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Fig. 8.1. Male of *Tipula trivittata* Say, (Nearctic, MND, fig. 7.1).

## Diagnosis

Small to large, typically slender-bodied flies with elongate legs (Fig. 1). Wing length 3–36 mm. Overall color various within family, sometimes with strongly contrasting coloration (e.g., *Hexatoma*, *Sigmatomera*). Ocelli absent. Rostrum small and inconspicuous in most Limoniinae, as long or longer than remainder of head and often with small apical projection (nasus) in Tipulinae (Fig. 2); mouthparts sometimes greatly elongate (e.g., *Elephantomyia*, *Toxorhina*). Antenna varied in length and structure, commonly with 11–14 flagellomeres (Figs. 8–14, 99); flagellomere shape various (globular, oval, cylindrical, sometimes branched), with length sometimes exceeding that of body (e.g., *Hexatoma*, *Rhabdomastix*). Thorax dorsally with V-shaped transverse mesonotal suture. Wings elongate, narrow, with at most weakly developed anal angle; wings sometimes reduced. Wing venation various with basal cells at least half the length of wing, with distinctive region near apical third of wing, the cord, where branching of Rs and M frequently occurs in an almost linear transverse line; two anal veins distinct and reaching margin;  $A_2$  moderately long (Figs. 15–19). Legs long and slender, usually unmodified, breaking readily at suture between trochanter and femur. Abdomen long, slender. Apex of male abdomen often with enlarged hypopygium, with two pairs of gonostyli usually present (Figs. 3–6). Apex of female abdomen usually with elongate, strongly sclerotized, acutely pointed ovipositor (Fig. 7), rarely short and fleshy (Fig. 145).

Larvae elongate, head capsule distinct but posterior two-thirds or more of head capsule enclosed and retractable within prothoracic segments (Figs. 147–148); capsule well sclerotized anteriorly, deeply incised ventrally and often dorsolaterally (may be reduced to sclerotized rods) (Figs. 149–151); mandibles opposed or nearly so, moving in horizontal or oblique plane (Fig. 151). Abdominal segments smooth or with transverse rows of fine hairs; transverse creeping welts or, less commonly, fleshy swellings sometimes present; usually functionally metapneustic (rarely apneustic), rarely with vestigial lateral spiracles; terminal segment with pair of posterior spiracles (Figs. 152–156), with disc surrounding spiracles often partially sclerotized, usually surrounded by lobelike projections of varied length, often fringed with hairs; anal papillae or membranous anal lobes usually present (Figs. 152–153), often elongate in aquatic species (Figs. 154–155).

Pupae elongate (Figs. 157–158), obtect (with head and thoracic appendages visible in connected sheaths), capable of some movement. Tarsal leg sheaths oriented side by side, not superimposed. Thoracic respiratory organs usually present, often extended and rodlike, but also as an acute spine, ear-shaped, or branched. One or more rows of spines usually present posteriorly on most abdominal segments, but sometimes absent or not spinelike. Genital sheaths usually ornamented with spinelike tubercles. Pupae sometimes enclosed in silken case.

Historically, tipulids were often grouped with other similar “crane fly” families, including Trichoceridae, Ptychopteridae, Blephariceridae, and Tanyderidae, but are easily recognized by the lack of ocelli, the V-shaped suture on the mesonotum, and the presence of two complete anal veins. Crane flies are sometimes confused with some other long-legged nematoceros Diptera (including Culicidae, large Cecidomyiidae (Lestremiinae), and some Mycetophiloidea), but the above characters as well as a complete costal vein at the wing tip will distinguish crane flies. Larval crane flies are often confused with larvae of Dolichopodidae or Sciomyzidae, because of the similarity of having posterior spiracles surrounded by lobes. The larvae of these two families have greatly reduced head capsules, with parallel, hooklike mandibles, whereas in crane flies, the head is often not so reduced and the mandibles are not parallel (if oblique, then the mandibles are not hooks, but more flattened with apical teeth). The integument in Dolichopodidae is generally smooth and striate, not covered in hairs as in crane flies.

## Biology

Crane flies are generally associated with humid environments, such as the margins of ponds and streams, but they are found also in forests and grasslands, and even in cultivated fields and urban and suburban yards (Alexander, 1920a, 1931); certain groups are adapted to arid and semiarid environments (Gelhaus, 2005). A few species are associated with the marine intertidal zone (Rogers, 1932), and some have been found to be true troglobites (Darlington & Gelhaus, 1994).

Adult flies may be found resting on vegetation adjacent to larval habitats and can be readily obtained by sweeping such areas with a net or by using Malaise or light traps (Young & Gelhaus, 2000; Contreras-Ramos & Gelhaus, 2002). In some species of Limoniinae, adults form aerial swarms, primarily of males (Pritchard, 1983). Adults show a wide variety of resting postures (e.g., Fig. 112, also see Byers, 1961), some of which are cryptic (Hynes, 1990), and certain taxa (e.g., *Trentepohlia*) are often tightly associated with arachnid webs (Robinson & Robinson, 1976). Some groups show mimetic coloration (e.g., *Hexatoma*, *Sigmatomera*, *Pselliophora*), and wing patterning can be correlated with vegetation type (Freeman, 1968). Adults are short lived and most do not appear to actively feed, although several genera have adults with lengthened mouthparts for taking nectar (e.g., *Geranomyia*, Figs. 104–106) (Rogers, 1926a).

Larvae occupy a large variety of habitats, from truly aquatic (mainly in well-oxygenated rapid streams) to semi-aquatic (e.g., shallow edges of aquatic habitats) and terrestrial (e.g., in forest soils) (Alexander & Byers, 1981). Pupae may be found in the same microhabitat as larvae or, in some aquatic species, in somewhat drier adjoining areas. The following lists some specific habitats and examples of Central American groups documented or likely to be found there:



- freshwater, especially rapidly flowing streams: *Cryptolabis*, *Leptotarsus* (*Pehlkea*), *Hexatoma*.
- aquatic to semiaquatic muddy or vegetated edge areas of streams and lakes: *Tipula* (*Bellardina*), *Zelandotipula*, *Dicranomyia*, and many Limnophilini and Chioneini.
- sandy, gravelly, or loamy soils with moderate humus, as found along stream borders: Chioneine groups such as *Gonomyia*, *Mesocyphona*.
- steep or vertical cliff faces kept wet by a film of water supporting algal growth: some species of *Dicranomyia*, *Orimarga* (Vaillant, 1950).
- intertidal zones or brackish water: *Dicranomyia*, particularly subgenus *Idioglochina*.
- phytotelmata (water held by bromeliads, bamboo canes, tree holes): *Sigmatomera*, *Trentepohlia*, (Picado, 1913; Louton et al., 1996).
- moist to wet cushions of mosses or liverworts: various Limoniini.
- dry to saturated decaying wood: *Atarba*, *Epiphragma*, *Eugnophomyia*, *Gnophomyia*, *Teucholabis*, *Lipsothrix*.
- rich organic earth or mud: numerous genera and species, including *Brachypremna*, *Molophilus*.
- decaying plant materials such as masses of leaves, stems, or fruits in various stages of putrefaction: *Styringomyia*, *Toxorhina*, *Rhipidia*.
- fungi, both woody and fleshy: several genera in Northern Hemisphere.
- on leaves of terrestrial higher plants: *Geranomyia recondita*.
- leaf litter and humus-rich soils of forested areas: *Nephrotoma*, *Dicranoptycha*.
- dry soil as found in lawns, pastures: *Nephrotoma*, *Tipula*.

The biology and immature stages of Neotropical crane flies are almost completely unknown, and little has been published on these topics; notable exceptions are Bruch (1939) and Picado (1913). Rearing of adults from immature stages is not difficult for most habitats (Rogers, 1937; Gelhaus, 1986) and will likely be rewarded with strikingly new information.

Crane flies are important members of aquatic and terrestrial biotic communities. The larval stage, which lasts a few weeks to up to a year or more, may be considered the most important ecologically, in comparison with the short adult stage. Larvae generally process dead organic matter (e.g., usually decaying plant material), but some are predaceous or even feed on living higher plants, algae, and fungi. A use-

ful classification of trophic categories for aquatic species is found in Byers & Gelhaus (2008). Herbivorous species may become economically important as a result of larval feeding in rangeland (Hartman & Hynes, 1977), turf (Jackson & Campbell, 1975), and crops (Rao & Gelhaus, 2004; Bishop & Portman, 1965). *Tipula oleracea* Linnaeus, a European crop and turf pest species, has been found in Ecuador (Young et al., 2000) and likely occurs in Central America. Adults may constitute important food sources for birds and other vertebrates, as well as for spiders and predaceous insects (cf., Alexander, 1920a; Alexander & Byers, 1981; Pritchard, 1983).

Because of their ecological importance, diversity, tendency to occupy specific stable microhabitats, and apparent propensity to be endemics, crane flies should be considered important subjects for biological conservation. Site diversity can range from a few species (e.g., 33 spp., Big Bend National Park, Texas, USA, J.K. Gelhaus, unpublished data) to several hundred (e.g., 198 spp., Michigan, Rogers, 1942; 263 spp., Virginia, Byers, 2002). Twenty-five species of crane flies emerged from a 4 m<sup>2</sup> area sampled over a small mountain stream in Puerto Rico (Livingston & Gelhaus, 1994). In temperate regions, many species of crane flies have a well-defined adult seasonal phenology (Young, 1978; Rogers, 1942) but this aspect of their biology has scarcely been examined in tropical regions (Gelhaus et al., 1993). Crane flies are excellent sources of information for phylogenetic and biogeographic studies (e.g., Oosterbroek, 1994; Tangelder, 1988). Nevertheless, a substantial effort for field studies, surveying, and identification should be exercised to provide the basic data for ecological, conservation, and historical biogeography studies. Without a good sampling of the fauna, we will continue to lack the information that will allow us to fully understand the extent, origins, and evolutionary and ecological relationships of Central America's biotic diversity as well as the impact of human activities on this biological diversity (Contreras-Ramos & Gelhaus, 2002).

## Classification

The family Tipulidae has been considered the most primitive or phylogenetically basal group within the Diptera (Wood & Borkent, 1989; Michelsen, 1996) but an alternative hypothesis places them in a more derived clade adjoining the Brachycera (Oosterbroek & Courtney, 1995). The family is generally agreed to be monophyletic (Oosterbroek & Theowald, 1991). Crane flies have an extensive fossil record (Evenhuis, 1994), with earliest fossils in the Upper Triassic already indicating a diverse fauna (Krzeminski, 1992a).

The bulk of the taxonomic literature treating the Neotropical fauna follows the higher-level classification of Alexander & Alexander (1970), with Tipulidae considered a single family subdivided in three subfamilies: Tipulinae, Cylindrotominae, and Limoniinae. This single family classification for crane flies is followed here to facilitate access to the primary literature, mostly that of Alexander (see Table 1). Other authors, particularly Europeans, consider crane flies (Tipu-

**Table 8.1.** Comparison of the classifications of Alexander (1970, who published most of the descriptive work on the crane flies of Central America), Oosterbroek (2005, the current online world catalog), and the classification used in this chapter.

Alexander and Alexander, 1970	Oosterbroek, 2005	This chapter
Family Tipulidae	Superfamily Tipuloidea	Family Tipulidae
Subfamily Tipulinae	Family Tipulidae	Subfamily Tipulinae
Subfamily Cylindrotominae	Family Cylindrotomidae	Subfamily Cylindrotominae
Subfamily Limoniinae	Family Limoniidae	Subfamily Limoniinae
Tribe Limoniini	Subfamily Limoniinae	Tribe Limoniini
Tribe Hexatomiini	Subfamily Limnophilinae	Tribe Limnophilini
Tribe Eriopterini	Subfamily Chioneinae	Tribe Chioneini
Tribe Pediciini	Family Pediciidae	Tribe Pediciini

loidea) to encompass three families (subfamilies elevated to families: Tipulidae sensu stricto, Limoniidae, Cylindrotomidae; see discussion by Byers, 1992) or four families (including Pediciidae; Starý, 1992). Phylogenetic analyses based on characters of the larvae and pupae (Oosterbroek & Theowald, 1991) and adults (Starý, 1992) support monophyly of all groups except for a paraphyletic Limoniinae (=Limoniidae).

The use of tribes in most subfamilies has not been consistently applied except for the Limoniinae. The subfamily Limoniinae has traditionally been subdivided into four tribes: Limoniini, Pediciini, Hexatomiini, and Eriopterini. Starý (1992) notes that the names Limnophilini (for the group Hexatomiini) and Chioneini (for the group Eriopterini) have priority, although not historic usage. In Central America, representatives of all subgroups have been recorded, with the exception of Pediciini and Cylindrotominae (both amphitropic in distribution, found in North America and southern South America only).

Almost no work has examined relationships among generic and subgeneric groups in any comprehensive way (but see Oosterbroek & Theowald, 1991 for Limoniinae sensu lato; Gelhaus, 2005 for *Tipula*; Ribeiro, 2008 for Limnophilini). C.P. Alexander, who nearly single-handedly studied the Central American crane fly fauna, favored large genera with subgenera; examples include *Erioptera*, *Gonomyia*, *Limonia* s.l., and *Tipula* (Alexander & Alexander, 1970). Workers in Europe have favored smaller genera, mostly without subgenera, and this classification has been followed in recent cataloging (Oosterbroek, 2003). Phylogenetic analyses of species relationships are few for the Neotropical Region (de Jong, 1989; Gelhaus & Young, 1995; Ribeiro & Amorim, 2002; Ribeiro, 2003) but include several temperate genera (Tangelder, 1985; Young, 1987; de Jong, 1994; Brodo, 1987; Gelhaus 2005). The applicability of crane flies for solving biogeographic questions (Oosterbroek, 1994; Tangelder, 1988; Contreras-Ramos & Gelhaus, 2002) should form an important part of revisionary studies of the Central American fauna.

Tipulidae sensu lato includes 15 246 recognized species worldwide, with Alexander having described 10 887 (Oosterbroek, 2003, 2005). In the Neotropical Region, 3546 species are considered valid, with 629 recorded for Central America.

Only 123 species are known from Costa Rica; this number is indicative of the few samples available for study during Alexander's working life, and accounts for probably one-third to one-fourth of that country's true crane fly fauna. Of these, 66 species are apparently endemic to Costa Rica, with an additional seven from Isla del Coco (Byers, 1981).

## Identification

The first species of crane fly described from Central America was by Bellardi in 1851, with several others described by Osten Sacken in 1886 and Williston in 1900 in the *Biologia Centrali-Americana* series. Alexander described about 95% of the Central American species from 1912 to 1981 (Oosterbroek, 2003). Oosterbroek & Theowald (1980) list all the 1000+ papers (mostly on crane flies) Alexander published. Byers (1982) provided a concise introduction to the Central American literature, and Contreras-Ramos & Gelhaus (2002) did the same for the Mexican fauna and literature (both papers in English and Spanish). Alexander & Alexander (1970) provided a catalog to the Neotropical species (through 1968), with Oosterbroek (2005) offering a searchable online world catalog. For many taxa, the use of both catalogs will guide the user through the many changes in generic and subgeneric assignments.

Adult crane flies can be studied both as dry specimens or in ethanol. Dry specimens are either field preserved in envelopes and mounted on paper points (Byers, 1961; Young & Gelhaus, 2000; Young, 2005) or directly pinned (Brodo, 1987). Because of the ease with which crane fly legs break from the thorax, dry specimens should be handled immediately after killing, or after 6–8 hours of storage in a tight container with slight moisture, to avoid the effects of rigor. For careful study, male and female genitalia need to be cleared from dry- and ethanol-preserved specimens using sodium or potassium hydroxide, following the method of Dieneske (1987).

Few of the important studied collections are housed in Central America. The majority of type specimens, and other studied specimens, are in the Alexander Collection at the Smithsonian Institution, Washington, D.C. Other important

curated and studied crane fly collections in the New World (all United States) include those at The Academy of Natural Sciences (Philadelphia, Pa.), California Academy of Sciences (San Francisco, Calif.), Carnegie Museum of Natural History (Pittsburgh, Pa.), University of Kansas (Lawrence, Kans.), and University of Michigan (Ann Arbor, Mich.). The specimens in Neotropical museums mostly remain unstudied and will reward the researcher with many new discoveries. Fieldwork is paramount, as few areas have been sampled thoroughly, the biology of most crane flies is unknown, and the pace of habitat alteration is great. Crane fly specialists have gathered for special meetings in recent years to exchange research results and participate in fieldwork together (Krzeminski, 1992b).

The larvae of fewer than 3% of the Central American species are described, but larvae for most genera are known from a few species from other regions. Larval preservation directly in alcohol may yield shrunken or distorted specimens, and where possible, specimens should be killed directly in hot (just boiled) water, and then transferred to 70%–80% ethanol for preservation, following the procedure of Gelhaus (1986). Identification of larvae below the family level for Central American specimens must rely on keys developed for North American genera and subgenera. The most comprehensive key is that of Alexander & Byers (1981), with only aquatic taxa keyed in Byers (1996), Byers & Gelhaus (2008), and Gelhaus (2000, 2002, 2008).

Revisions of Nearctic groups of crane flies not listed in the Synopsis section may prove useful to researchers on Central American crane flies. These groups include *Dolichopeza* (Byers, 1961); *Dicranoptycha* (Young, 1987); *Nephrotoma* (Tangelder, 1983, 1985, 1988; Oosterbroek, 1984); *Prionocera* (Brodo, 1987); subgenera *Eremotipula*, *Lunatipula* of *Tipula* (Gelhaus, 2005). General species keys as part of faunal studies might also prove useful, in that they key out several widespread species that occur in Central America (eastern North America: Alexander, 1943a; California: Alexander, 1967a).

