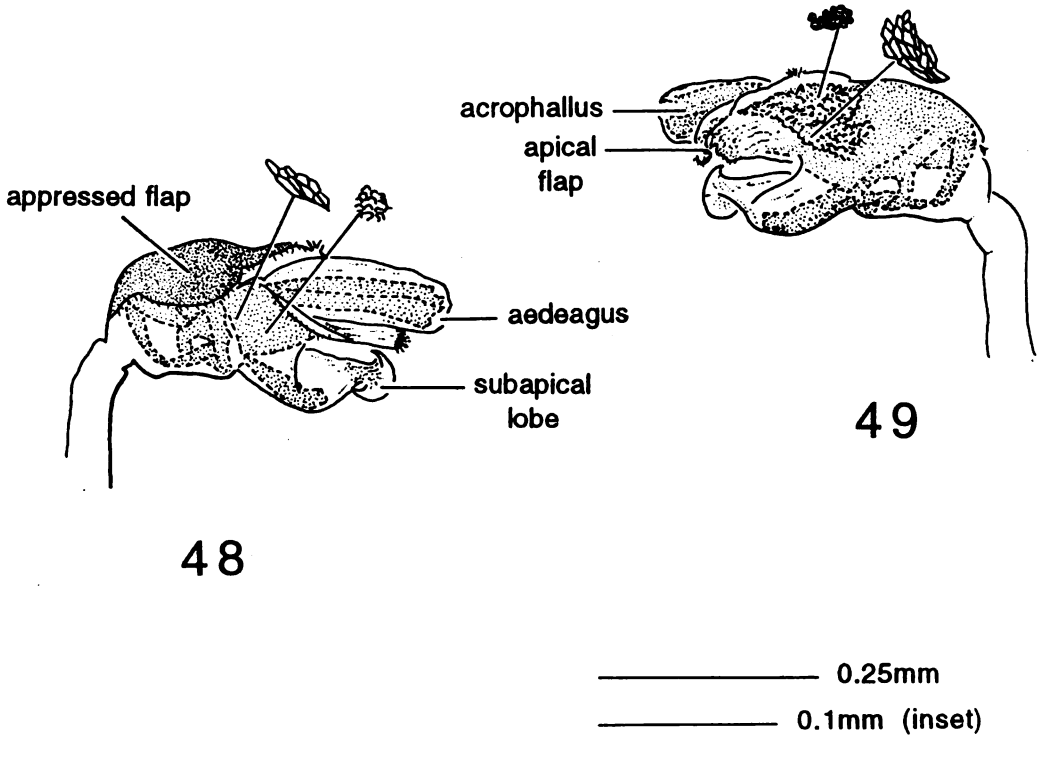
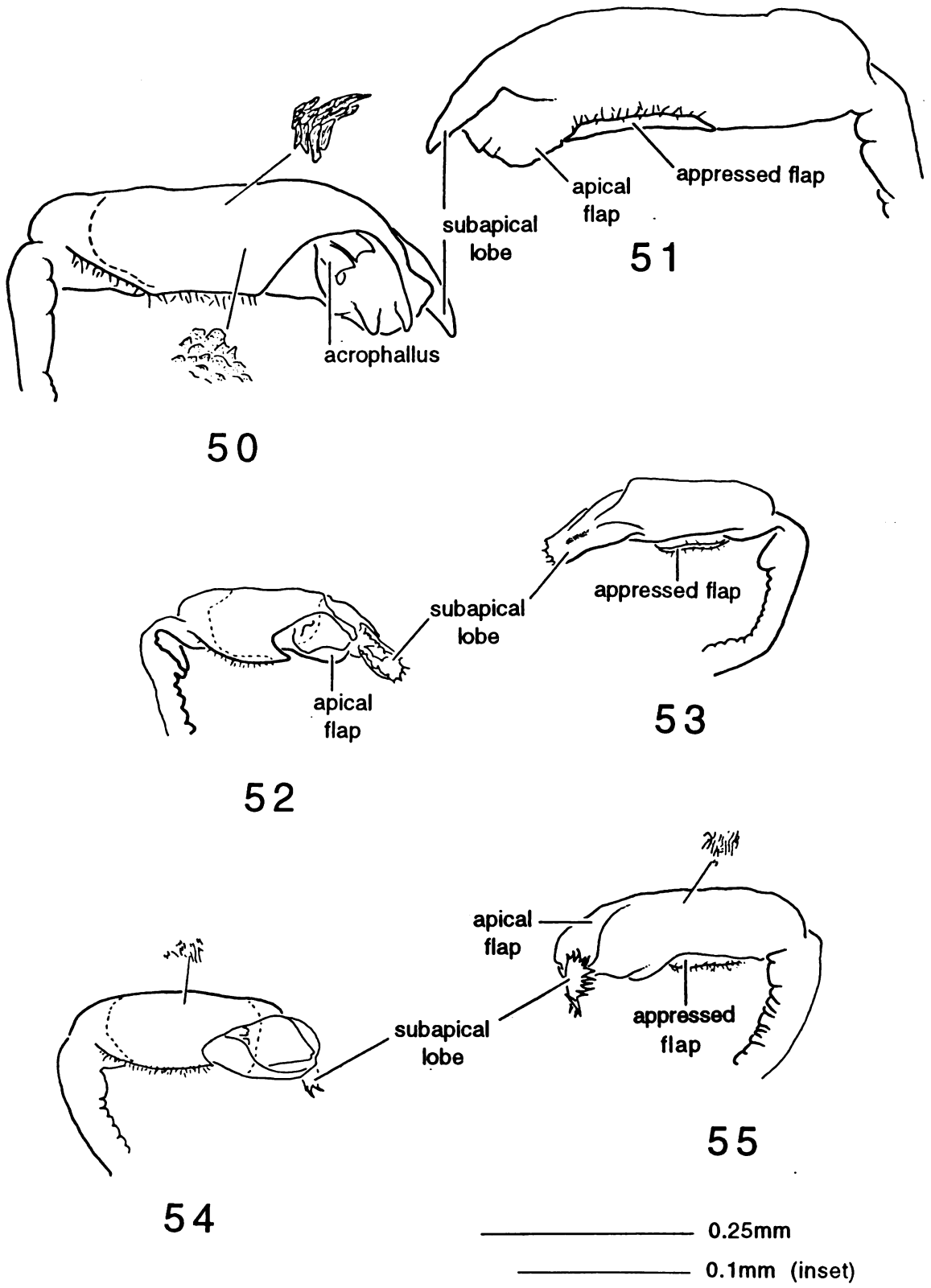
Figures 42—45, Distiphallus. 42—43, *Paraterellia immaculata*, right and left lateral views. 44—45, *Oedicarena persuasa*, right and left lateral views.