The morphological terminology for the key generally follows that of Alexander & Byers (1981). Cell “dm” as used

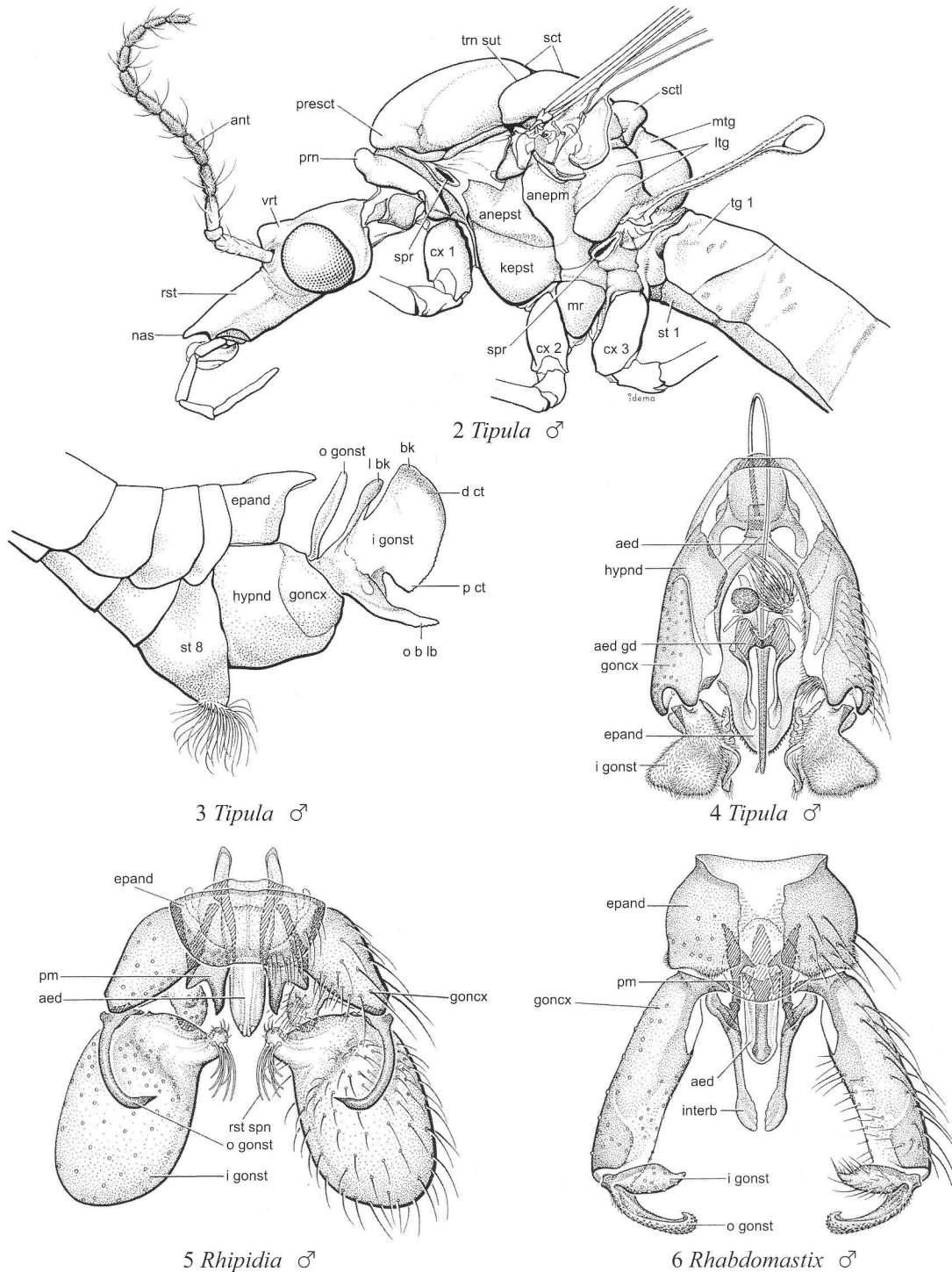
in the following key was commonly called the discal cell or first  $M_2$  cell in previous literature, and presence or absence of the cell often was called a “closed” or “open” cell. The veins designated as the “basal transverse section of  $CuA_1$ ” and “distal section of  $CuA_1$ ” as used here in the key were called the crossvein “m-cu” and vein “ $M_4$ ”, respectively, in much of the older literature (Byers, 1989); the true “m-cu” crossvein is found in only a few taxa (e.g., *Megistocera*, Fig. 20, labeled bm-cu). The crossvein “sc-r” was called “ $Sc_2$ ” in much of the previous literature. Crane fly venation can be surprisingly prone to individual anomalies, including addition of crossveins, and therefore the user should always check both wings before deciding on the interpretation of the venation (see comments of Edwards, 1938).

The male genitalic terms gonocoxite and gonostylus used in the key are equivalent to basistyle and dististyle used in the older literature. The term rostrum is used for two different structures: the extension of the head containing the labellum, palps, and nasus; and an extension of the ventral gonostylus found in some Limoniini. In the male, epandrium and hypandrium are used here instead of ninth tergite and ninth sternite. Although this provides consistency within the Diptera, the latter terms are predominant in previous crane fly literature. In addition, the term parameres is used in the key instead of gonopophyses.

The homology of the gonostyles is unclear within the Tipulidae, and this uncertainty is reflected in the inconsistent application of terms to these structures (e.g., inner and outer gonostyles in Tipulinae, dorsal and ventral gonostyles in Limoniini). Ribeiro (2006) reviewed the homology and suggested a new set of terms (clasper, lobe) reflecting the supposed functions of the structures; he also presented a table comparing the variety of terms used historically. In this chapter, the terms inner gonostylus and outer gonostylus are used to reflect homology and use within the past literature. Clearly further study of the homology of these structures is indicated, including a broader sampling within the Tipulidae and considering situations where only one or more than two gonostyles are found.

### Key to the genera and subgenera of Tipulidae of Central America

1. Fully winged; other characters various . . . . . 2
- Subapterous (Fig. 34); rostrum with nasus (Fig. 2); antenna with 11 flagellomeres; TIPULINAE; . . . . . *Tipula* (*Eumicrotipula*) Alexander, in part
2. Rostrum usually well developed, but longer than remainder of head, usually with anteriorly projecting, sharply pointed nasus (Fig. 2); antenna commonly with 11 flagellomeres (Fig. 13), 14 flagellomeres in some *Tipula* (*Eumicrotipula*), 6 in *Megistocera*;  $CuA$  slightly constricted (or bent) at branching of  $CuA_1$  and  $CuA_2$  (Fig. 15); terminal segment of palpus elongate (in dry specimens may be wrinkled and contracted in length), usually much longer than three preceding ones together (Fig. 2);  $Sc_1$  usually weakening distally or absent (Fig. 15) but sometimes rudiment present (in *Leptotarsus*, *Nephrotoma*, *Megistocera*, *Brachypremna*, Figs. 20–21); size large, wing commonly over 10 mm long, usually much longer; TIPULINAE. . . . . 3



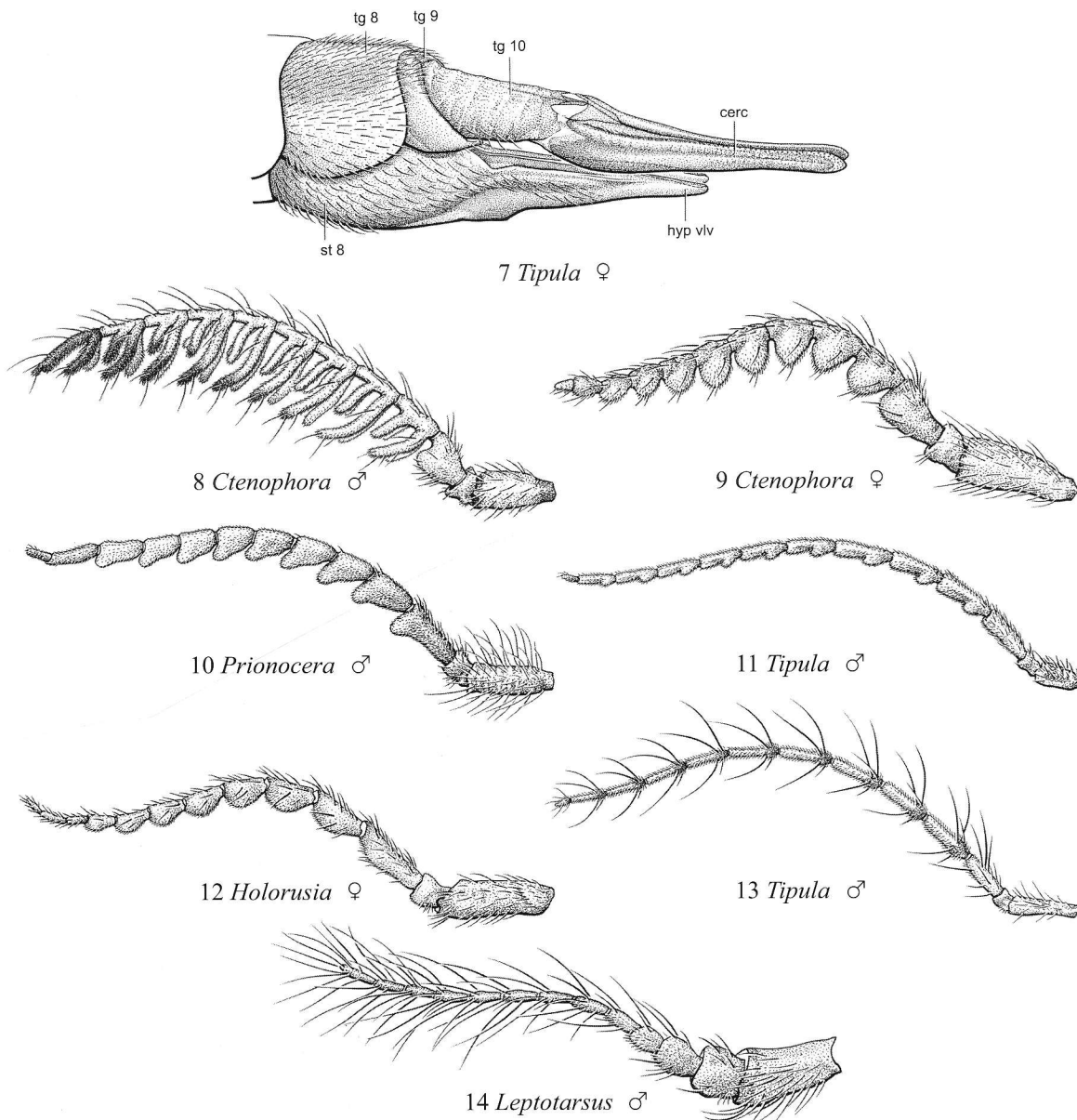
**Figs. 8.2–6.** Head, thorax, and male terminalia: lateral view of head and thorax of (2) *Tipula trivittata* Say, (Nearctic, MND, fig. 7.2); lateral view of terminal abdominal segments of (3) *Tipula (Lunatipula) monticola* Alexander, (Nearctic, MND, fig. 7.3); posteroventral view of male terminalia of (4) *Tipula (Yamatotipula) eluta* Loew, (Nearctic, MND, fig. 7.4); dorsal view of male terminalia (5) *Rhipidia lecontei* Alexander, (Nearctic, MND, fig. 7.5); and (6) *Rhabdomastix subfascigera* Alexander (Nearctic, MND, fig. 7.6).

Abbreviations: aed, aedeagus; aed gd, aedeagal guide; anepm, anepimeron; anepst, anepisternum; ant, antenna; bk, beak; cx, coxa; d ct, dorsal crest; epand, epandrium; goncx, gonocoxite; i gonst, inner gonostylus; interb, interbase; kepst, katepisternum; l bk, lower beak; ltg, laterotergite; mr, meron; mtg, mediotergite; nas, nasus; o b lb, outer basal lobe; o gonst, outer gonostylus; p ct, posterior crest; pm, paramere; presct, prescutum; prn, pronotum; rst, rostrum; rst spn, rostral spine; sct, scutum; sctl, scutellum; spr, spiracle; st, sternite; tg, tergite; trn sut, transverse suture; vrt, vertex.

- Rostrum usually short and nasus absent (Figs. 109a–c), but when lengthened as in *Geranomyia*, *Elephantomyia*, and *Toxorhina* (Figs. 104, 105, 106), mouthparts greatly extended, usually exceeding half length of body; antenna usually with 12 or 14 flagellomeres (Fig. 99), 11 in *Dicranota* (known from Central Mexico), but sometimes with fewer flagellomeres (two to six in some Limnophilini, one in a *Helius* sp.); CuA straight, not constricted at meeting of CuA<sub>1</sub> and CuA<sub>2</sub> (Figs. 16–19); terminal segment of palpus short, no longer than two preceding ones together (Fig. 102); Sc<sub>1</sub> complete (Figs. 16–19); size small or medium, rarely large, wing commonly under 10 mm length, usually much smaller; LIMONIINAE . . . . . 16
- 3. R<sub>2+3</sub> strongly angulated, often with short spur at median angle (Fig. 20); crossvein extending from vein M to CuA<sub>1</sub> (sometimes considered true bm-cu crossvein); antenna with six flagellomeres (Fig. 88); southeastern United States, Caribbean, South America. . . . [*Megistocera* Wiedemann]
- R<sub>2+3</sub> gently curved (Figs. 21, 23); crossvein absent with distal section of vein CuA<sub>1</sub> arising directly from vein M or forming posterior border of cell dm; antenna usually with 11 flagellomeres (Figs. 13, 14) . . . . . 4
- 4. R<sub>1+2</sub> strongly bent vertically toward costa (Fig. 21); veins M2, M3, and CuA<sub>1</sub> narrowly whitened at or close to the wing margin . . . . . *Brachypremna* Osten Sacken
- R<sub>1+2</sub> extending more toward wing tip (Fig. 15); M<sub>2</sub>, M<sub>3</sub>, and CuA<sub>1</sub> not usually whitened near wing margin, although white spots may be present along cell margins, not veins, in some *Tipula* . . . . 5
- 5. Male (and sometimes female) antenna with branches on flagellomeres (not beadlike as in some *Tipula* (*Microtipula*) and (*Eumicrotipula*)) (Figs. 89, 90, 91); female antenna with flagellomeres, at least, produced to give serrate appearance (as in Fig. 9); wing usually with cell m<sub>1</sub> sessile (Fig. 22) . . . . . 6
- Male and female without branched antennal flagellomeres, although lower faces of flagellomeres may be enlarged (Figs. 10–14); wing with cell m<sub>1</sub> usually pedicillate (Fig. 15) (except *Nephrotoma*, some *Leptotarsus*) . . . . . 8
- 6. Antennae with flagellomeres 2–10 with four long branches that exceed length of flagellomeres (Fig. 90); terminal flagellomere appearing trifid with pair of subequal basal branches . . . . . *Pselliophora* Osten Sacken
- Flagellomeres 2–7 with one or two branches (Figs. 89, 91); remaining flagellomeres unbranched; *Ozodicera* Macquart. . . . . 7
- 7. Flagellomeres each with single branch (Fig. 89) . . . . . *Ozodicera* (*Ozodicera*) Macquart
- Each flagellomere with two branches (although one branch may arise off another) (Fig. 91) . . . . . *Ozodicera* (*Dihexaclonus*) Enderlein
- 8. Wing with cell r<sub>3</sub> constricted at midlength (Fig. 24); antenna filiform, not produced and with few, if any, short verticillate setae (Fig. 92); wing often with spot or cloud over origin of Rs, and patch at base and middle of cell bm (Fig. 24); male inner gonostylus of characteristic shape (Fig. 113); when viewed laterally resembling bird's head, set with blackened nodules, those of head and lateral lobe often closely approximated; female hypogynial valves short, with emargination at tip (Fig. 144) . . . . . *Zelandotipula* Alexander
- Wing with cell r<sub>3</sub> straight (Fig. 15), or if slightly constricted, then antenna with flagellomeres with basal enlargements (may be only slight enlarged) and verticils longer than flagellomeres; wing otherwise pigmented or lacking patterning (Figs. 26, 29, 31, 32); form of male inner gonostylus otherwise, but may have blackened nodules (Figs. 114, 117, 118); hypogynial valves may be short, although apex usually rounded or pointed, not emarginate (Figs. 7, 145) . . . . . 9



9. Antenna with proximal flagellomeres conspicuously lobed on outer half to produce subpectinate to pectinate appearance, basal enlargements lacking (as in Fig. 10); verticils reduced; cell  $cua_1$  unusually wide at wing margin, nearly equaling the extent of  $M_1-M_3$  (Fig. 25); vein M arched before branching . . . . . *Ischnotoma* (*Neotipula*) Alexander
- Antenna with proximal flagellomeres not lobed, although basal part of flagellomeres may be significantly enlarged (Fig. 13); verticils usually present (Figs. 13, 14); cell  $cua_1$  not unusually wide, about equal to extent of cell  $m_3$  (Figs. 15, 26); vein M straight. . . . . 10

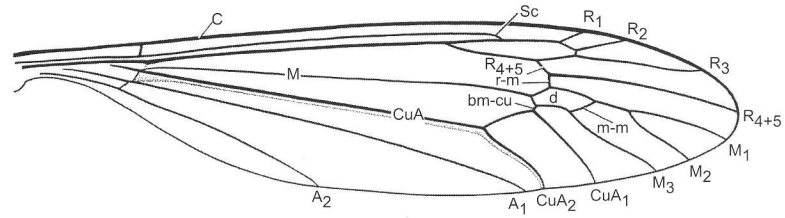
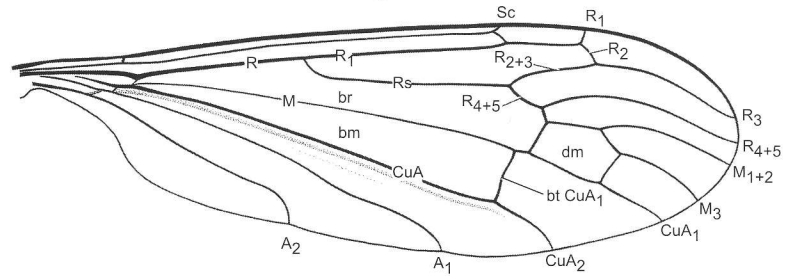
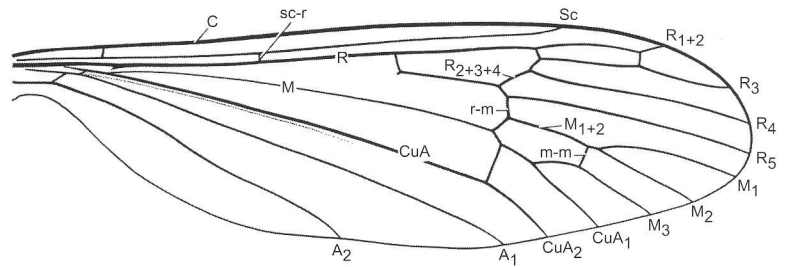
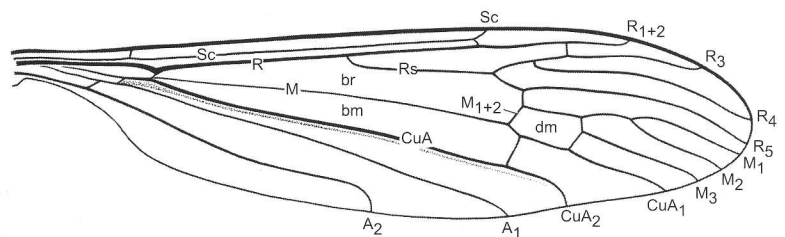
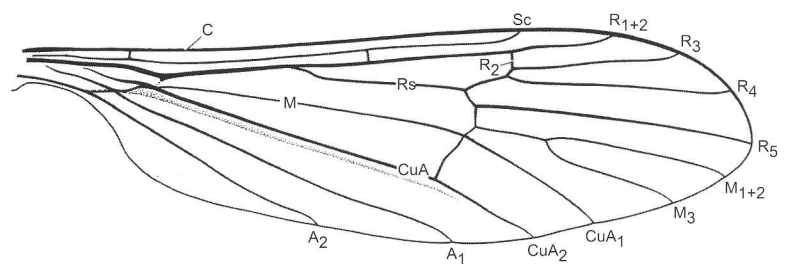


**Figs. 8.7–14.** Ovipositor and antennae: lateral view of ovipositor of (7) *Tipula* (*Yamatotipula*) *noveboracensis* Alexander, (Nearctic, MND, fig. 7.7); antenna of male (8) and female (9) of *Ctenophora apicata* Osten Sacken, (Nearctic, MND, figs. 7.8–9); (10) *Prionocera parrii* (Kirby), (Nearctic, MND, fig. 7.10); (11) *Tipula* (*Angarotipula*) *illustris* Doane, (Nearctic, MND, fig. 7.11); (12) *Holorusia hespera* Arnaud & Byers, (Nearctic, MND, fig. 7.12); (13) *Tipula* (*Lunatipula*) *triplex* Walker, (Nearctic, MND, fig. 7.13); and (14) *Leptotarsus testaceus* (Loew), (Nearctic, MND, fig. 7.14).

Abbreviations: cerc, cercus; hyp vlv, hypogynial valve; st, sternite; tg, tergite.

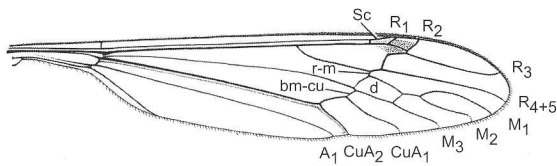


10. Antennae short, scarcely longer than head (Fig. 14); abdomen elongate, often extending past wings; male hypopygium simple in structure with elongate gonocoxites not extensively fused with sternite (Fig. 114); gonostyli terminal in position; inner gonostylus of male with modified spinoid setae, often in longitudinal series; *Leptotarsus* Guérin-Ménéville . . . . . 11
- Antennae longer (Fig. 2); abdomen shorter, wings usually extending well past end of abdomen (Fig. 1); inner gonostylus without spinoid setae (Figs. 115–118) (*Nephrotoma* and some *Tipula* have similar setae on epandrium, not gonostylus). . . . . 12
11. One or more supernumerary crossveins in cell bm (Fig. 26); Colombia. . . . . [ *Leptotarsus (Pehlkea)* Enderlein ]
- Without supernumerary crossveins in cell bm (Fig. 27) . . . . . *Leptotarsus (Tanyprema)* Osten Sacken
12. Vein Sc ending nearly opposite origin of Rs (Fig. 28); Rs short, oblique; cell  $m_1$  sessile or with short petiole; basal transverse section of  $CuA_1$  uniting with M for short distance before or at fork of M; body usually highly polished, often black and yellow. . . . . *Nephrotoma* Meigen
- Vein Sc longer, Sc meeting  $R_1$  beyond origin of Rs (including *Tipula (Microtipula)* where Rs is short) (Figs. 15, 29), Rs usually longer, usually exceeding basal transverse section of  $CuA_1$ ; cell  $m_1$  usually with long petiole (can be short in some *Tipula (Bellardina)*); basal transverse section of  $CuA_1$  meeting M beyond its fork; body coloration usually opaque, pruinose, but may be polished; *Tipula* Linnaeus. . . . . 13
13. Calypter with several strong setae (as in Fig. 30); male antenna not elongate . . . . . 14
- Calypter without strong setae (Fig. 2); male antenna usually elongate, often one-third of body length . . . . . 15
14. Wing with darkened pattern conspicuously mottled, with marginal whitened spot along margin of outer cells; male hypandrium modified into paired fleshy appressed lobes (Fig. 116) . . . . . *Tipula (Bellardina)* Edwards
- Wing with darkened border encompassing leading edge of wings (costal and subcostal cells) only; adults grayish overall; male hypandrium not so modified (Fig. 115); Old World, one species introduced into South America. . . . . [ *Tipula (Tipula)* Linnaeus ]
15. Length of Rs short, slightly less or slightly more than length of basal transverse section of  $CuA_1$  (Fig. 31); wing often scarcely patterned (may be colored); antenna of male with basal enlargements small; male terminalia with posterior margin of epandrium usually bi- or tri-lobed; lobe margins with black, short setae (Fig. 117); membranous proctiger prominent, often as large as epandrium, sometimes hairy or with sclerotized teeth; both gonostyli similar in size, outer gonostylus not fleshy, inner gonostylus not elongate with prominent upper and lower beaks; female with fleshy, short ovipositor (Fig. 145); female not subapterous. . . . . *Tipula (Microtipula)* Alexander
- Length of basal section of Rs long, 1.5–3× length of basal transverse section of  $CuA_1$  (Figs. 32–33); wing often with darkened mottled pattern (Fig. 32); male antenna in some species with extreme bases of flagellomeres each with knoblike enlargement to present a beadlike appearance (Figs. 93–94); epandrium without dark setae, margin usually incised (Fig. 118); proctiger not as described above; inner gonostylus with elongate body with prominent upper and lower beaks, outer gonostylus smaller and fleshy, sometimes absent (Fig. 118); female ovipositor long and strongly sclerotized (as in Fig. 7); female sometimes subapterous (Fig. 34). . . . . *Tipula (Eumicrotipula)* Alexander, in part
16. Eye hairy, with short hairs between ommatidia;  $Sc_1$  long, extending distally past fork of Rs (Figs. 17, 35); sc-r basal to origin of Rs; North America south to central Mexico . . . . . [ PEDICIINI; *Dicranota* Zetterstedt ]

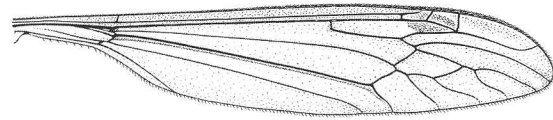
15 *Tipula* ♂16 *Limonia* ♂17 *Dicranota* ♂18 *Pseudolimnophila* ♂19 *Ormosia* ♀

**Figs. 8.15–19.** Wings: dorsal view of (15) *Tipula* (*Yamatotipula*) *tricolor* Fabricius, (Nearctic, MND, fig. 7.15); (16) *Limonia* (*Metalimnobia*) *triocellata* (Osten Sacken), (Nearctic, MND, fig. 7.16); (17) *Dicranota* (*Eudicranota*) *pallida* Alexander, (Nearctic, MND, fig. 7.17); (18) *Pseudolimnophila inornata* (Osten Sacken), (Nearctic, MND, fig. 7.18); and (19) *Ormosia monticola* (Osten Sacken) (Nearctic, MND, fig. 7.19).

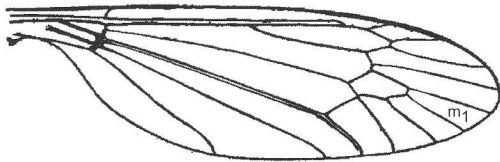
Abbreviation: bt CuA<sub>1</sub>, basal transverse section of vein CuA<sub>1</sub>.



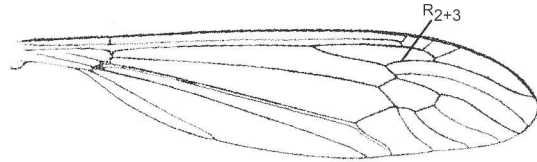
20 *Megistocera* ♂



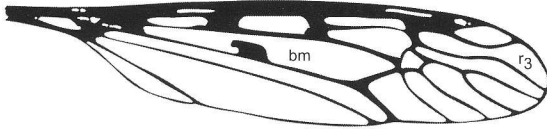
21 *Brachypremna* ♀



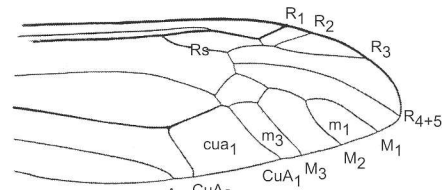
22 *Pselliophora*



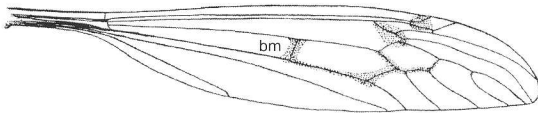
23 *Ozodicera* (*Ozodicera*)



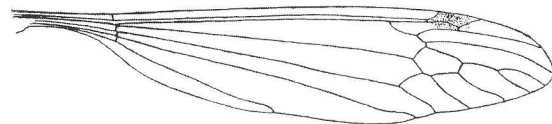
24 *Zelandotipula*



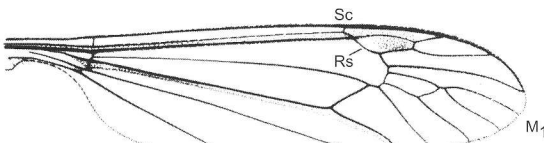
25 *Ischnotoma*



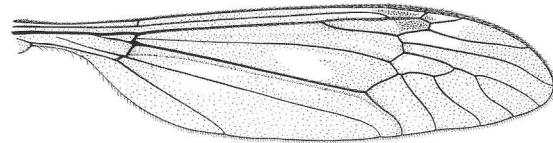
26 *Leptotarsus* (*Pehlkea*)



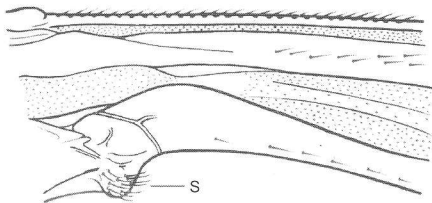
27 *Leptotarsus* (*Tanypremna*)



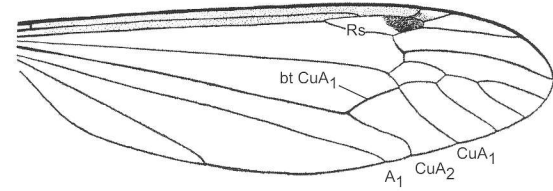
28 *Nephrotoma* ♂



29 *Tipula* (*Lunatipula*) ♂



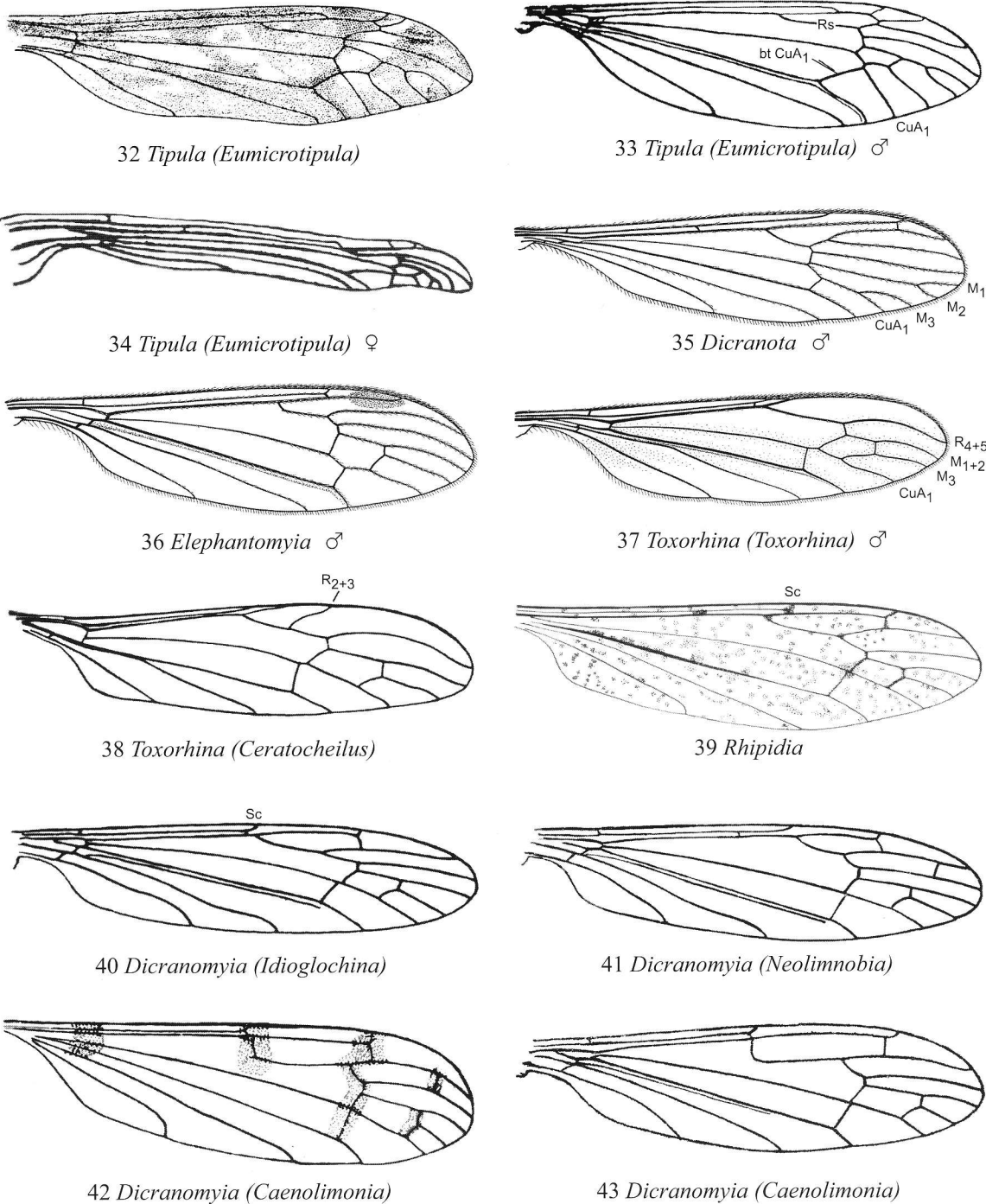
30 *Zelandotipula*



31 *Tipula* (*Microtipula*)