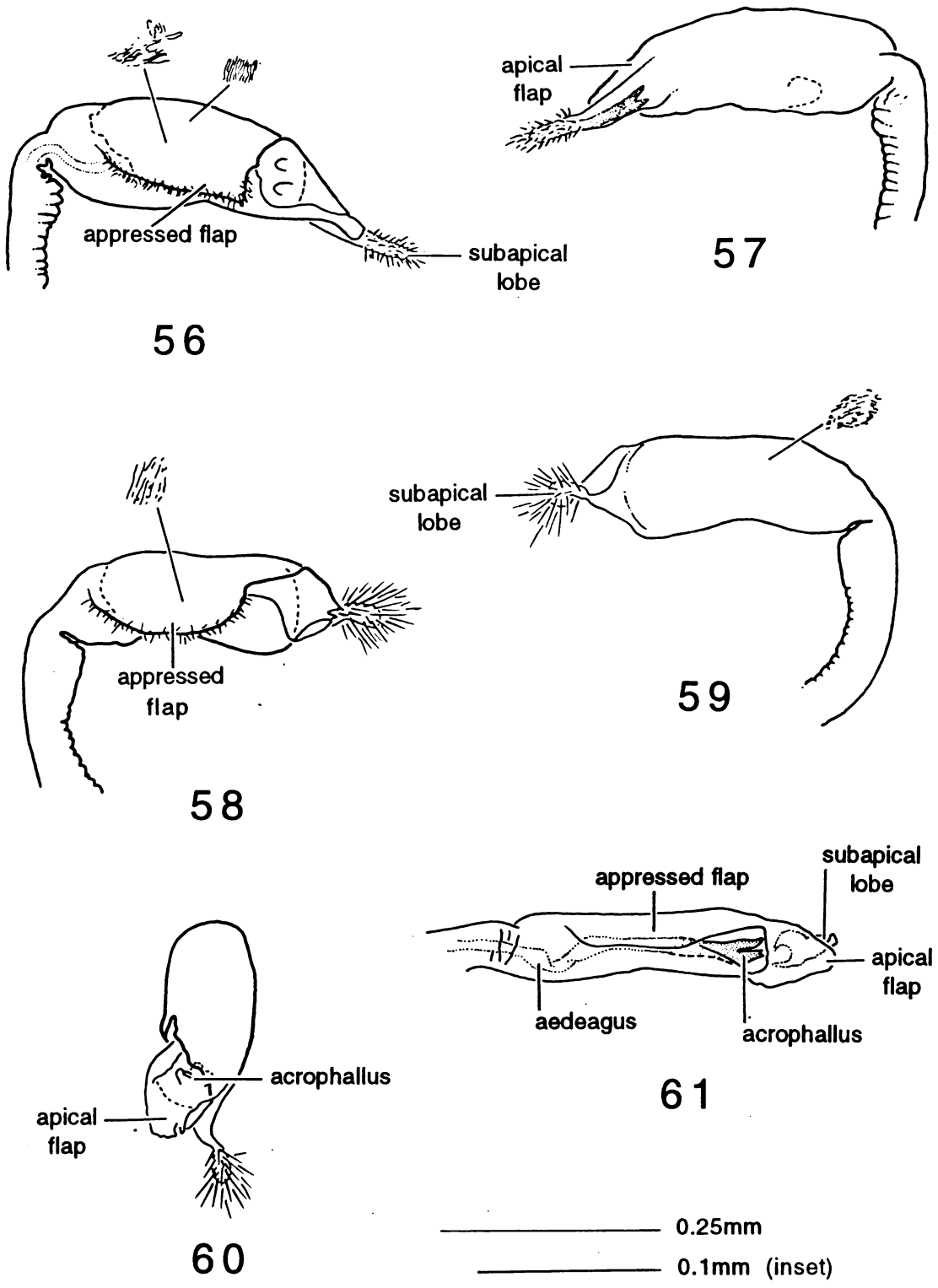




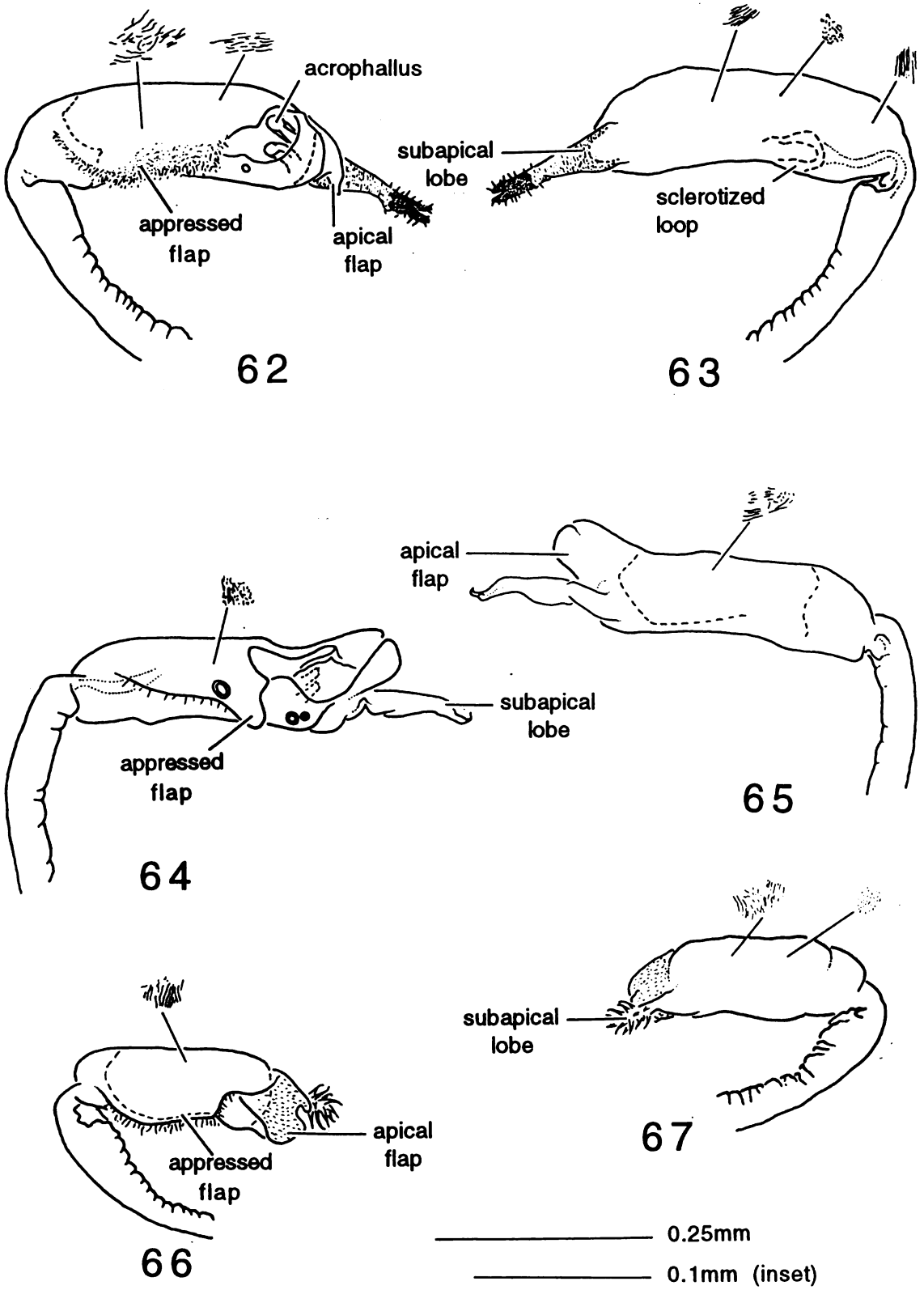
Figures 46—49, Distiphallus, right and left lateral views. 46—47, *Trypeta inaequalis*. 48—49, *Epochra canadensis*.



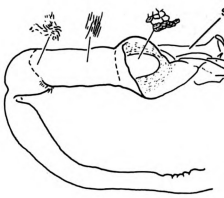
Figures 50—55, Distiphallus, right and left lateral views. 50—51, *Rhagoletis adusta*. 52—53, *Rhagoletis cerasi*. 54—55, *Rhagoletis cingulata*.



Figures 56—61, Distiphallus. 56—57, *Rhagoletis nova*, right and left lateral views. 58—59, *Rhagoletis pomonella*, right and left lateral views. 60, *Rhagoletis pomonella*, dorsoapical view. 61, *Rhagoletis magniterebra*, dorsolateral view.



Figures 62—67, Distiphallus, right and left lateral views. 62—63, *Rhagoletis psalida*. 64—65, *Rhagoletis striatella*. 66—67, *Rhagoletis suavis*.



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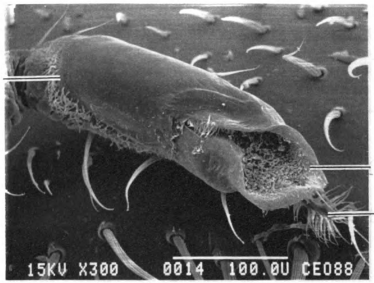

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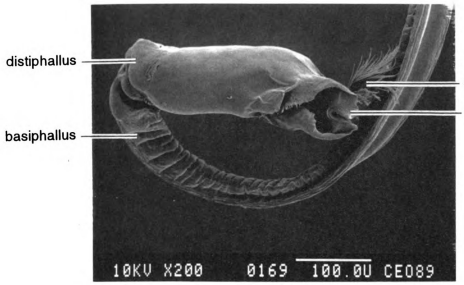
Figures 68—69, Distiphallus, right lateral view. 68, *Chetostoma rubidium*. 69, Micrograph, *Rhagoletis suavis*.



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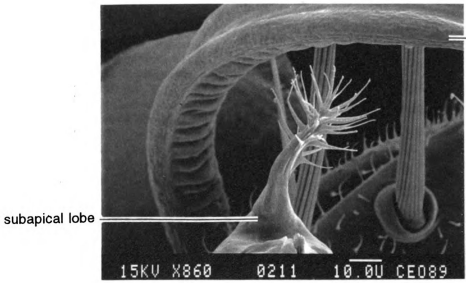

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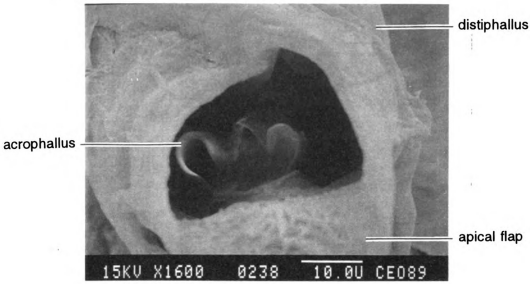
Figures 70—71, Micrographs, distiphallus, right lateral view. 70, *Rhagoletis pomonella*. 71, *Rhagoletis suavis*.