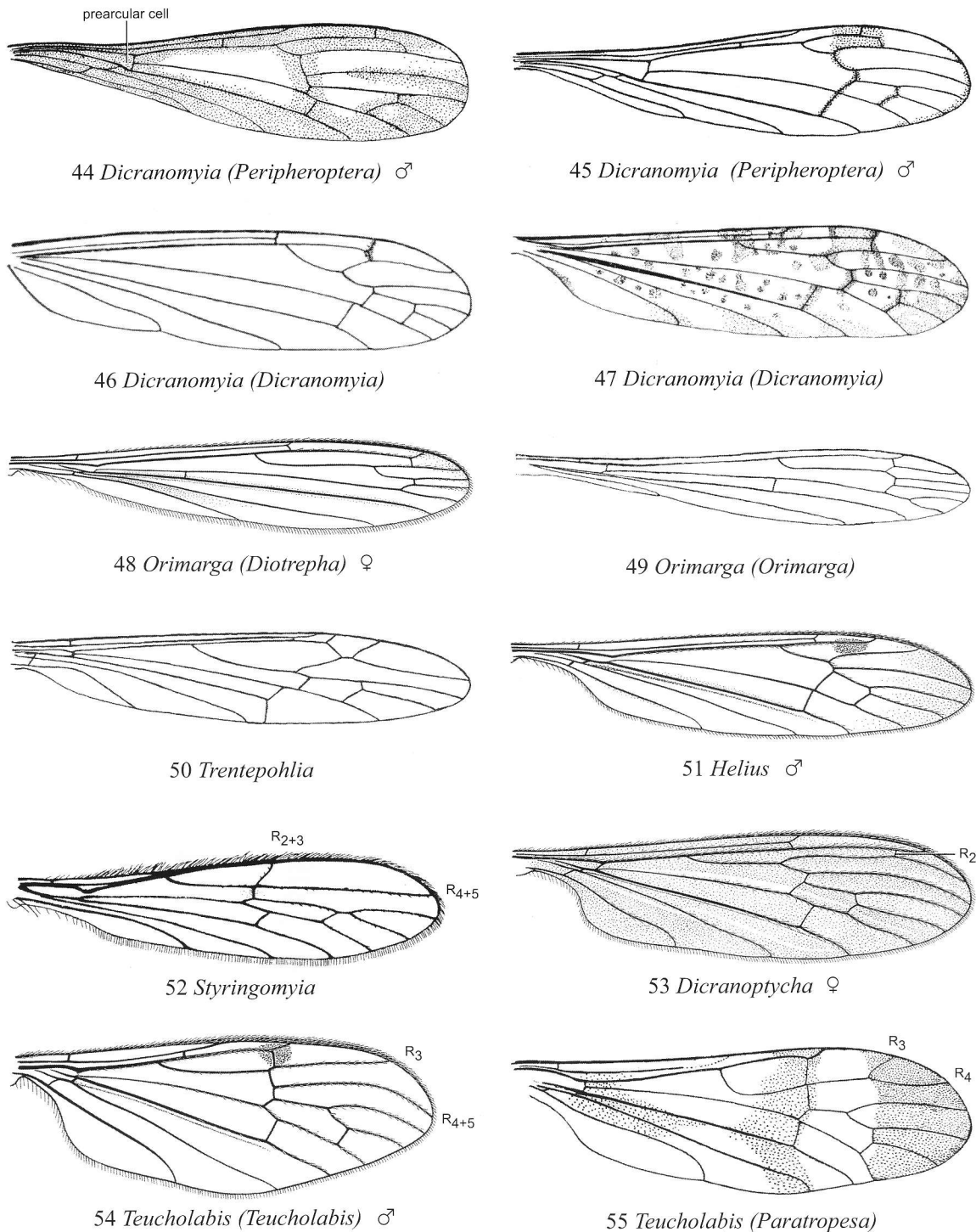
**Figs. 8.20–31.** Wings (*continued*): dorsal view of (20) *Megistocera longipennis* (Macquart), (Nearctic, MND, fig. 7.20); (21) *Brachypremna dispellens* (Walker), (Nearctic, MND, fig. 7.21); (22) *Pselliophora margarita* (Alexander), (Alexander, 1969a, fig. 21); (23) *Ozodicera eurystyla* Alexander, (South America, Alexander, 1969a, fig. 49); (24) *Zelandotipula associans* (Walker), (Vane-Wright, 1967, fig. 12); (25) *Ischnotoma* (*Neotipula*) *maya* (Alexander), (Alexander, 1912d, plate 24a); (26) *Leptotarsus* (*Pehlkea*) *colombianus* (Enderlein), (South America, Alexander, 1914b, fig. 3); (27) *Leptotarsus* (*Tanypremna*) *opilio* (Osten Sacken), (Alexander, 1914b, fig. 2); (28) *Nephrotoma ferruginea* (Fabricius), (Nearctic, MND, fig. 7.24); (29) *Tipula* (*Lunatipula*) *dorsimacula* Walker, (Nearctic, MND, fig. 7.25); wing base of (30) *Zelandotipula gracilipes* (Walker), (South America, Vane Wright, 1967, fig. 16); dorsal view of wing, base omitted, of (31) *Tipula* (*Microtipula*) *aymara* Alexander, (South America, Alexander, 1912d, fig. b).

Abbreviation: bt CuA<sub>1</sub>, basal transverse section of vein CuA<sub>1</sub>; s, setae.

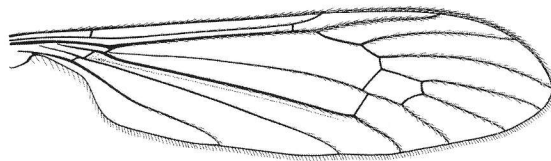
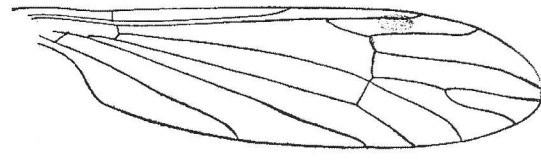
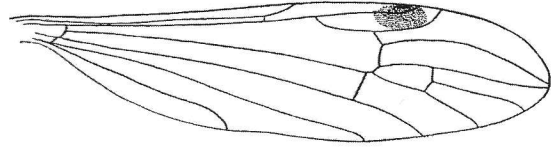
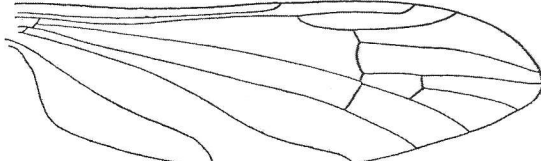
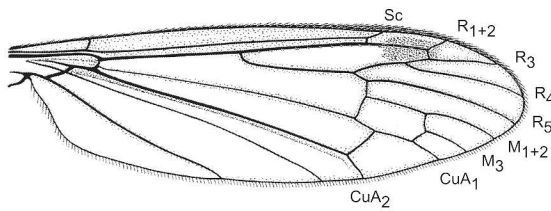
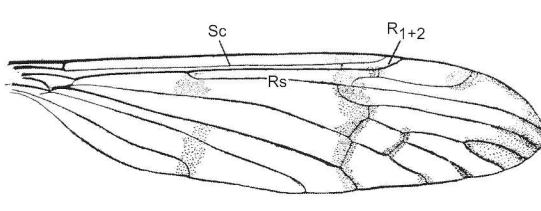
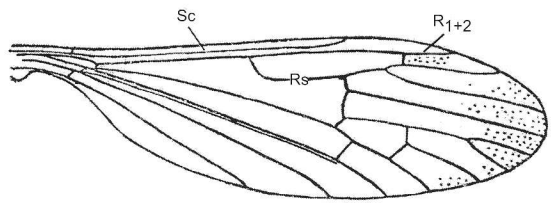
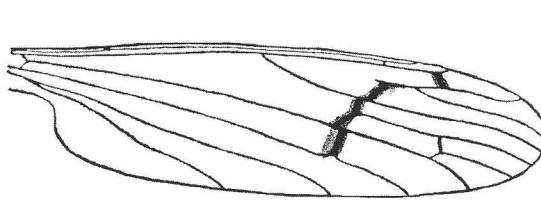
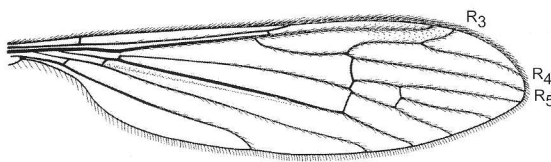
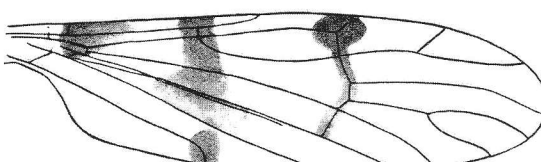
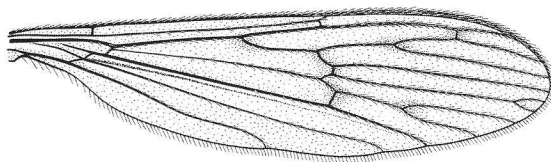
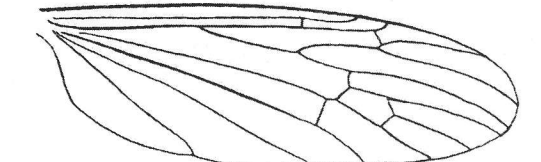


**Figs. 8.32–43.** Wings (*continued*): dorsal views of (32) *Tipula (Eumicrotipula) monilifera* Loew, (South America, Alexander, 1916a, plate 3, fig. 5); (33) *Tipula (Eumicrotipula) michoacana* Alexander, male (Alexander, 1946a, fig. 7); (34) *Tipula (Eumicrotipula) michoacana* Alexander, female (Alexander, 1946a, fig. 8); (35) *Dicranota tenuipes* (Osten Sacken), (Nearctic, MND, fig. 7.39); (36) *Elephantomyia (Elephantomyia) westwoodi* Osten Sacken, (Nearctic, MND, fig. 7.42); (37) *Toxorhina (Toxorhina) magna* Osten Sacken, (Nearctic, MND, fig. 7.50); (38) *Toxorhina (Ceratocheilus) americana* (Alexander), (Alexander, 1913c, fig. E); (39) *Rhipidia (Rhipidia) multiguttata* Alexander, (Alexander, 1912c, fig. A); (40) *Dicranomyia (Idioglochina) marmorata* Osten Sacken, (Nearctic, Alexander, 1967a, fig. 59); (41) *Dicranomyia (Neolimnobia) diva* (Schiner), (Alexander, 1964b, fig. 18, pattern omitted); (42) *Dicranomyia (Caenolimonia) translucida* (Alexander), (Alexander, 1912b, fig. r); and (43) *Dicranomyia (Caenolimonia) distantia* (Alexander), (Alexander, 1971, fig. 2, pattern omitted).

Abbreviation: bt CuA<sub>1</sub>, basal transverse section of vein CuA<sub>1</sub>.

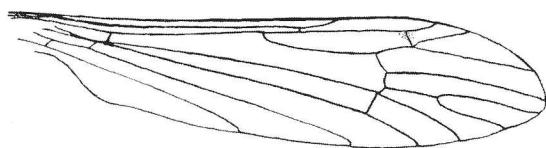
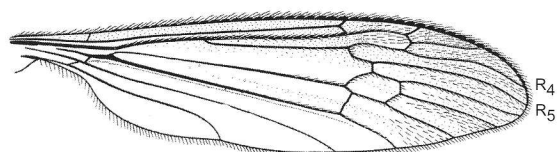
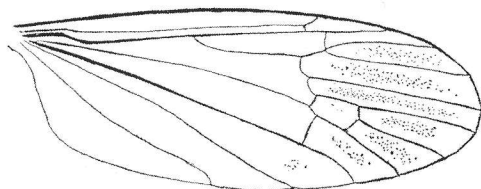
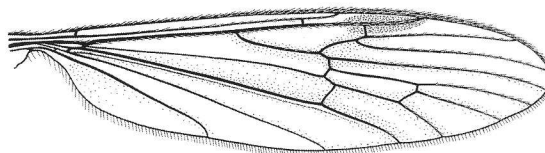
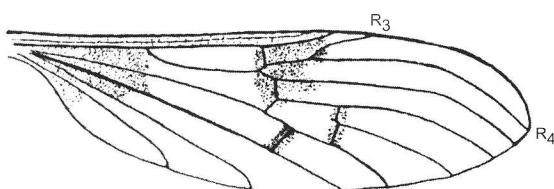
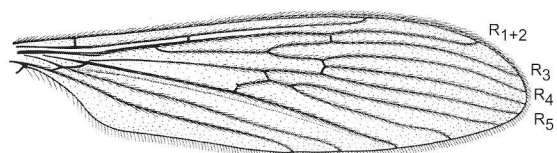
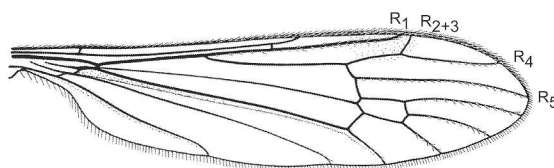
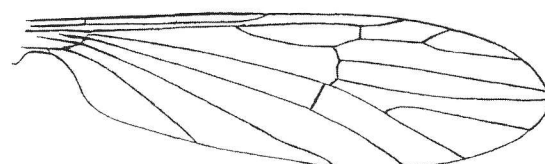
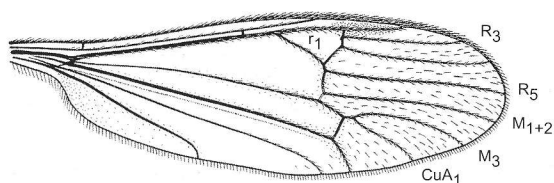
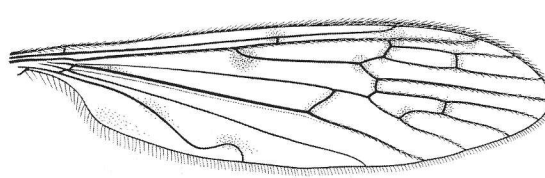
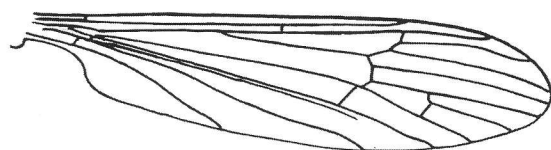


**Figs. 8.44–55.** Wings (continued): dorsal view of (44) *Dicranomyia (Peripheroptera) eudorae* (Alexander), (South America, Alexander, 1913d, fig. 7); (45) *Dicranomyia (Peripheroptera) arcuata* (Alexander), (South America, Alexander, 1913d, fig. 8); (46) *Dicranomyia (Dicranomyia) knabi* (Alexander), (Alexander, 1912b, fig. m); (47) *Dicranomyia (Dicranomyia) gloriosa* (Alexander), (Alexander, 1912b, fig. j); (48) *Orimarga (Diotrepha) mirabilis* (Osten Sacken), (Nearctic, MND, fig. 7.35); (49) *Orimarga (Orimarga) niveitarsis* Alexander, (Alexander, 1915, fig. 5); (50) *Trentepohlia (Paramongoma) dominicana* Alexander, (Caribbean, Alexander, 1970a, fig. 60); (51) *Helius (Helius) flavipes* Macquart, (Nearctic, MND, fig. 7.32); (52) *Styringomyia paulista* Alexander, (South America, Ribeiro, 2003, fig. 7); (53) *Dicranoptycha germana* (Osten Sacken), (Nearctic, MND, fig. 7.33); (54) *Teucholabis (Teucholabis) complexa* Osten Sacken, (Nearctic, MND, fig. 7.51), and (55) *Teucholabis (Paratropesa) collaris* (Osten Sacken), (South America, Alexander, 1913d, fig. 9).

56 *Atarba (Atarba)* ♀57 *Gonomyia (Neolipophleps)*58 *Gonomyia (Paralipophleps)*59 *Gonomyia (Leiponeura)*60 *Hexatoma* ♀61 *Lecteria*62 *Paradelphomyia*63 *Sigmatomera (Sigmatomera)*64 *Gonomyia (Gonomyia)* ♀65 *Teucholabis (Euparatropesa)*66 *Polymera* ♀67 *Sigmatomera (Austrolimnobia)*

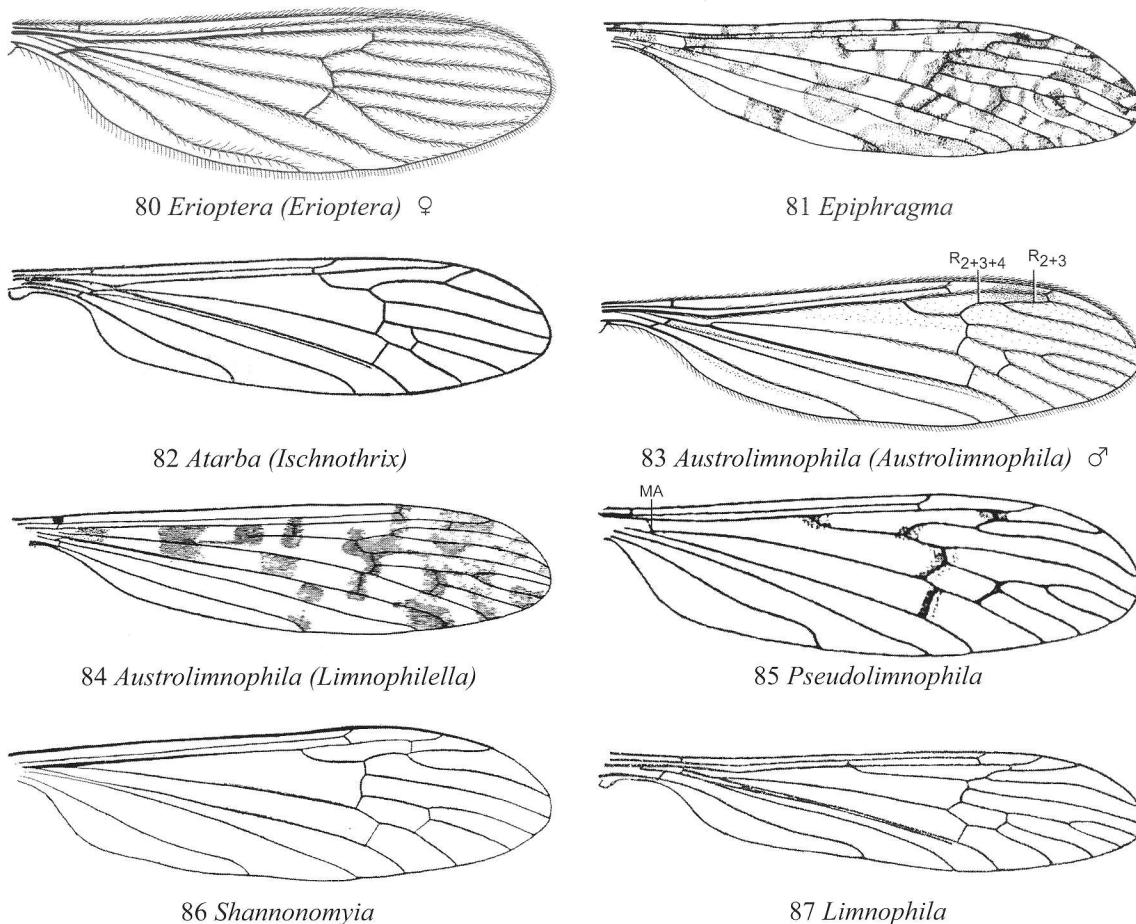
**Figs. 8.56–67.** Wings (*continued*): dorsal view of (56) *Atarba (Atarba) picticornis* Osten Sacken, (Nearctic, MND, fig. 7.43); (57) *Gonomyia (Neolipophleps) alexanderi* (Johnson), (Nearctic, Alexander, 1919a, fig. 86); (58) *Gonomyia (Paralipophleps) pleuralis* (Williston), (Alexander, 1916c, fig. 20); (59) *Gonomyia (Leiponeura) puer* Alexander, (Alexander, 1916c, fig. 21); (60) *Hexatoma (Eriocera) longicornis* (Walker), (Nearctic, MND, fig. 7.41); (61) *Lecteria (Lecteria) armillaris* (Fabricius), (Alexander, 1913a, fig. 42); (62) *Paradelphomyia (Oxyrhiza) oaxacensis* (Alexander), (Alexander, 1948b, fig. 2); (63) *Sigmatomera (Sigmatomera) occulta* Alexander, (Reidel, 1921, fig. A, as *flavipennis*); (64) *Gonomyia (Gonomyia) subcinerea* Osten Sacken, (Nearctic, MND, fig. 7.54); (65) *Teucholabis (Euparatropesa) lindneri* Alexander, (South America, Alexander, 1933, fig. 1); (66) *Polymera (Polymera) rogersiana* Alexander, (Nearctic, MND, fig. 7.45); and (67) *Sigmatomera (Austrolimnobia) magnifica* (Alexander), (Alexander, 1913a, fig. 31).



68 *Ellipteroides (Progonomyia)*69 *Lipsotrix* ♀70 *Eugnophomyia*71 *Gnophomyia* ♀72 *Neognophomyia*73 *Molophilus* ♂74 *Rhabdomastix* ♂75 *Cheilotrichia (Empeda)*76 *Cryptolabis* ♀77 *Symplecta (Symplecta)*78 *Symplecta (Trimicra)*79 *Erioptera (Mesocyphona)*

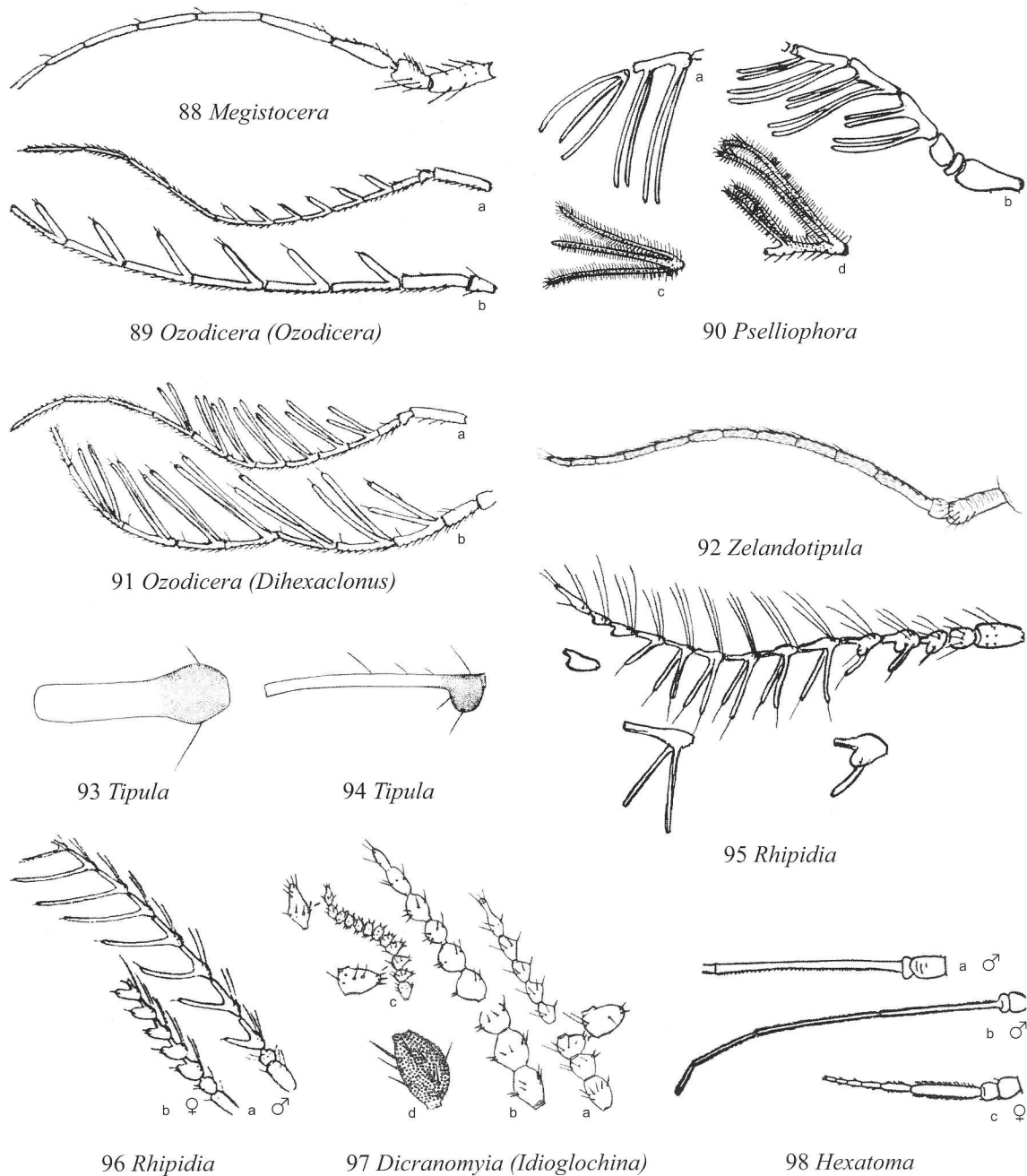
**Figs. 8.68–79.** Wings (*continued*): dorsal view of (68) *Ellipteroides (Progonomyia) slossonae* (Alexander), (Alexander, 1914d, fig. 26); (69) *Lipsotrix nigrilinea* (Doane), (Nearctic, MND, fig. 7.55); (70) *Eugnophomyia luctuosa* (Osten Sacken), (Alexander, 1913a, fig. 29); (71) *Gnophomyia tristissima* (Osten Sacken), (Nearctic, MND, fig. 7.53); (72) *Neognophomyia hirsuta* (Alexander), (South America, Alexander, 1913a, fig. 30); (73) *Molophilus nitidus* Coquillett, (Nearctic, MND, fig. 7.56); (74) *Rhabdomastix (Rhabdomastix) californiensis* Alexander, (Nearctic, MND, fig. 7.58); (75) *Cheilotrichia (Empeda) tanneri* Alexander, (Alexander, 1970b, fig. 5); (76) *Cryptolabis (Cryptolabis) paradoxa* (Osten Sacken), (Nearctic, MND, fig. 7.57); (77) *Symplecta (Symplecta) cana* (Walker), (Nearctic, MND, fig. 7.62); (78) *Symplecta (Trimicra) pilipes* (Fabricius), (Alexander, 1967a, fig. 450); and (79) *Erioptera (Mesocyphona) eiseni* Alexander, (Alexander, 1913a, fig. 26).

- Eye glabrous (without hairs);  $Sc_1$  of varied length; when sc-r basal to origin of  $R_s$ ,  $Sc_1$  not extending past fork of  $R_s$  (Fig. 45) . . . . . 17
- 17.  $R_s$  one or two branched, two or three branches of  $R$  reaching wing margin (Figs. 38, 39, 56) . . 18
  - $R_s$  three branched ( $R_3$  may be short as in *Lecteria* (*Psaronius*) and *Rhabdomastix*), four branches of  $R$  reaching wing margin (Fig. 60) . . . . . 47
- 18. Head with rostrum and mouthparts long and slender, greatly exceeding length of head, usually half of body length or more (equal to head and thorax or longer) (Figs. 104–106) . . . . . 19
  - Rostrum usually not elongated, rarely as long as head (e.g., *Helius*, Fig. 102) . . . . . 22
- 19.  $R_2$  present; elongate rostrum formed of mouthparts, particularly prominent labial palpi and hypopharynx (Fig. 104); antenna with 12 flagellomeres; male hypopygium with inner gonostylus swollen with medial rostrum (Fig. 119) . . . . . *Geranomyia* Haliday



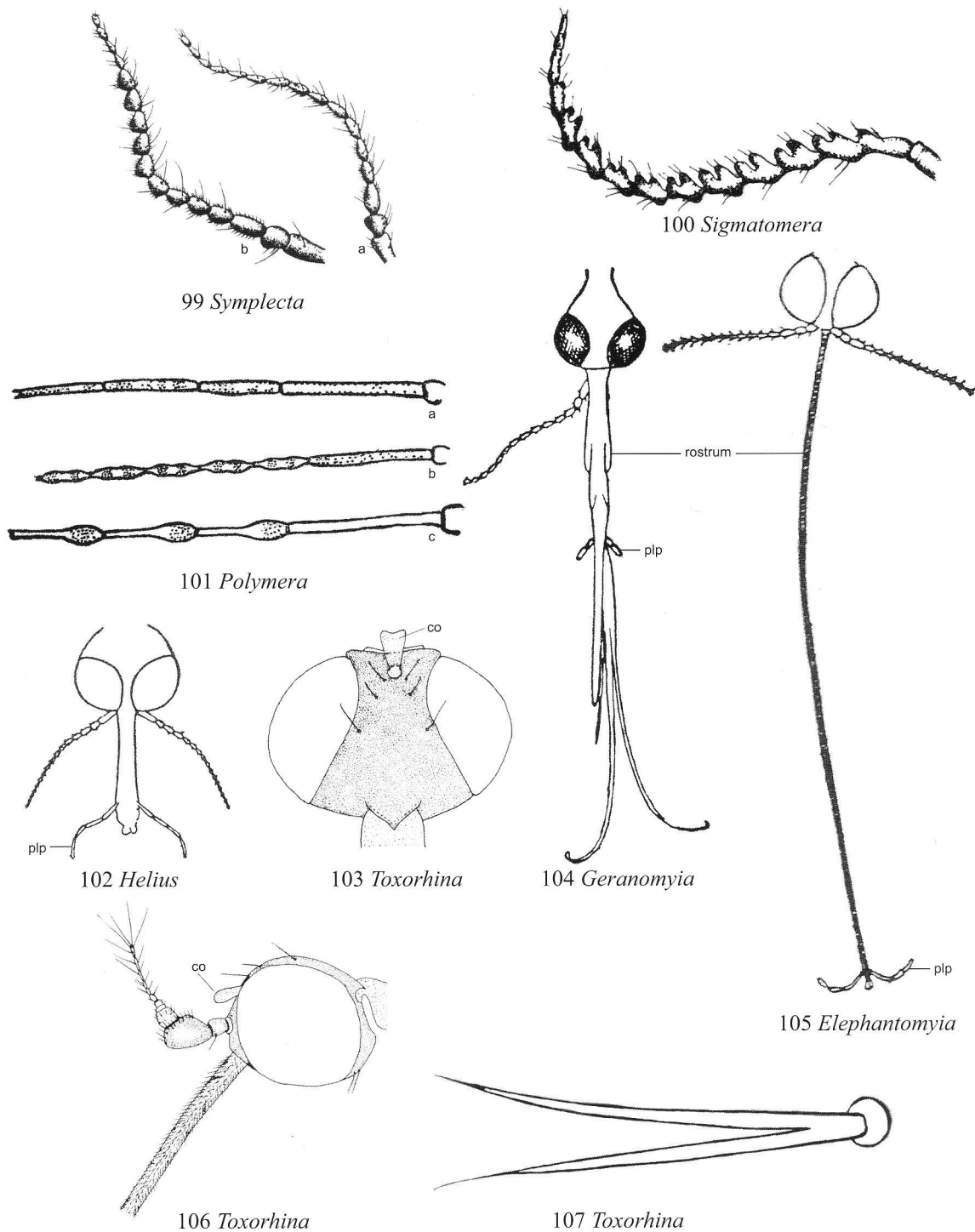
**Figs. 8.80–87.** Wings (*concluded*): dorsal views of (80) *Erioptera* (*Erioptera*) *septentrionis* Osten Sacken, (Nearctic, MND, fig. 7.63); (81) *Epiphragma* (*Epiphragma*) *gracilicorne* Alexander, (South America, Alexander, 1916a, fig. 11); (82) *Atarba* (*Ischnothrix*) *voracis* Alexander, (South America, Alexander, 1948a, fig. 21); (83) *Austrolimnophila* (*Austrolimnophila*) *toxoneura* (Osten Sacken), (Nearctic, MND, fig. 7.48); (84) *Austrolimnophila* (*Limnophilella*) *victor* Alexander, (Alexander, 1919b, fig. 6A); (85) *Pseudolimnophila* (*Pseudolimnophila*) *luteipennis* (Osten Sacken), (Alexander, 1919a, fig. 135); (86) *Shannonomyia* (*Shannonomyia*) *lentooides* (Alexander), (Alexander, 1913a, fig. 21); and (87) *Limnophila* (*Limnophila*) *guttulatissima* Alexander, (Alexander, 1948a, fig. 6).

- $R_2$  absent (Fig. 36); rostrum formed from frons, with reduced mouthparts, including palpi, at extreme tip (Fig. 105); antenna with 13–14 flagellomeres; rarely with 10 flagellomeres in some *Toxorhina* (*T.*); male genitalia with ventral gonostylus not swollen, without rostrum (Fig. 120) . . . . . 20
- 20. Origin of  $R_s$  before *sc-r* (Fig. 36); basal third of veins  $Cu$  and  $A_1$  not particularly close together; setae on legs simple; tibial spurs present but short . . . . . *Elephantomyia* Osten Sacken
- $R_s$  originating beyond *sc-r* (Fig. 37); basal third of veins  $Cu$  and  $A_1$  close together, then abruptly divergent more distally; setae on legs bifid (Fig. 107); tibial spurs absent; *Toxorhina* Loew . . . . . 21
- 21.  $R_s$  with two branches (Fig. 38); anterior vertex with soft, pale triangular sac (corniculus) (Figs. 103, 106) . . . . . *Toxorhina* (*Ceratocheilus*) Wesche
- $R_s$  unbranched (Fig. 37); anterior vertex without corniculus . . . . . *Toxorhina* (*Toxorhina*) Loew
- 22. Antenna with 12 flagellomeres (sometimes last flagellomere constricted and appearing as 13th flagellomere);  $R_2$  present (but may be faint); LIMONIINI . . . . . 23
- Antenna with 13–14 flagellomeres;  $R_2$  present or absent . . . . . 36
- 23. Flagellomeres of antenna of male and female more or less produced to give antenna serrate or pectinate appearance (Figs. 96, 97; in some females and males, this modification is slight) . . . . . 24
- Flagellomeres of both sexes ranging from subglobular to oval to elongate, not produced to appear serrate or pectinate in appearance . . . . . 25
- 24. Flagellomeres of male antenna commonly bipectinate, unipectinate, or subpectinate (Figs. 95, 96); flagellomeres in female and some males less developed, often slightly to scarcely produced, although if subpectinate, often at least flagellomeres 12 and 13 are abruptly lighter in color (*L. domestica* species group); *Sc* usually ending well beyond the origin of  $R_s$  (Fig. 39); wing usually spotted or clouded, sometimes strongly so; inner gonostylus with two or more rostral spines (Fig. 121); not marine. . . . . *Rhipidia* Meigen
- Intermediate flagellomeres with lower (ventral) surface produced into flattened lobe producing nearly serrate appearance (Fig. 97), verticils shorter than flagellomeres, stout, and encircling mid-length and on extended portion; antenna uniformly dark, not with abruptly lighter flagellomeres; *Sc* ending before or opposite origin of  $R_s$  (Fig. 40); wing with light brown clouds, not strongly spotted; inner gonostylus without rostral spines (Fig. 122); marine, Pacific coasts of Chile and North America . . . . . [*Dicranomyia* (*Idioglochina*) Alexander]
- 25.  $R_{1+2}$  longer than  $R_2$  (=terminal section of  $R_1$ , i.e., the section beyond point of fusion with  $R_2$ ) continuing in direction of  $R_1$  and longer than  $R_2$  (often at least two times longer than  $R_2$ ); male gonostylus simple, undivided; North America, Colombia, Chile . . . [*Limonia* (*Limonia*) Meigen]
- Terminal section of  $R_1$  in nearly transverse position, not continuing in the direction of basal section of  $R_1$  and about as long as  $R_2$  (Figs. 41, 47); male gonostylus divided. . . . . 26
- 26. Cell  $r_3$  with supernumerary crossvein (Fig. 41); femora with dark rings. . . . . 27
- Cell  $r_3$  without extra crossvein; femora various. . . . . 28
- 27. Wing with reticulated patterning;  $R_s$  gently curved (Fig. 41); male inner gonostylus large, swollen (Fig. 123); prescutum dark brown with three yellowish-brown stripes. . . . . *Dicranomyia* (*Neolimnobia*) Alexander
- Wing patterning restricted, not heavily reticulated (Fig. 42);  $R_s$  with strong bend or curve near origin; male hypopygium with smaller inner gonostylus (Fig. 124); whitish or yellow thorax with narrow darkened median line on prescutum . . . . . *Dicranomyia* (*Caenolimonia*) Alexander
- 28. Vein *Sc* short, ending before or opposite of origin of  $R_s$  (Figs. 44, 45) . . . . . 29
- Vein *Sc* longer, ending beyond origin of  $R_s$ , opposite one-third length or more of  $R_s$  (Fig. 47). . . . . 31



**Figs. 8.88–98.** Antennae: scape, pedicel, and basal flagellomeres of (88) *Megistocera longipennis* (Macquart), (Alexander, 1969a, fig. 5); (89) *Ozodicera (Ozodicera) cinereipennis* Alexander, (South America, Alexander, 1969a, fig. 52); (90) *Pselliophora margarita* (Alexander), (Alexander, 1969a, fig. 22); (91) *Ozodicera (Dihexaclonus) macracantha*, (South America, Alexander, 1969a, fig. 51); (92) *Zelandotipula laevis* (Alexander), (South America, Vane-Wright, 1967, fig. 18); fifth flagellomere of (93) *Tipula (Eumicrotipula) exilis* Alexander, (South America, Alexander 1916a, plate 4, fig. 5); and (94) *Tipula (Eumicrotipula) armillatus* Alexander, (South America, Alexander, 1916a, plate 4, fig. 8); scape, pedicel, and flagellomeres of (95) *Rhipidia (Rhipidia) willistoniana* (Alexander), (Alexander, 1970a, fig. 28); and male (96a) and female (96b) of *Rhipidia (Rhipidia) subcostalis* Alexander, (Alexander, 1962b, fig. 23); various flagellomeres of (97a–d) *Dicranomyia (Idioglochina)* spp., (Austropacific, Alexander, 1972, figs. 67–69); scape, pedicel, and basal flagellomeres of males (98a, b) and female (98c) of *Hexatoma (Eriocera)* spp., (Nearctic, Alexander, 1919a, figs. 125, F, G, H).