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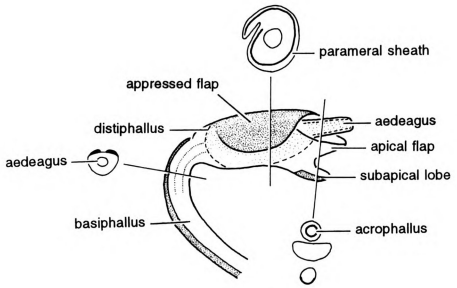
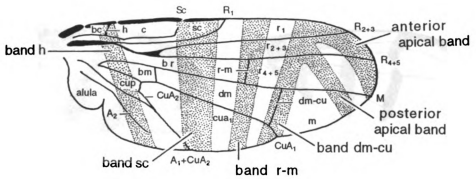


73

Figures 72—73, Phallus. 72, *Rhagoletis completa*, apical view. 73, Phallus ground plan, right lateral view (cross sections: bold lines = sclerotized, plain lines = membranous).



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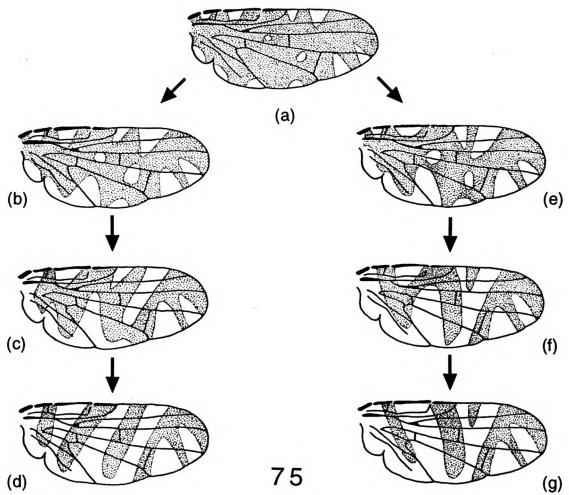
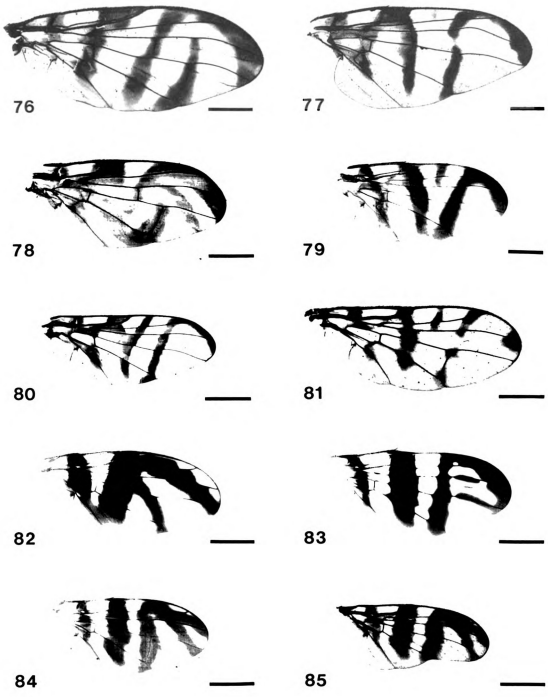
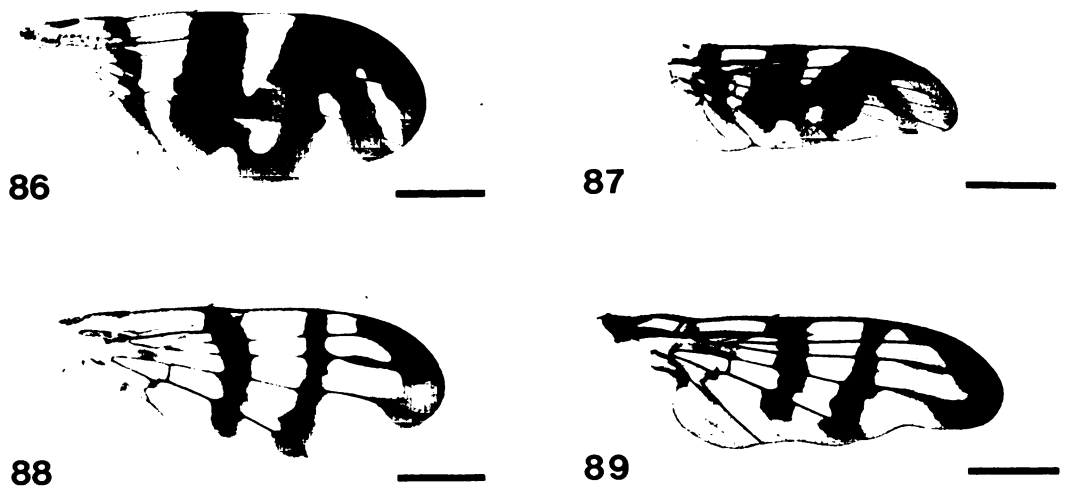


75

Figures 74—75. 74, Generalized wing showing venation and names of wing bands. 75, Evolution of banded wing patterns in the Trypetini. (a) Hypothetical ground plan pattern. (b—d) Evolution of wing pattern with proximal subcostal band prominent and band r-m complete. (e—g) Evolution of wing pattern with distal subcostal band prominent and band r-m truncated. See text.



Figures 76—85. Wing patterns of trypetines. 76, *Epochra canadensis*. 77, *Chetostoma curvinerve*. 78, *Euleia fratria*. 79, *Zonosemata electa*. 80, *Paraterellia ypsilon*. 81, *Oedicarena nigra*. 82, *Rhagoletis pomonella*. 83, *Rhagoletis zoqui*. 84, *Rhagoletis chionanthi* (normal wing shape). 85, *Rhagoletis chionanthi* (abnormal wing shape). Scale bars equal 1mm.



Figures 86—89. Wing patterns of *Rhagoletis*. 86, *Rhagoletis fausta* (normal wing shape). 87, *Rhagoletis fausta* (abnormal wing shape). 88, *Rhagoletis juglandis* (normal wing shape). 89, *Rhagoletis juglandis* (abnormal wing shape). Scale bars equal 1mm.