- 29. Wing apex usually obtusely rounded (most developed in males); vein  $A_2$  lying close to wing margin at least in basal half (Figs. 44, 45);  $R_s$  short, equal to or only slightly longer than  $R_2$ ; wing with prearcular cell large and prominent although wing base narrowed (width of prearcular cell measured transversely at arcular crossvein one-quarter of wing width measured at same location), females of some species indistinguishable from those of subgenus *Dicranomyia* . . . . . *Dicranomyia (Peripheroptera)* Schiner
- Wing apex more narrowly rounded; vein  $A_2$  not following close to wing margin (Figs. 43, 46, 47); vein  $R_s$  usually much longer than  $R_2$ ; wing with prearcular cell usually small and wing base not narrowed (width of prearcular cell one-sixth or less of wing width). . . . . 30
- 30.  $R_s$  strongly bent at origin, sometimes bent slightly toward wing base (Fig. 43); thorax yellow with narrow darkened median line on pronotum and prescutum; femora yellow with darker rings; mesal face of male gonocoxite with several coarse black setae (Fig. 124) . . . . . *Dicranomyia (Caenolimonia)* Alexander
- $R_s$  various but usually not strongly bent beyond origin (Figs. 46, 47); coloration of thorax and legs various; gonocoxite otherwise (Figs. 125, 126) . . . . . *Dicranomyia (Dicranomyia)* Stephens
- 31. Eyes in both sexes nearly holoptic, with borders at dorsal side parallel for some distance, leaving only narrow strip of vertex between them; male hypopygium complicated (Fig. 127): with large apical lobe of gonocoxite, no rostral spines on rostral prolongation of small inner gonostylus, and proctiger prominent, forming several separate lobes . . . . . *Atypophthalmus* Brunetti
- Eyes with their borders at dorsal side rounded and clearly separated above; male hypopygium not as in Fig. 127; . . . . . 32
- 32. Male hypopygium with single gonostylus (Figs. 128, 130) . . . . . 33
- Male hypopygium with two pairs of gonostyli, outer gonostylus forming curved rod (Figs. 125, 126, 129) . . . . . 34
- 33. Male gonostylus complicated (Fig. 128), apex often forming spine; mesal face of gonocoxite often with various lobes and protuberances tufted with setae . . . . . *Dicranomyia (Caenoglochina)* Alexander
- Male gonostylus simple in structure with dark furrow present (Fig. 130); gonocoxite with one or two simple lobes, with scattered setae, not tufted with setae . . . . . *Dicranomyia (Neolimonia)* Alexander
- 34. Antenna with verticils elongate apically, some exceeding flagellomeres upon which they arise; apical flagellomeres elongate, not globular, with terminal flagellomere exceeding length of penultimate flagellomere . . . . . 35
- Antennae with verticals not conspicuously long; flagellomeres usually globular or oval, not with extended apical flagellomeres . . . . . *Dicranomyia (Dicranomyia)* Stephens
- 35. Male outer gonostylus with microscopic serrations (“scabrous”), best seen in slide mount (Fig. 129); inner gonostylus not bilobed, without rostral spines, rostrum glabrous, compressed, blade shaped, with pale area at midlength . . . . . *Dicranomyia (Neoglochina)* Alexander
- Male outer gonostylus smooth (Fig. 131); inner gonostylus deeply bilobed with two rostral spines, rostral section large and stout, often pale and peglike, surrounded by areas of delicate, silken hairs (Fig. 131) . . . . . *Dicranomyia (Neolimonia)* Alexander
- 36.  $R_2$  at oblique angle toward anterior margin of wing, giving appearance of confluence of veins forming X-shape (Fig. 50); cell  $dm$  present: cell  $cu$  nearly closed at wing margin owing to end of vein  $CuA_2$  being abruptly bent toward  $A_1$ ; male hypopygium with single pair of gonostyli (Fig. 134) . . . . . *Trentepohlia (Paramongona)* Brunetti



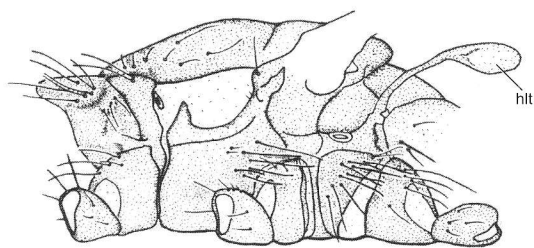
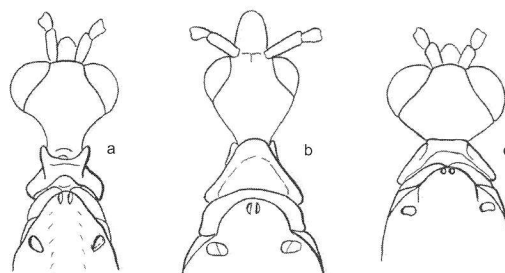
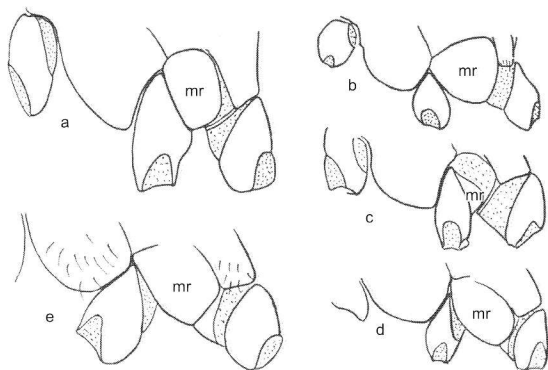
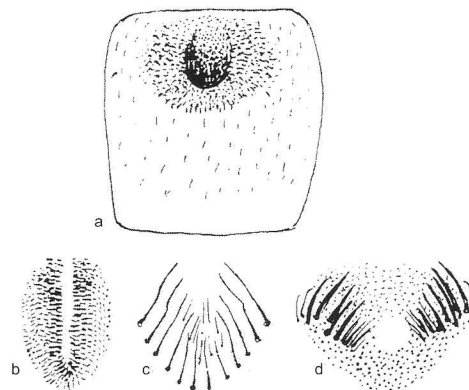
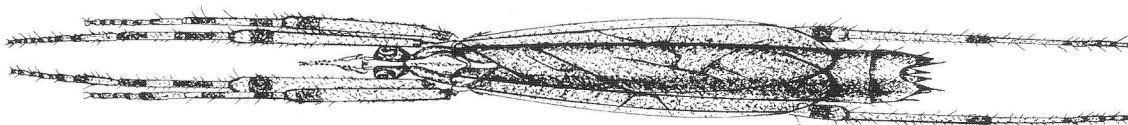
**Figs. 8.99–107.** Antennae and heads: of (99a) *Symplecta* (*Symplecta*) *hybrida* (Meigen), (99b) *Symplecta* (*Trimicra*) *pilipes* (Fabricius), (Palearctic, Reusch & Oosterbroek, 1997, fig. 122); (100) *Sigmatomera* (*Sigmatomera*) *occulta* Alexander, (Reidel, 1921, fig. B, as *flavipennis*); (101) *Polymera* (*Polymera*) spp., (hairs omitted), (Alexander, 1948b, figs. 31–33); anterior views of heads of (102) *Helius* (*Helius*) *flavipes* Macquart, (Nearctic, Alexander, 1919a, fig. 124B); (103) *Toxorhina* (*Ceratocheilus*) sp., (Afrotropical, Tjeder, 1981, fig. 1); (104) *Geranomyia* *canadensis* (Westwood), (left antenna omitted), (Nearctic, Alexander, 1943a, fig. 34C); (105) *Elephantomyia* (*Elephantomyia*) *westwoodi* Osten Sacken, (Nearctic, Alexander, 1919a, fig. 124D); lateral view of head of (106) *Toxorhina* (*Ceratocheilus*) sp., (Afrotropical, Tjeder, 1981, fig. 2); leg seta of (107) *Toxorhina* (*Ceratocheilus*) sp., (Afrotropical, Tjeder, 1981, fig. 4).

Abbreviation: co, corniculus; plp, palpus.



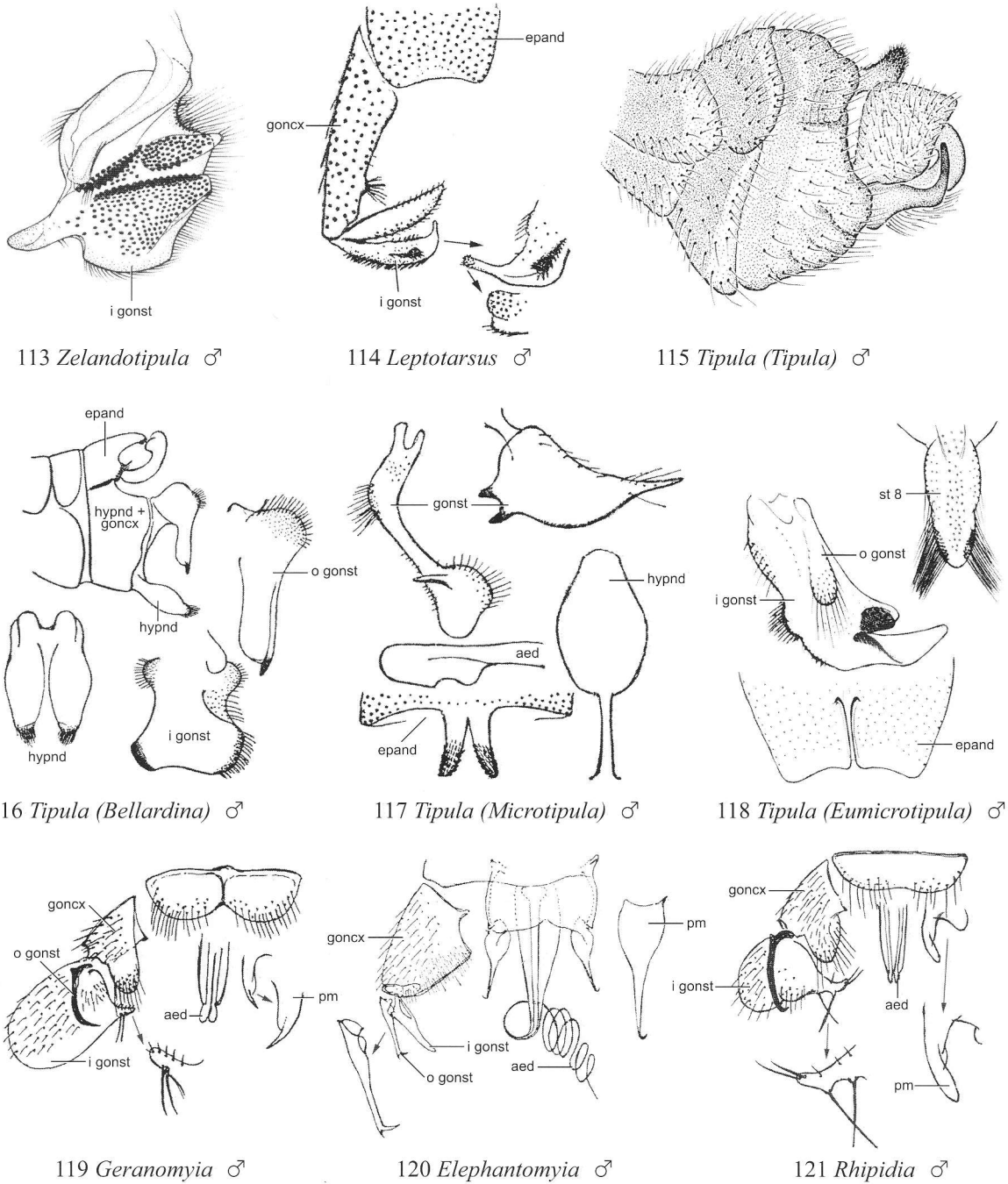
- Wing with  $R_2$  in more transverse position (in relation to axis of wing) or absent; cell dm present or absent; apex of  $CuA_2$  not abruptly bent; male hypopygium with two pairs of gonostyli (one pair in *Styringomyia*) . . . . . 37
- 37. Basal transverse section of  $CuA_1$  located well before first branch of vein M, in basal third to basal half of wing (Figs. 48, 49); cell dm absent; wings narrow, four to five times as long as wide (at greatest width); *Orimarga* Osten Sacken . . . . . 38
- Basal transverse section of  $CuA_1$  located shortly before, at, or after branching of vein M, in apical half of wing (Fig. 51); cell dm present; wings usually not greatly narrowed, four times as long as wide . . . . . 39
- 38. M with three branches reaching wing margin (Fig. 49); basal transverse section of  $CuA_1$  reaching M normally near midlength of wing . . . . . *Orimarga* (*Orimarga*) Osten Sacken
- M with two branches reaching wing margin (Fig. 48); basal transverse section of  $CuA_1$  reaching M far before fork of M, at or near one-third to one-fourth of wing length . . . . . *Orimarga* (*Diotrepha*) Osten Sacken
- 39. Ventral part of head extended with rostrum about as long as remainder of head (Fig. 102);  $R_2$  absent (Fig. 51) . . . . . *Helius* (*Helius*) Lepeletier & Serville
- Ventral part of head not produced, rostrum shorter or longer than remainder of head; where rostrum longer, then  $R_2$  present (some *Teucholabis*) . . . . . 40
- 40. Two branches of Rs strongly divergent, nearly perpendicular (Fig. 52);  $R_1$  short, not reaching midlength of wing; thorax strongly dorsoventrally compressed (Fig. 108) . . . . . *Styringomyia* Loew
- Branches of Rs parallel to divergent, but not perpendicular;  $R_1$  reaching midlength of wing, usually longer; thorax not dorsoventrally compressed . . . . . 41
- 41.  $R_2$  present (Figs. 16, 53) . . . . . 42
- $R_2$  absent (Fig. 56) . . . . . 44
- 42.  $R_2$  situated beyond level of distal end of cell dm (Fig. 53); conspicuous pale fold present in outer end of cell  $cua_2$ ; males without depressions (sternal pockets) on abdominal sternites 5 and 6 . . . . . *Dicranoptycha* Osten Sacken
- $R_2$  opposite crossvein r-m or slightly beyond (Figs. 54, 55); no fold in cell  $cua_2$ ; males with depressions (sternal pockets) on abdominal sternites 5 and 6 (Figs. 111a–d); pockets with various modified setae (at least one species from Colombia lacks these); *Teucholabis* Osten Sacken . . . . . 43
- 43. Cell dm with three veins arising from it and ending in wing margin (Fig. 54); two single veins of Rs reaching wing margin . . . . . *Teucholabis* (*Teucholabis*) Osten Sacken
- Cell dm with four veins arising from it and ending in wing margin (Fig. 55); Rs with only one branched vein apparent, with  $R_3$  and  $R_4$  reaching wing margin ( $R_5$  arises from cell dm) . . . . . *Teucholabis* (*Paratropesa*) Schiner
- 44. Two branches of Rs nearly parallel, with only slight divergence at wing tip (Fig. 56); male antenna usually of medium length to elongate, one-third to three times body length; tibial spurs present . . . . . *Atarba* (*Atarba*) Osten Sacken
- Two branches of Rs strongly divergent, at least at wing margin (Figs. 57–59); antenna short, no longer than thorax, one-fifth or less of total body length; tibial spurs absent (although some may have two dark setae in similar position); *Gonomyia* Meigen, in part . . . . . 45

45. Cell dm absent in all Central American species (Fig. 57), costal border of wing usually broadly whitened; legs conspicuously banded with white, forelegs different from remainder; male hypopygium with three to four apparent gonostyli terminal in position (apical extension of gonocoxite absent) (Fig. 135), intermediate gonostylus complicated and longest, outer gonostylus forms thin spine, inner gonostylus usually fleshy, sometimes with dark spine . . . . . *Gonomyia* (*Neolipophleps*) Alexander
- Cell dm present (Figs. 58–59); legs and wings without pattern or patterned differently; hypopygium usually with apical extension of gonocoxite (Figs. 132–133); one gonostylus present . . . 46

108 *Styringomyia*109 a. *Pseudolimnophila*, b. *Limnophila*,  
c. *Palaria*110 a. *Neolimnophila*, b. *Crypteria*,  
c. *Gonomyia*, d. *Rhabdomastix*, e. *Erioptera*111 *Teucholabis* ♂112 *Styringomyia*

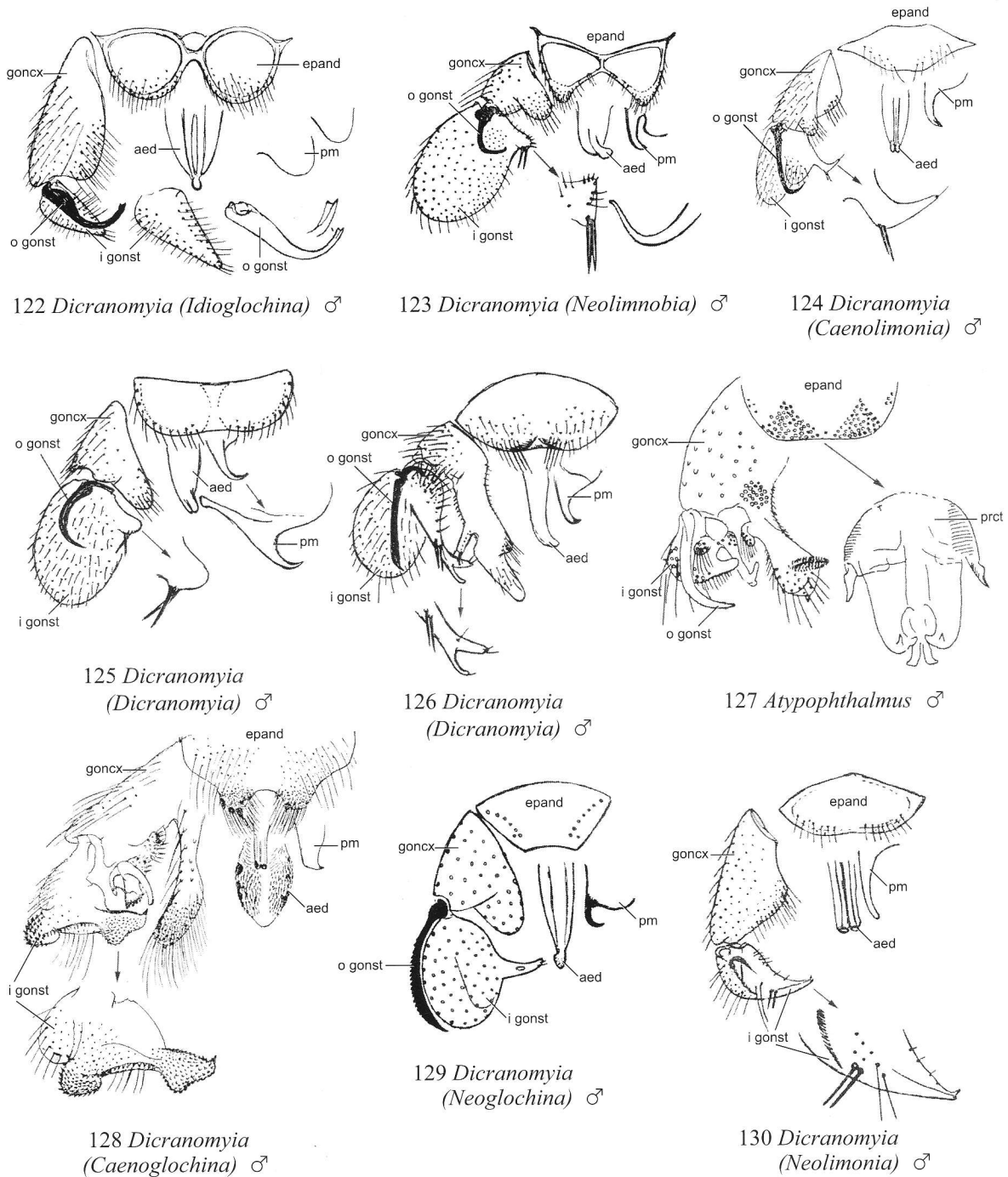
**Figs. 8.108–112.** Thoraces, heads and adjacent pronota, pleura, sternal pockets, and adult posture: lateral view of thorax of (108) *Styringomyia* sp., (South America, Ribeiro, 2003, fig. 6); dorsal view of head (flagellum omitted), prothorax, and adjacent scutum of (109a) *Pseudolimnophila* sp., (109b) *Limnophila* sp., and (109c) *Palaria* sp., (Palearctic, Edwards, 1938, fig. 13); lateral view of lower part of pleuron, including katepisternum, meron, and coxae of (110a) *Neolimnophila* sp., (110b) *Crypteria* sp., (110c) *Gonomyia* sp., (110d) *Rhabdomastix* sp., and (110e) *Erioptera* sp., (Palearctic, Edwards, 1938, fig. 17, membranous areas stippled); sternal pockets of (111a–d) *Teucholabis* spp., (South America, from Alexander, 1980, figs. 36, 37, 42); adult resting posture of (112) *Styringomyia* sp., (Austropacific, Hynes, 1990, fig. 5).

Abbreviation: hlt, halter; mr, meron.



**Figs. 8.113–121.** Male terminalia: anterolateral view of inner gonostylus (outer gonostylus omitted) of (113) *Zelandotipula associans* (Walker), (Vane-Wright, 1967, fig. 31); dorsal view of male terminalia (left gonopod omitted, with inset of inner gonostylus, facing opposite direction, as well as apex of same) of (114) *Leptotarsus (Tanypremna) incompletus* (Alexander), (South America, Alexander, 1944c, fig. 3); lateral view of male terminalia of (115) *Tipula (Tipula) oleracea* Linnaeus, (Young et al., 2000, fig. 1); lateral view of male terminalia and components of (116) *Tipula (Bellardina) cydippe* Alexander, (Alexander, 1947c, fig. 2); dorsal views of male terminalia of (117) *Tipula (Microtipula) contemplata* Alexander, (Alexander, 1951, fig. 10), (118) *Tipula (Eumicrotipula) ligulipenicillata* Alexander, (Alexander, 1946a, fig. 12); (119) *Geranomyia subviresens* (Alexander), (Alexander, 1970a, fig. 22); (120) *Elephantomyia (Elephantomyia) orthorhabda* Alexander, (Alexander, 1971, fig. 29); and (121) *Rhipidia (Rhipidia) willistoniana* (Alexander), (Alexander, 1970a, fig. 28).

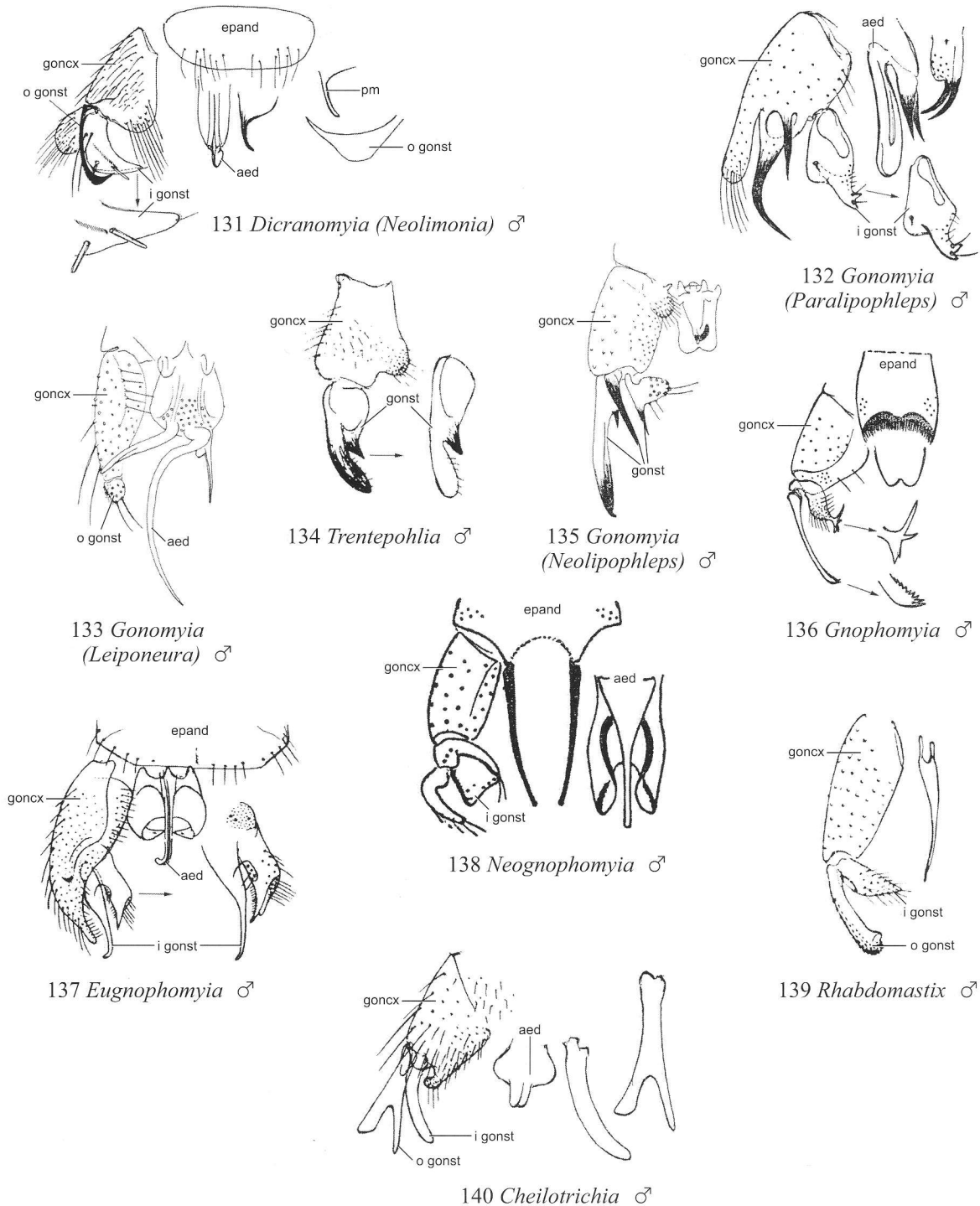
Abbreviations: aed, aedeagus; epand, epandrium; goncx, gonocoxite; hypnd, hypandrium; i gonst, inner gonostylus; o gonst, outer gonostylus; pm, paramere.



**Figs. 8.122–130.** Male terminalia (*continued*): dorsal views of (122) *Dicranomyia (Idioglochina) marmorata* Osten Sacken, (Nearctic, Alexander 1967a, fig. 254); (123) *Dicranomyia (Neolimnobia) diva* (Schiner), (Alexander, 1964b, fig. 25); (124) *Dicranomyia (Caenolimonia) distantia* (Alexander), (Alexander 1971, fig. 6); (125) *Dicranomyia (Dicranomyia) omisa* (Alexander), (Alexander, 1970a, fig. 12); (126) *Dicranomyia (Dicranomyia) divisa* (Alexander), (Nearctic, Alexander 1970a, fig. 11); (127) *Atyphthalmus (Atyphthalmus) umbratus* (de Meijere), (Alexander 1926, fig. 12); (128) *Dicranomyia (Caenoglochina) lotax* (Alexander), (Alexander, 1971, fig. 5); (129) *Dicranomyia (Neoglochina) sciasma* Alexander, (South America, Alexander, 1950, fig. 20); and (130) *Dicranomyia (Neolimonia) cuzcoensis* (Alexander), (South America, Alexander, 1967b, fig. 48).

Abbreviations: aed, aedeagus; epand, epandrium; goncx, gonocoxite; hypnd, hypandrium; i gonst, inner gonostylus; o gonst, outer gonostylus; pm, paramere; prct, proctiger.

46. Wing with conspicuous dark-brown pterostigmal spot (Fig. 58); pleura strongly patterned with brown and yellow stripes; gonocoxite produced into apical outer fleshy lobe and one or more blackened spines or spinous points (arising from apex of gonocoxite) (Fig. 132) . . . . . *Gonomyia (Paralipophleps)* Alexander
- Wing with pterostigmal spot lacking or virtually so (Fig. 59); pleural stripes indistinct or faintly indicated; gonocoxite with or without apical fleshy lobe, gonostylus sometimes with spine, but no other additional darkened spines arising from gonocoxite (Fig. 133) . . . . . *Gonomyia (Leiponeura)* Skuse
47. Antenna with nine or fewer flagellomeres, although they may be greatly elongated, often with vestiture of basal flagellomeres with spinous setae (Figs. 98a–c); male antennae short to long (exceeding body length). . . . . *Hexatoma* Latreille, subgenus *Eriocera* Macquart
- Antennae with more than 11 flagellomeres, length various but usually short . . . . . 48
48. Tibial spurs absent (some *Gonomyia* and others have distinct small, dark setae in the “spur” position, with these setae slightly distinct from the remainder but lack thickness and finer hair found on spurs); cell  $m_1$  usually absent; CHIONEINI and LIMNOPHILINI, in part . . . . . 49
- Tibial spurs present, cell  $m_1$  often present; LIMNOPHILINI in part. . . . . 70
49. Cells  $m_1$  and  $dm$  present (Fig. 61), three branches of M and distal section of  $CuA_1$  reaching wing margin . . . . . 50
- Cell  $m_{1+2}$  present, cell  $dm$  present or absent (Figs. 63, 65), two branches of M and distal section of  $CuA_1$  reaching wing margin (Fig. 63); if three branches of M, then cell  $dm$  absent (*Polymera*, Fig. 66). . . . . 51
50.  $R_2$  present, macrotrichia absent in outer wing cells (Fig. 61); large species, 13–18 mm body length; Sc long, extending to fork of Rs and in close proximity to  $R_{1+2}$ ; Rs long, parallel to  $R_1$ , and in alignment with  $R_{2+3+4}$  and  $R_4$  . . . . . *Lecteria (Lecteria)* Osten Sacken
- $R_2$  weak or absent; macrotrichia in outer wing cells (Fig. 62); small species, less than 10 mm body length; Sc not reaching Rs fork and distant from  $R_{1+2}$ ; Rs shorter and curved near origin, not in straight line alignment with  $R_{2+3+4}$  and  $R_4$  . . . . . *Paradelphomyia (Oxyrhiza)* De Meijere, in part
51. Antennal flagellomeres of both sexes strongly binodose (Fig. 100); apex of female cerci tridentate (Fig. 146) . . . . . *Sigmatomera (Sigmatomera)* Osten Sacken
- Antennal flagellomeres of both sexes not strongly binodose, if with developed nodes, then nodes with whorls of hairs and wing with cell  $m_1$  present (*Polymera*); apex of female cerci simple, pointed . . . . . 52
52. Coxae of mid- and hind legs only slightly separated by meral region; meron small, not exceeding coxa in diameter (Figs. 110a, c) . . . . . 53
- Coxae of mid- and hind legs widely separated by large meron producing “pot-bellied” appearance, meron subequal to or larger than coxa (Figs. 110d, e) . . . . . 61
53. Cell  $r_3$  shorter than vein  $R_{2+3+4}$  (its petiole) (as measured along  $R_3$ ; Fig. 64) . . . . . 54
- Cell  $r_3$  longer than its petiole . . . . . 55
54.  $R_2$  present, before or just after the end of Rs,  $R_{2+3+4}$  short or lacking (Fig. 65);  $R_1$  gently bent caudad where it meets  $R_2$ ; males with depressions (sternal pockets) on abdominal sternites 5 and 6 (Fig. 111); pockets with various modified setae (at least one species from Colombia lacks these); body often highly polished, and pleura often with pruinose or silvery stripe . . . . . *Teucholabis (Euparatropesa)* Alexander
- $R_2$  absent (Fig. 64); males without sternal pockets; body not polished, pleura with dark-brown stripe if present. . . . . *Gonomyia (Gonomyia)* Meigen