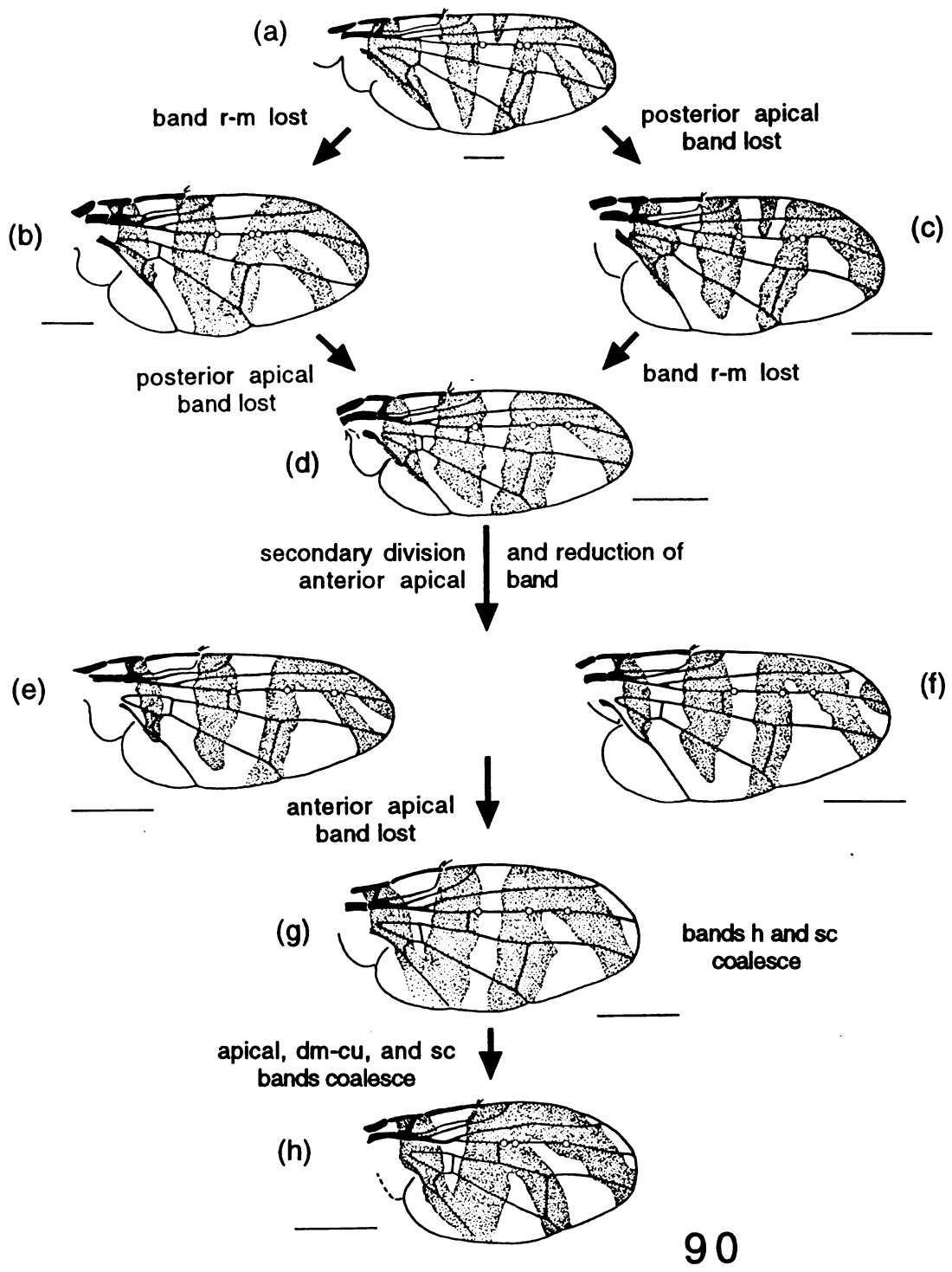


Figure 90. Transformation series for wing patterns in *Rhagoletis*. (a) *Rhagoletis blanchardi*, (b) *Rhagoletis striatella*, (c) *Rhagoletis cerasi*, (d) *Rhagoletis completa*, (e) *Rhagoletis indifferens*, (f) *Rhagoletis cingulata*, (g) *Rhagoletis tabellaria*, (h) *Rhagoletis zephyria*. Circles on vein R_{4+5} indicate position of campaniform sensilla. Scale bars equal 1mm. Drawings of wings were made using a drawing tube attached to a stereo microscope.

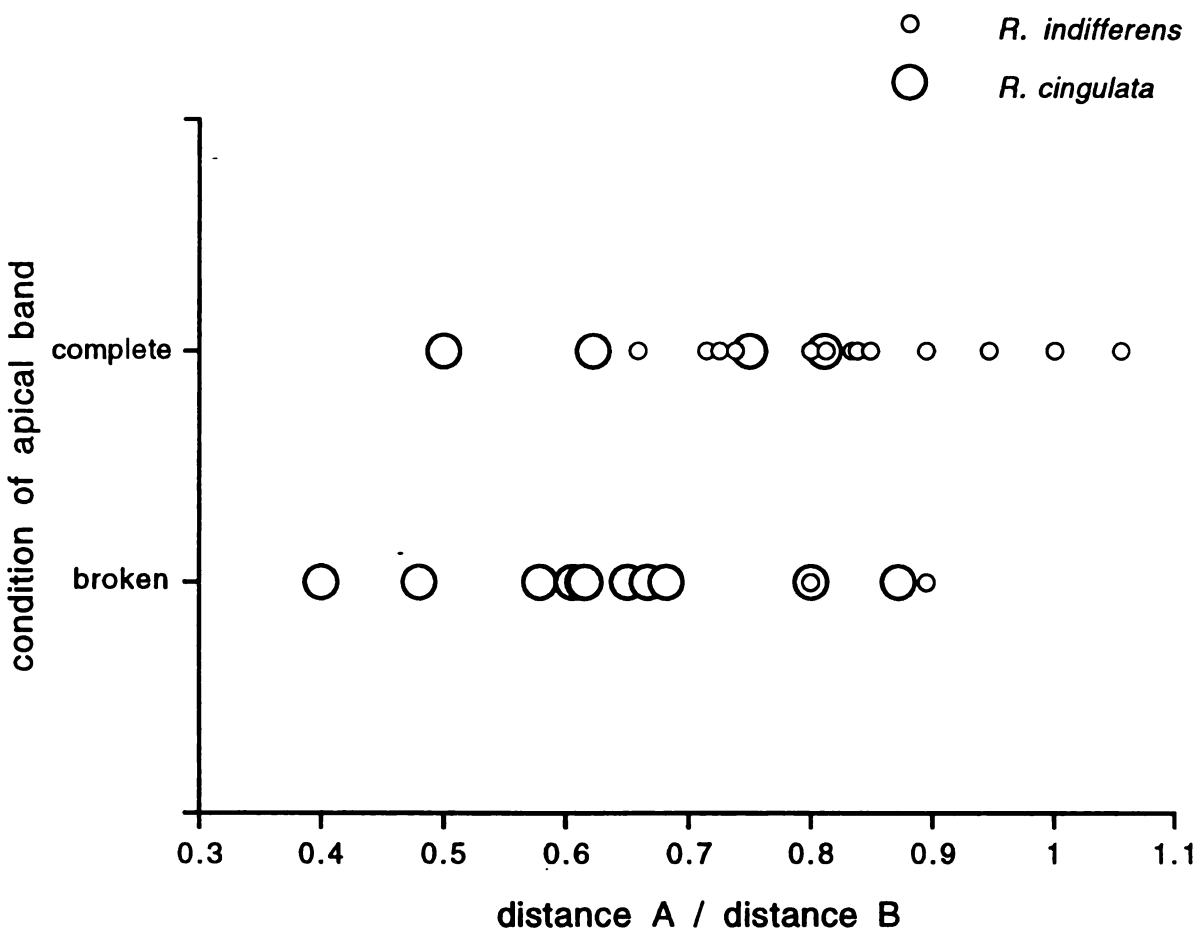
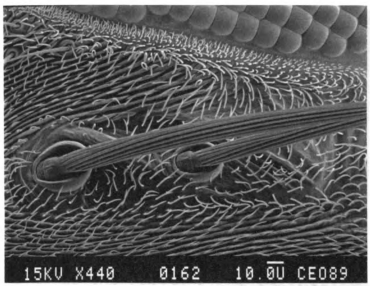


Figure 91. Relationship between condition of apical band and ratio of distance between the two distal sensilla on vein R4+5 (distance A) to the distance between the distal most sensillum and apex of vein R4+5 (distance B) in *R. cingulata* and *R. indifferens*.



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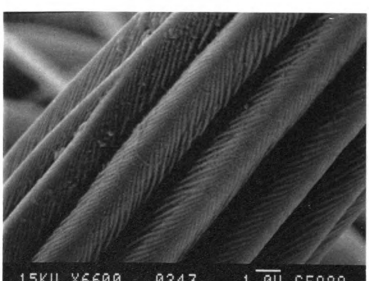

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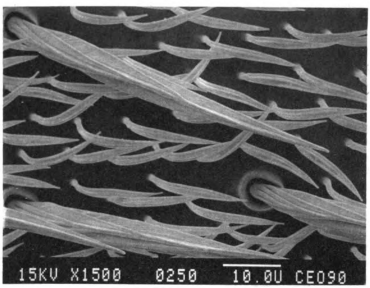
Figures 92—93. Scanning electron micrographs of setae of *Rhagoletis* species. 92, Right orbital setae of *R. pomonella* showing longitudinal grooves. 93, Right upper frontal seta of *R. completa* showing oblique striations lying in longitudinal grooves.



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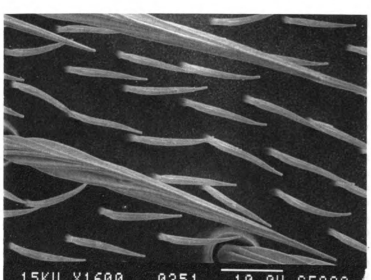

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Figures 94—95. Scanning electron micrographs of scutal microtrichia of *Rhagoletis pomonella*. 94, Microtrichia from lateral microtrichiose stripe. 95, Microtrichia from between sublateral and lateral microtrichiose stripes.

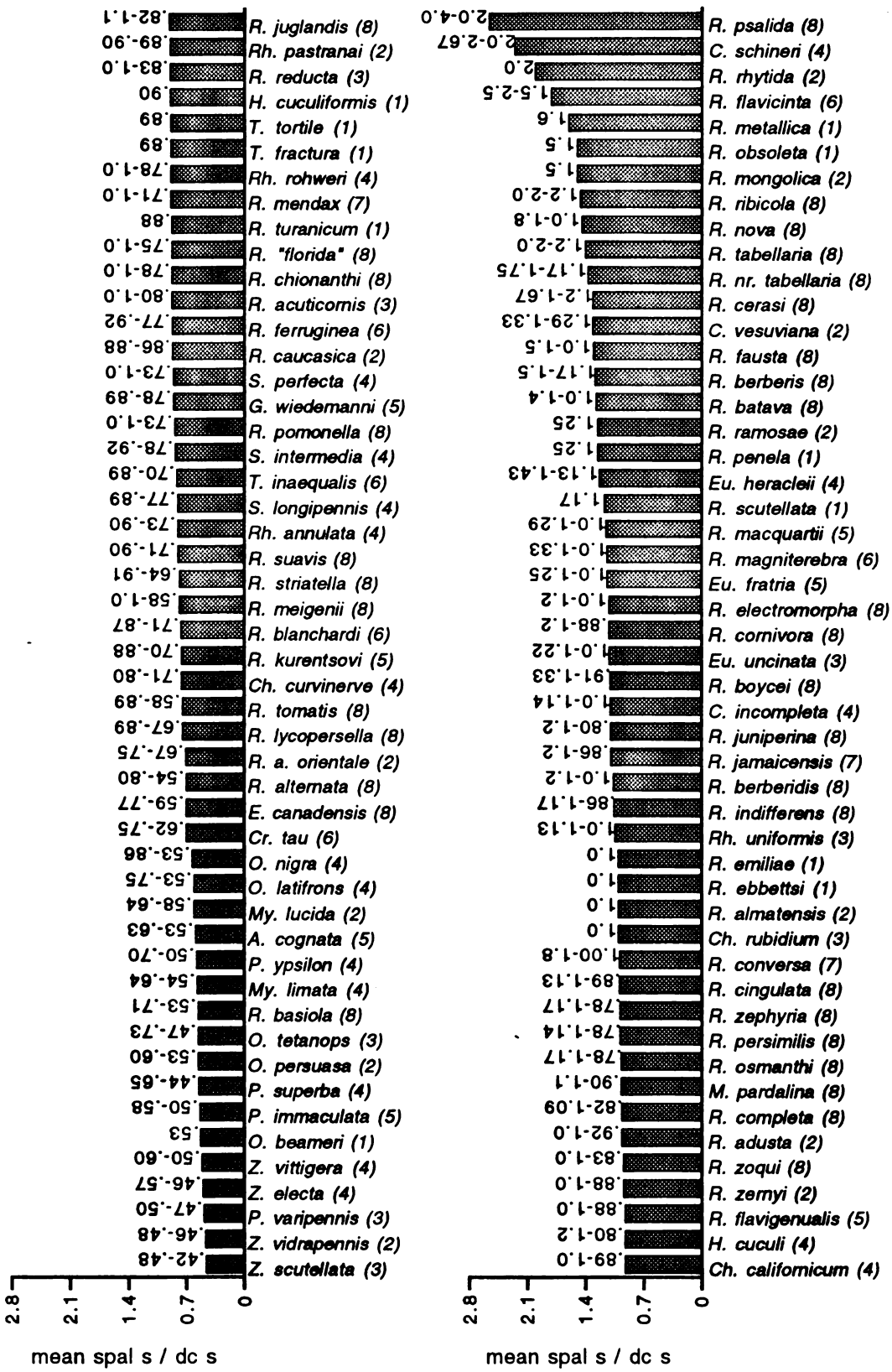


Figure 96. Mean ratio of distance, measured from transverse suture, of the supra-alar seta (spal s) to the dorsocentral seta (dc s). Number in parentheses after species is sample size; range of the ratio is given above bars. See text.

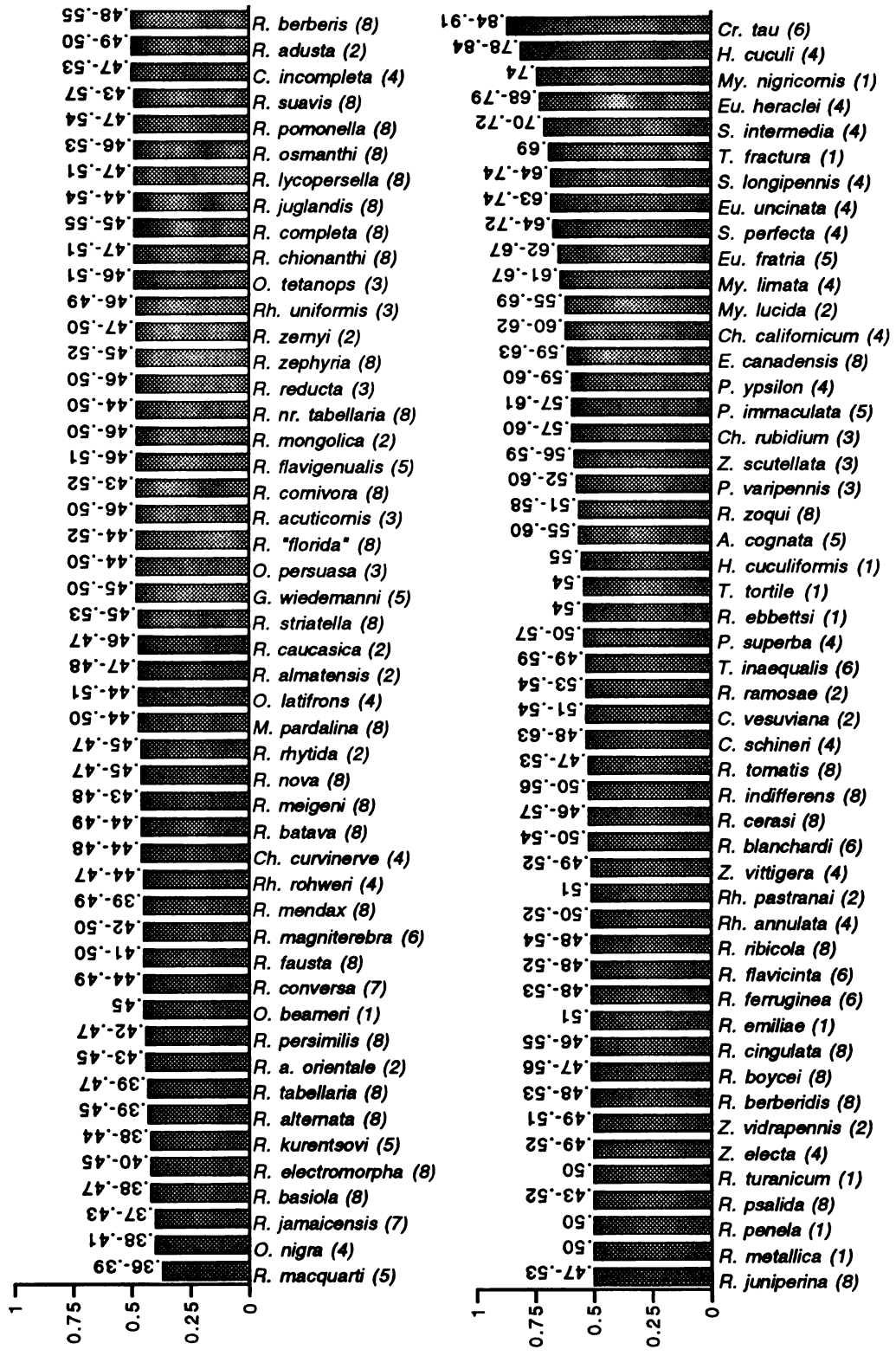


Figure 97. Mean position of crossvein r-m along vein M. Number in parentheses after species name is sample size; range of the ratio is given above bars. See text.

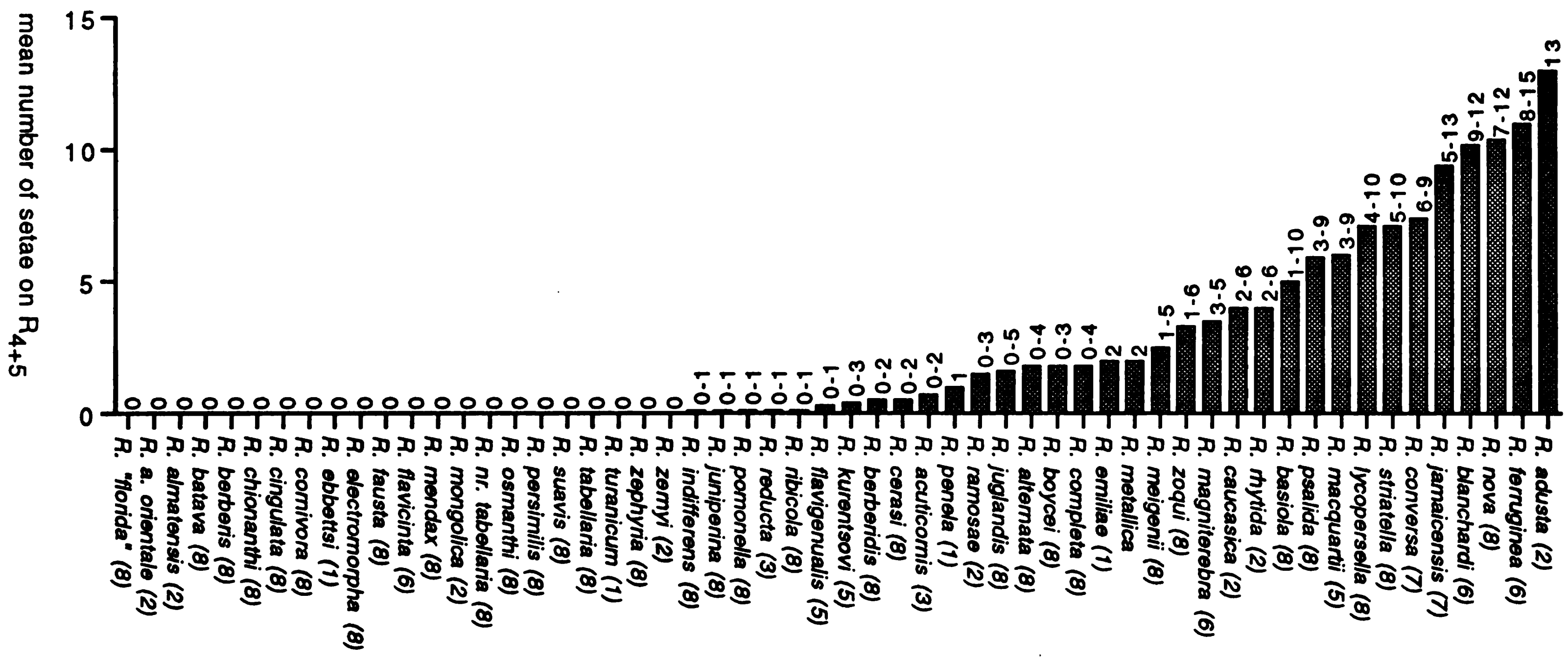


Figure 98. Mean number of setae on vein R4+5 dorsally beyond branching of vein Rs in *Rhagoletis*. Number in parentheses after species is sample size; range in number of setae is given above bars.

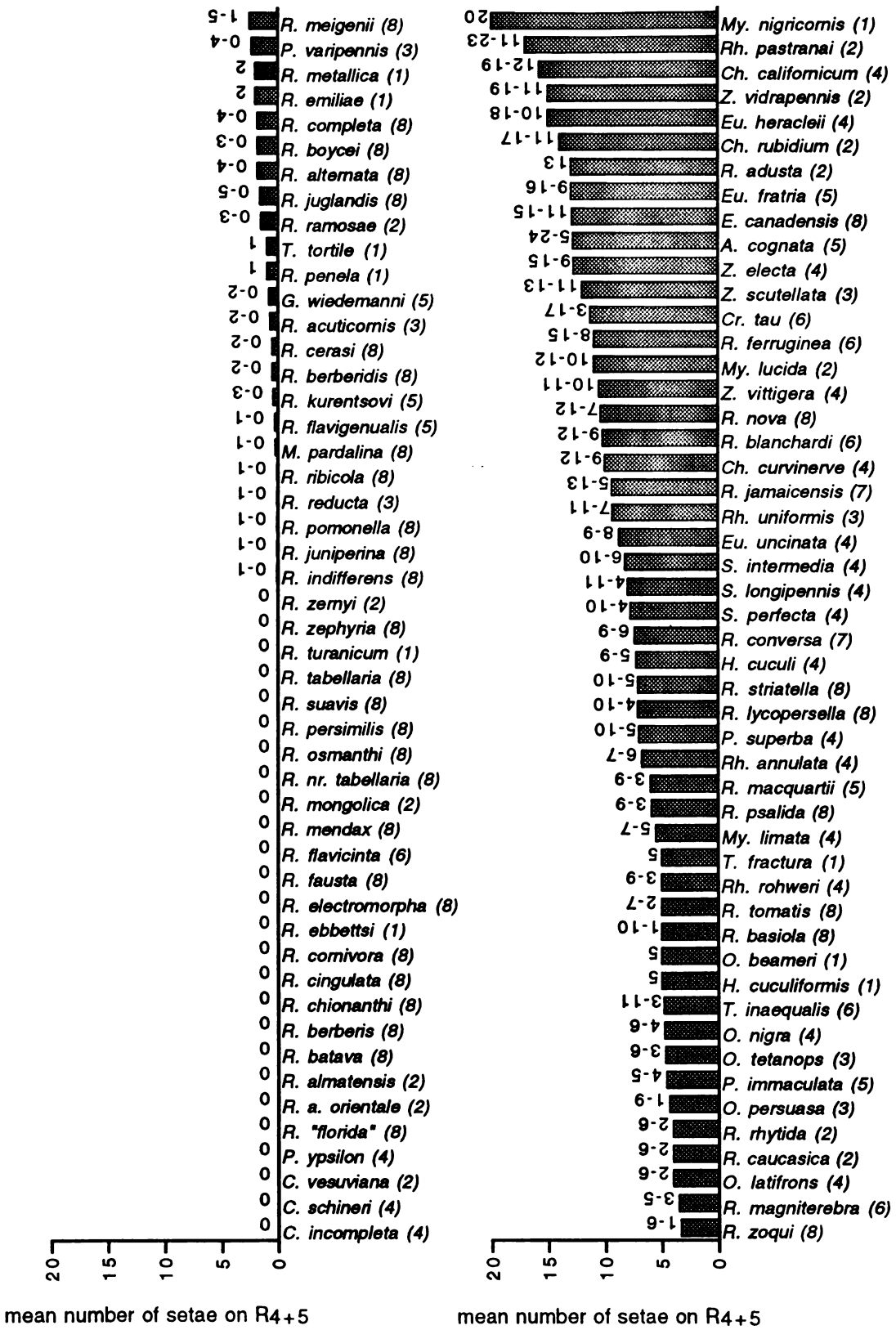


Figure 99. Mean number of setae on vein R4+5 dorsally beyond branching of vein Rs. Numbers in parentheses after species is sample size; range for number of setae is given above bars.

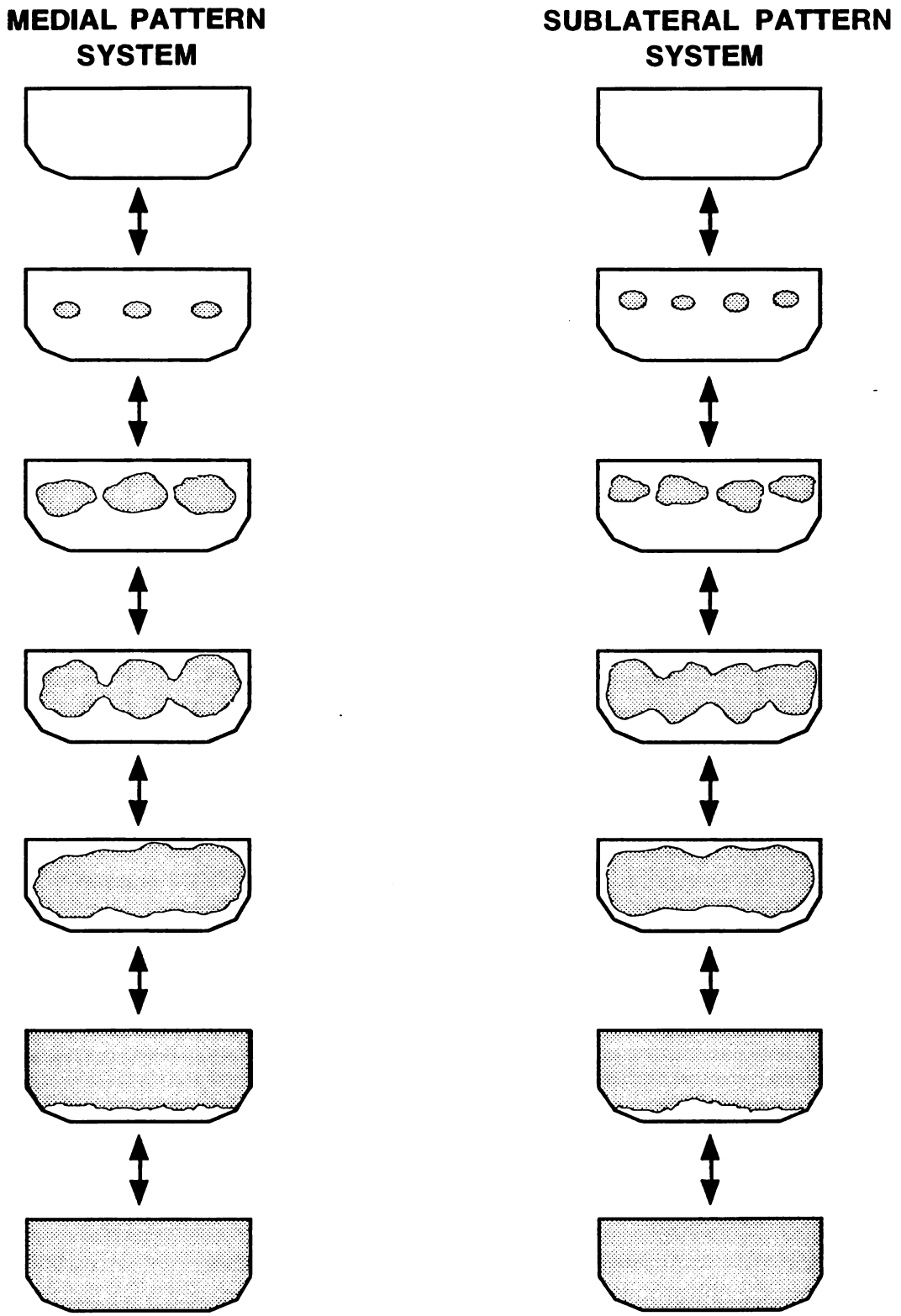


Figure 100. Transformation series for medial and sublateral pattern systems of tergal coloration. See text.

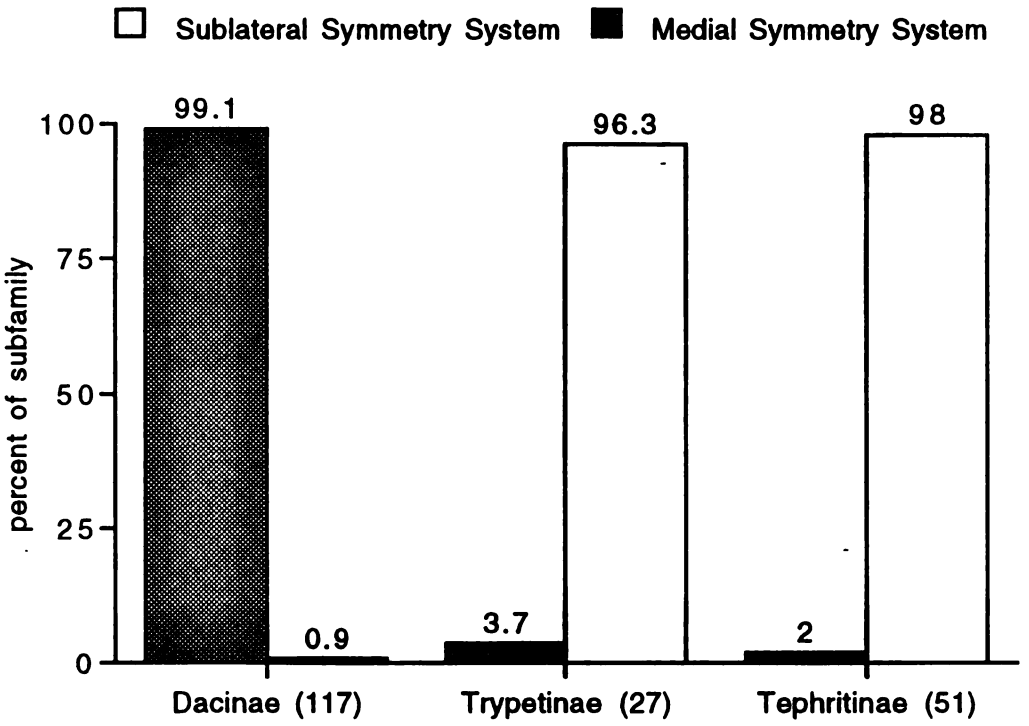
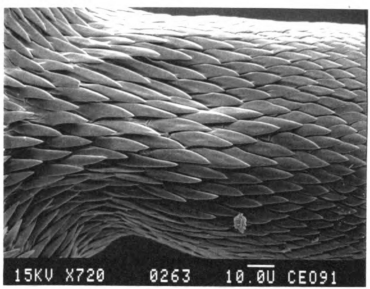


Fig. 101. Percent of species by symmetry system within subfamilies. Number in parentheses after subfamily is sample size. See text.



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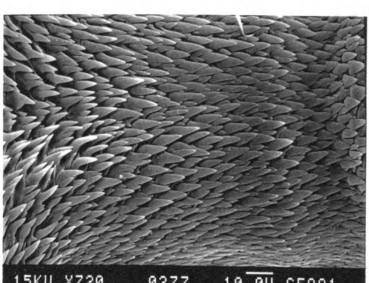

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Figures 102—103. Scanning electron micrographs of denticles on eversible ovipositor sheath of *Rhagoletis* species. 102, *R. cornivora*. 103, *R. pomonella*.

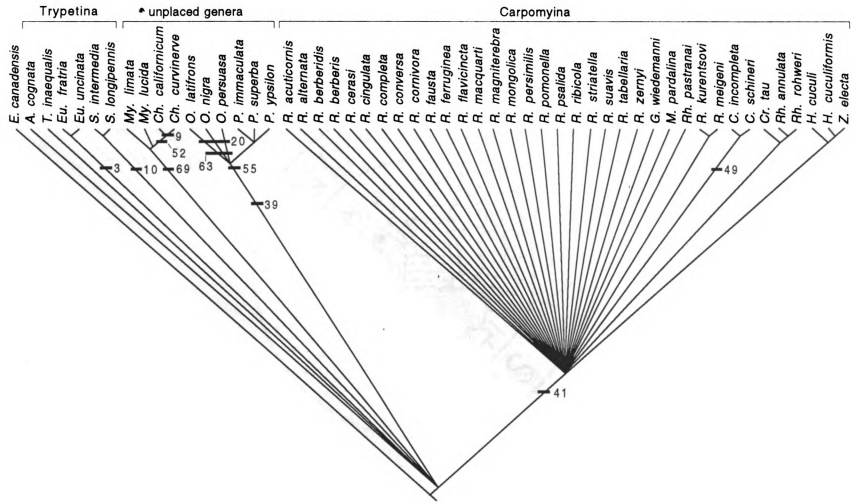

Figure 104. Strict consensus tree of 18,691 cladograms of length = 135, CI = 0.417, and RI = 0.748 (uninformative characters ignored). Bars represent synapomorphies; numbers refer to characters in Table 7. Subtribes are indicated along the top of the tree.

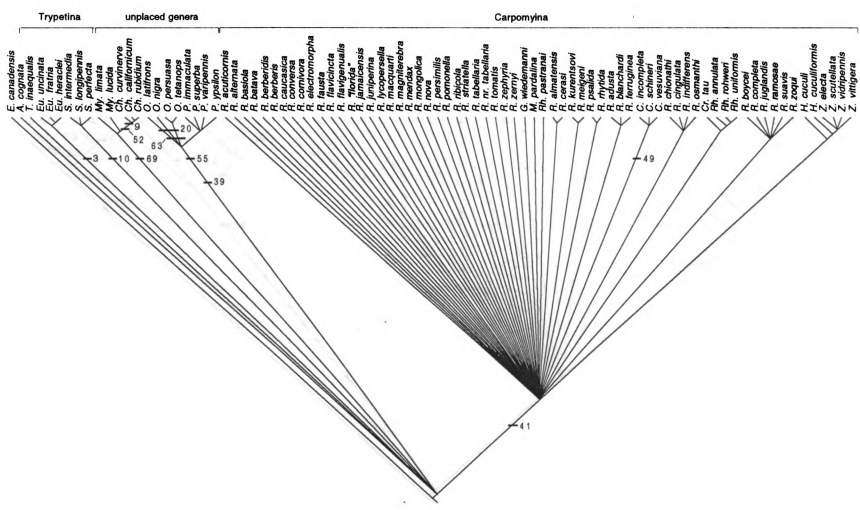

Figure 105. Strict consensus tree of 1,000 cladograms of length = 135, CI = 0.430, and RI = 0.848. Bars represent synapomorphies; numbers refer to characters. Subtribes are indicated along the top of the tree.

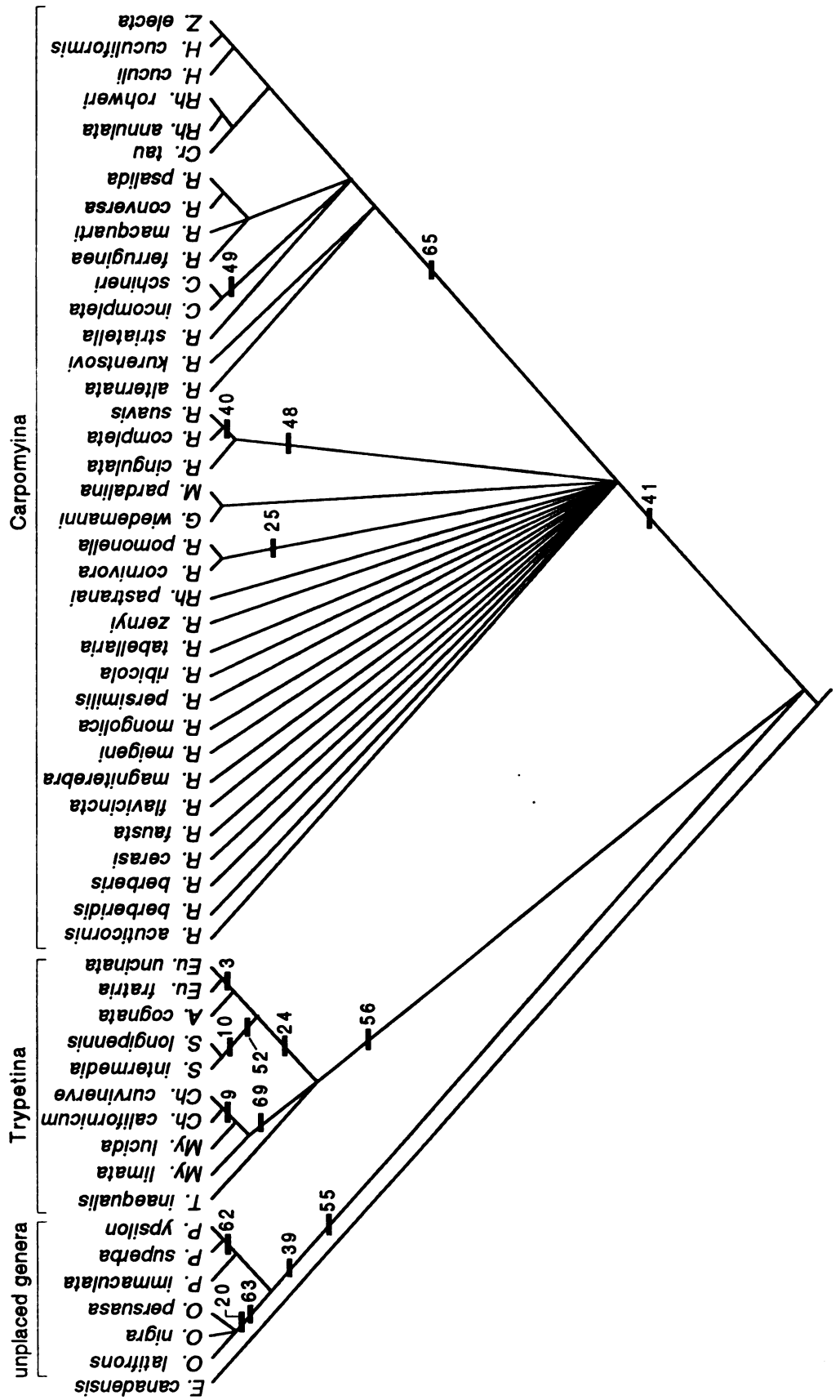

Figure 106. Strict consensus tree of 12,061 cladograms of length = 37,433, CI = 0.671, and RI = 0.900 (reweighted data). Bars represent synapomorphies; numbers refer to characters in Table 7. Subtribes are indicated along the top of the tree.

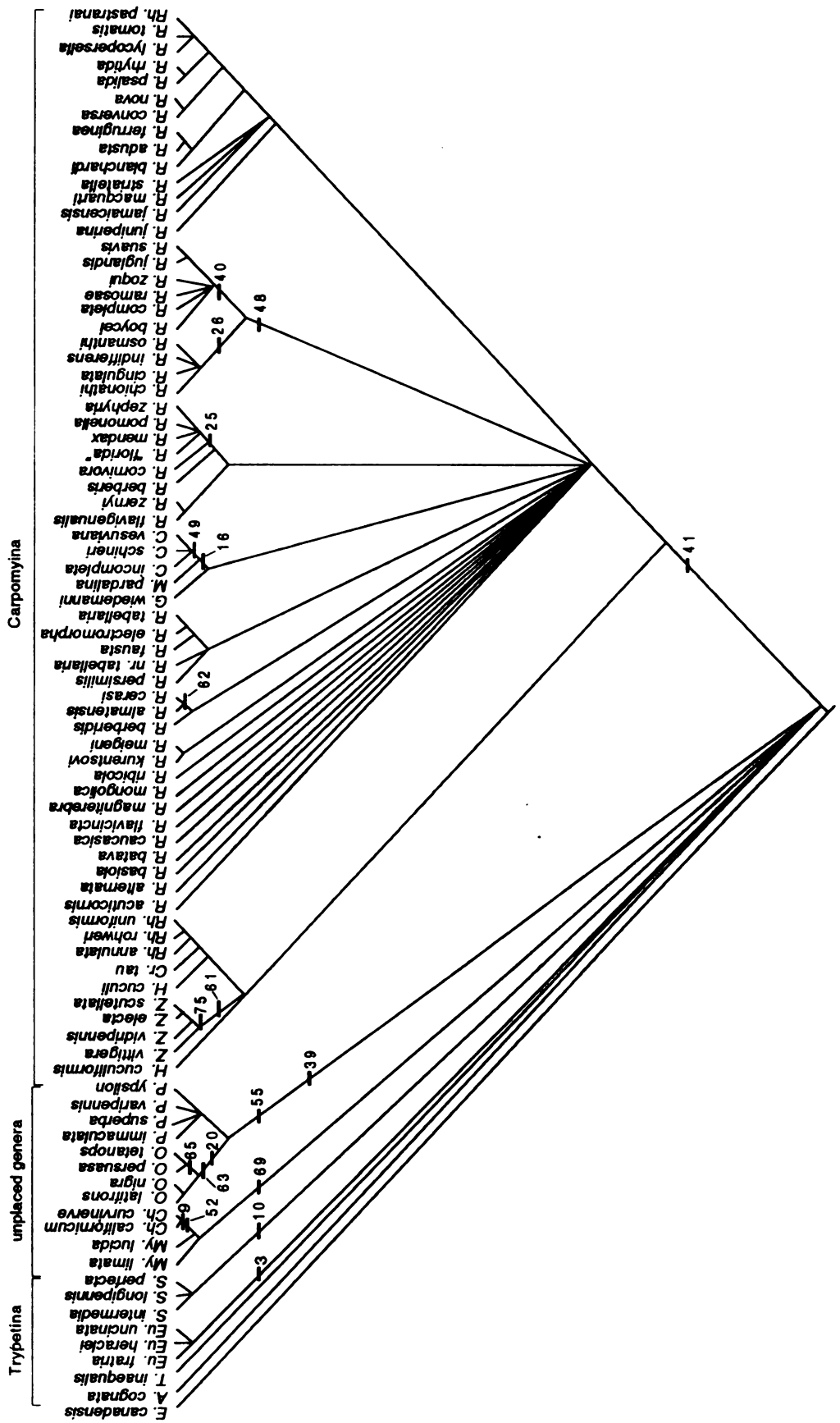

Figure 107. Strict consensus tree of 13,100 cladograms of length = 306, CI = 0.281, and RI = 0.789. Bars represent synapomorphies; numbers refer to characters in Table 7. Subtribes are indicated along the top of the tree.

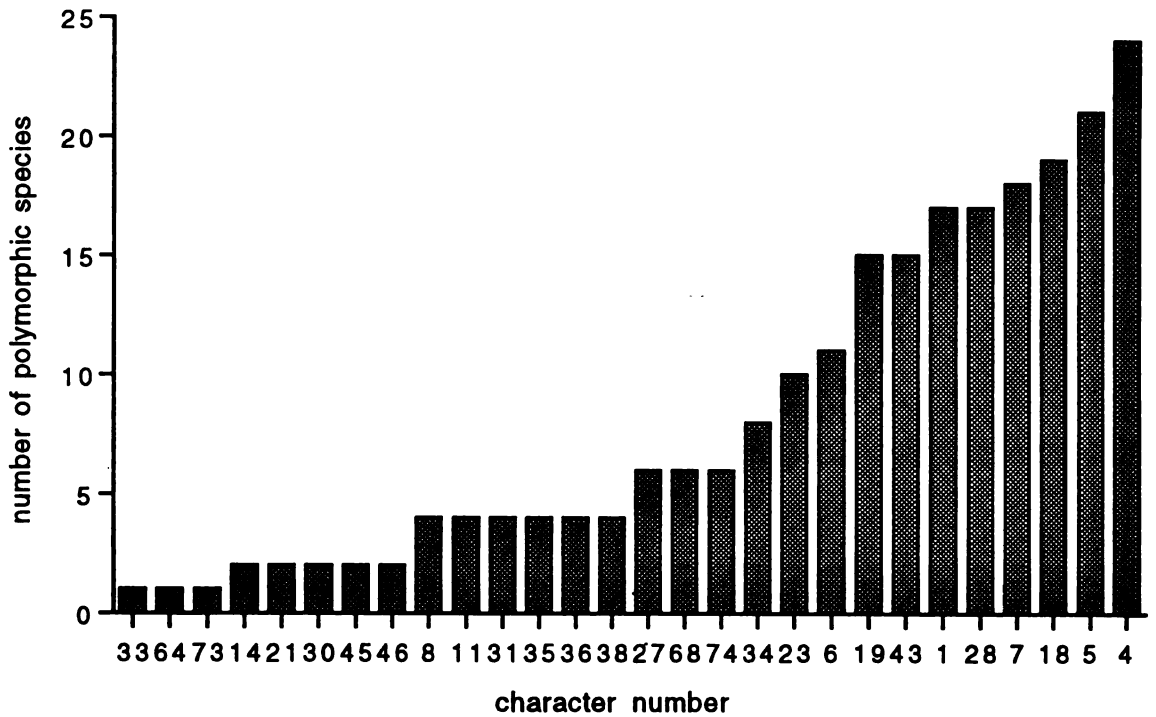

Figure 108. Number of polymorphic species by character.

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