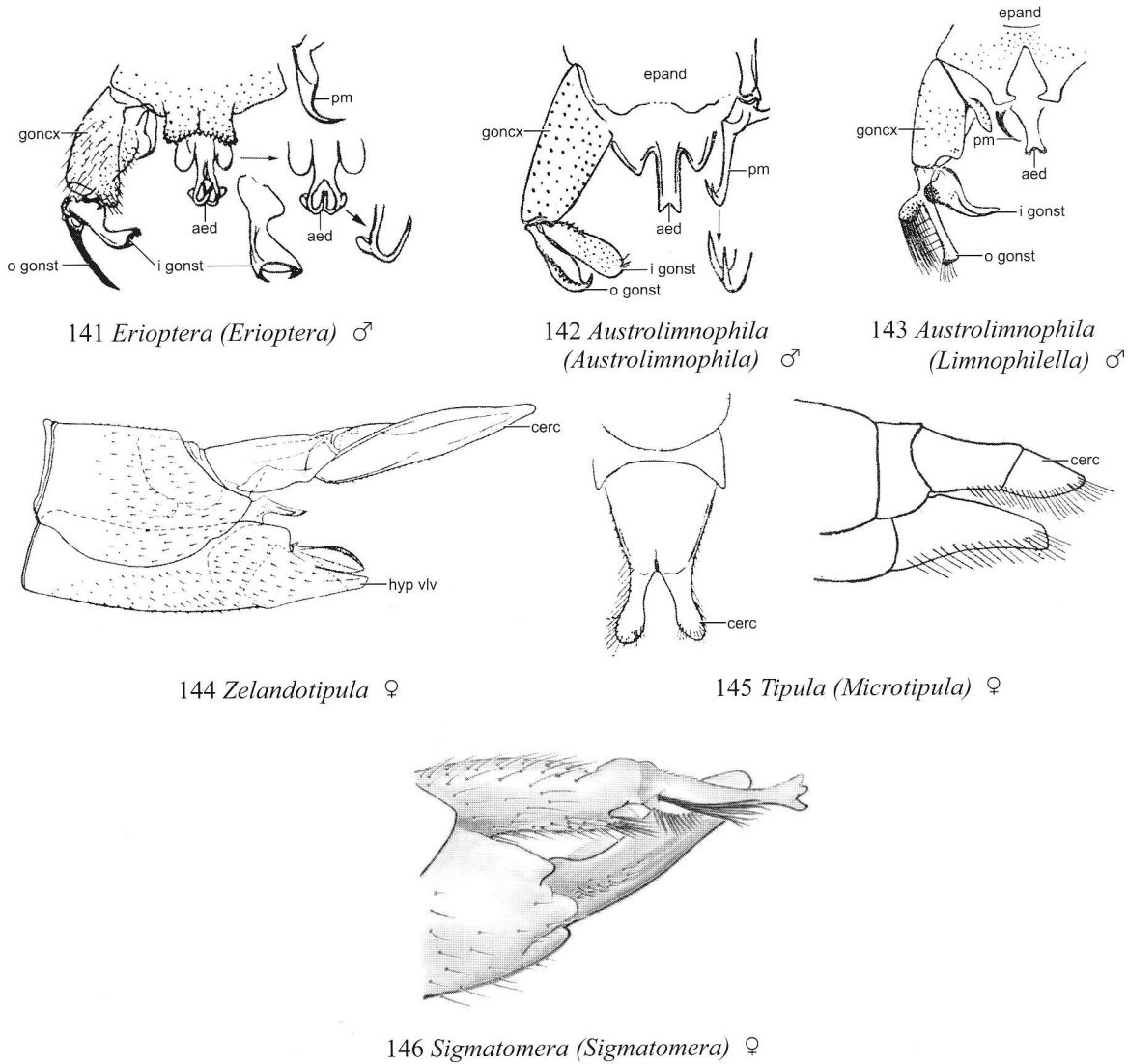
**Figs. 8.131–140.** Male terminalia (*continued*): dorsal views of (131) *Dicranomyia (Neolimonia) gurneyi* (Alexander), (Caribbean, Alexander, 1970a, fig. 13); (132) *Gonomyia (Paralipophleps) pleuralis* (Williston), (Alexander, 1964b, fig. 87); (133) *Gonomyia (Leiponeura) haploa* Alexander, (Alexander, 1926, fig. 18); (134) *Trentepohlia (Paramongoma) aequivena* Alexander, (South America, Alexander, 1980, fig. 27); (135) *Gonomyia (Neolipophleps) strigilis* Alexander, (Alexander, 1926, fig. 14); (136) *Gnophomyia triceps* Alexander, (Alexander, 1947b, fig. 9); (137) *Eugnophomyia apache* (Alexander), (Nearctic, Alexander, 1967a, fig. 401); (138) *Neognophomyia adara* Alexander, (South America, Alexander, 1949, fig. 27); (139) *Rhabdomastix (Rhabdomastix) plaumanni* Alexander, (Alexander, 1947a, fig. 2); and (140) *Cheilotrichia (Empeda) tanneri* Alexander, (Alexander, 1970b, fig. 9).

Abbreviations: aed, aedeagus; epand, epandrium; goncx, gonocoxite; hypnd, hypandrium; i gonst, inner gonostylus; o gonst, outer gonostylus; pm, paramere.



55. Male antenna long, often as long as or longer than body; usually flagellomeres strongly nodulose (appearing beadlike) with whorls of long verticils at nodes and fine hairs overall (Fig. 101), in some species flagellomeres elongate and cylindrical with long verticils over entire length; cell dm absent (Fig. 66). . . . . *Polymera* Wiedemann, subgenus *Polymerodes* Alexander  
 – Male antennae not as above; cell dm usually present (absent in *Ellipteroides* with short cell  $r_3$ ) . . . 56
56.  $R_{1+2}$  and  $R_2$  short, subequal or  $R_{1+2}$  less than twice length of  $R_2$  ( $R_2$  may be faint); vein  $R_{2+3+4}$  (petiole of cell  $r_3$ ) long, one-third or more length of vein  $R_4$  . . . . . 57  
 –  $R_{1+2}$  much longer than  $R_2$ , over twice length of  $R_2$ ; vein  $R_{2+3+4}$  (petiole of cell  $r_3$ ) usually short, one-quarter or less of length of vein  $R_4$  . . . . . 59
57. Sc-r ending opposite or beyond the fork of Rs (Fig. 67); large species, wing 13 mm or more, wing and body contrastingly colored orange and black . . . . *Sigmatomera* (*Austrolimnobia*) Alexander  
 – Sc-r ending before fork of Rs; smaller species, wing length less than 10 mm, usually much smaller; body and wing not so colored. . . . . 58
58.  $Sc_1$  ending before fork of Rs; cell dm absent (Fig. 68) . . . *Ellipteroides* (*Progonomyia*) Alexander  
 –  $Sc_1$  ending opposite or beyond fork of Rs; cell dm present (Fig. 69) . . . . . *Lipsothrix* Loew
59. Macrotrichia present in outer wing cells (rarely absent) (Fig. 70); male hypopygium with gonocoxite produced far beyond point of insertion of gonostyli (Fig. 137); many species colored black and orange . . . . . *Eugnophomyia* Alexander  
 – No macrotrichia on wing cell membranes (Fig. 71); male gonostyli terminal, without apical development of gonocoxite (Figs. 136, 138); body mostly black with yellow or differently colored. . . . 60
60. Veins  $R_3$  and  $R_4$  greatly different in length, with  $R_4$  strongly curved to tip of wing; wing margin between  $R_3$  and  $R_4$  several times longer than that between  $R_4$  and  $R_5$  (Fig. 72); posterior border of male epandrium with pair of elongate lateral tergal spines (Fig. 138) . . . . . *Neognophomyia* Alexander  
 – Veins  $R_3$  and  $R_4$  similar in length, and  $R_4$  not strongly curved to wing tip (Fig. 71); wing margin between  $R_3$  and  $R_4$  less than two times longer than that between  $R_4$  and  $R_5$ ; posterior margin of male epandrium variously shaped, sometimes with median lobe or row of short setae, but not with pair of elongate lateral spines (Fig. 136) . . . . . *Gnophomyia* Osten Sacken
61. Cell  $r_3$  sessile; Rs forking into  $R_{2+3}$  and  $R_{4+5}$  (Fig. 73) . . . . . *Molophilus* (*Molophilus*) Curtis  
 – Cell  $r_3$  petiolate; Rs forking into  $R_{2+3+4}$  and  $R_5$  . . . . . 62
62. Cell  $r_3$  (as measured along vein  $R_3$ ) shorter than its petiole ( $R_{2+3+4}$ ) (Figs. 74, 75) . . . . . 63  
 – Cell  $r_3$  at least as long as its petiole . . . . . 64
63.  $R_2$  absent;  $R_3$  short, suberect, close to  $R_1$  at margin, longer and more oblique in some species;  $R_3$  commonly about one-third length of  $R_4$  or less (Fig. 74); antenna of male greatly lengthened, more than three times length of wing, with abundant pale setae restricted to one face of flagellomere; gonostylus of male terminalia terminal; outer gonostylus simple, densely spinose outwardly (Figs. 6, 139); interbase long and slender . . . . . *Rhabdomastix* (*Rhabdomastix*) Skuse  
 –  $R_2$  present (Fig. 75); combination of other characters not as above; hypopygium as Fig. 140 . . . . . *Cheilotrichia* Rossi, subgenus *Empeda* Osten Sacken
64. Wing membrane with sparse to abundant macrotrichia in wing cells (if viewed in alcohol, only trichial bases may be visible) (Fig. 76) . . . . . 65  
 – Wing membrane without macrotrichia. . . . . 66

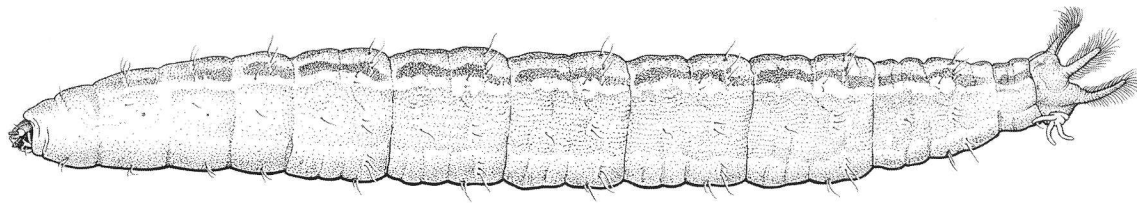
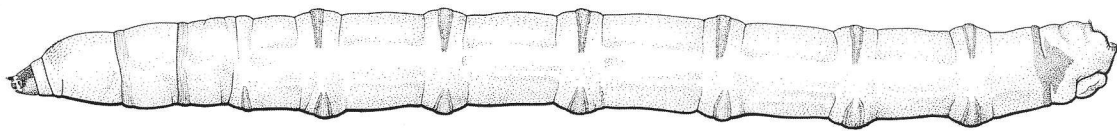
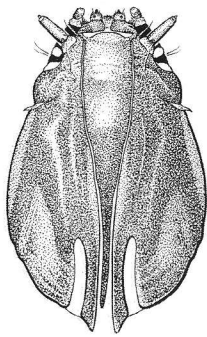
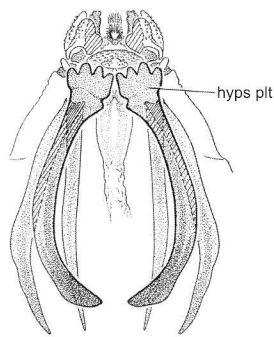
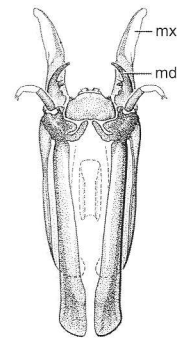
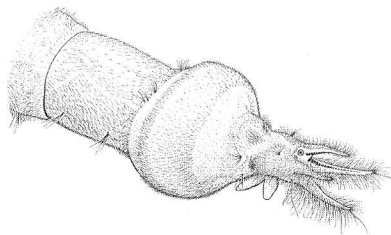
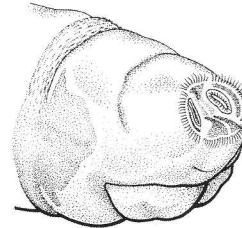
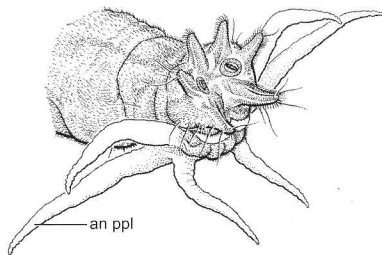
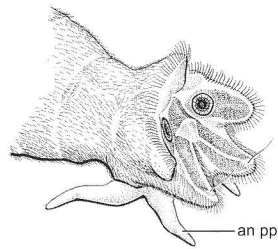
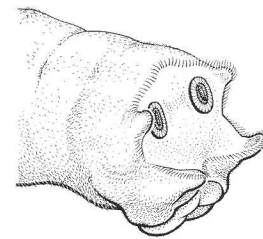
65. Vein  $R_{2+3+4}$  strongly arched, with cell  $r_1$  forming triangle, sometimes nearly equilateral (Fig. 76); cell  $dm$  absent (“open”); female cercus and hypogynial valve short and fleshy . . . . . *Cryptolabis* (*Cryptolabis*) Osten Sacken
- Vein  $R_{2+3+4}$  not strongly arched, with cell  $r_1$  extended, not triangular (as in Fig. 79); cell  $dm$  present; female cercus and hypogynial valve sclerotized. . . . . *Erioptera* Meigen (*Mesocyphona* Osten Sacken), in part (*E. costalis* Alexander group)



**Figs. 8.141–146.** Male terminalia (concluded) and female terminalia: dorsal view of male terminalia of (141) *Erioptera* (*Erioptera*) *acucuspis* Alexander, (South America, Alexander, 1976, fig. 7); (142) *Austrolimnophila* (*Austrolimnophila*) *microsticta* Alexander, (South America, Alexander, 1948b, fig. 14); and (143) *Austrolimnophila* (*Limnophilella*) *schunkeana* Alexander, (South America, Alexander, 1948b, fig. 9); lateral view of female terminalia of (144) *Zelandotipula novarae* (Schiner), (New Zealand, Vane-Wright, 1967, fig. 14); (145) *Tipula* (*Microtipula*) *smithi* Alexander, (South America, Alexander, 1912d, figs. w, w1); and (146) *Sigmatomera* (*Sigmatomera*) *seguyi* Alexander (drawn by S. Podenas).

Abbreviations: aed, aedeagus; cerc, cercus; epand, epandrium; goncx, gonocoxite; hyp vlv, hypogynial valve; i gonst, inner gonostylus; o gonst, outer gonostylus; pm, paramere.

66. Supernumerary crossvein in cell  $r_3$ , and vein  $A_2$  strongly sinuous at its distal end (Fig. 77). . . . .  
 . . . . . *Symplecta* (*Symplecta*) Meigen
- Supernumerary crossvein lacking in cell  $r_3$  (Fig. 78); vein  $A_2$  weakly sinuous or nearly straight (Figs. 78, 80) . . . . . 67
67. Terminal three to four flagellomeres abruptly smaller than others (Fig. 99b); cell dm present (Fig. 78) . . . . . *Symplecta* (*Trimicra*) Osten Sacken
- Terminal flagellomeres gradually and progressively smaller than others (Fig. 99a); cell dm absent . . . . . 68
68. Vein  $M_3$  arising from  $M_{1+2}$  (Fig. 79). . . . . *Erioptera* (*Mesocyphona*), in part
- Vein  $M_3$  arising from distal section of  $CuA_1$  (Fig. 80). . . . . 69
69. Legs (trochanters through proximal end of basistarsus) with abundant elongate scales, remainder of tarsi with typical setae; wings with trichia of veins stout or with scales (scales may be lost in specimens in fluid); aedeagus of male long, slender, with acute tip . . . . . *Eriopterodes* Alexander
- Legs and wings with typical trichia, without scales or strongly thickened setae; aedeagal apex bifurcate (Fig. 141). . . . . *Erioptera* (*Erioptera*) Meigen
70. Cell c with one or more crossveins in addition to basal crossvein; wing strongly patterned with brown, usually ocelliform (ringlike) markings but may be finely spotted (Fig. 81); legs often banded with black or yellow . . . . . *Epiphragma* (*Epiphragma*) Osten Sacken
- Cell c without extra crossvein, only one crossvein present . . . . . 71
71. Crossvein  $R_2$  lacking or only faintly indicated. . . . . 72
- Crossvein  $R_2$  present . . . . . 73
72. Antenna not elongate, length one-fifth or less of wing length; macrotrichia usually in outer wing cells; cell dm present; vein  $R_3$  of moderate length, half or more length of  $R_{4+5}$  (Fig. 62) . . . . .  
 . . . . . *Paradelphomyia* Alexander, subgenus *Oxyrhiza* de Meijere, in part
- Antenna elongate, especially in male, usually one third to three times wing length; macrotrichia absent on wing membrane; cell dm absent in Central American species (*A. patens*); vein  $R_3$  short, oblique to transverse to wing edge, one-quarter length of  $R_{4+5}$  (Fig. 82). . . . .  
 . . . . . *Atarba* (*Ischnothrix*) Bigot
73. Cell dm absent (present in one species), often with both cell  $m_1$  and cell  $m_3$  present (rarely  $M_1$  absent) (Fig. 66); male antenna long, often longer than wing or body, flagellomeres usually strongly nodulose (appearing beadlike) with whorls of long verticils at nodes (Fig. 101c); in some species flagellomeres elongate and cylindrical with long verticils over entire length (Figs. 101a, b); female antenna much shorter, not nodulose (females may key to *Erioptera*) . . . . .  
 . . . . . *Polymera* (*Polymera*) Wiedemann
- Cell dm usually present (absent in one species of *Shannonomyia* with large  $m_3$  cell); cell  $m_1$  often present (not in most *Shannonomyia*); male antenna short to moderate in length, shorter than body or wing length; male and female antennae not strongly nodulose, although may have long verticils . . . . . 74
74. Wing with MA (anterior branch of the medius, arculus) lacking (Figs. 83, 84); wings clear or patterned with bands or spots; *Austrolimnophila* Alexander . . . . . 75
- Wing with MA present (Fig. 85); wing unpatterned or patterning restricted. . . . . 76

147 *Prionocera*148 *Limonia*149 *Prionocera*150 *Molophilus*151 *Limnophila*152 *Limnophila*153 *Limonia*154 *Tipula*155 *Gonomyia*156 *Epiphragma*

**Figs. 8.147–156.** Larvae: lateral view of larvae of (147) *Prionocera* sp., (Nearctic, MND, fig. 7.66); and (148) *Limonia* sp., (Nearctic, MND, fig. 7.85); dorsal view of larval head capsule of (149) *Prionocera* sp., (Nearctic, MND, fig. 7.67, as *P. dimidiata*); (150) *Molophilus* sp. (Nearctic, MND, fig. 7.76); and (151) *Limnophila* sp., (Nearctic, MND, fig. 7.83); posterolateral view of terminal segments of (152) *Limnophila* sp. (Nearctic, MND, fig. 7.84); (153) *Limonia* sp., (Nearctic, MND, fig. 7.85); (154) *Tipula* (*Yamatotipula*) *strepens* Loew, (Nearctic, MND, fig. 7.86); (155) *Gonomyia* sp., (Nearctic, MND, fig. 7.80); and (156) *Epiphragma fascipenne* (Say), (Nearctic, MND, fig. 7.86, as *E. fascipennis*).

Abbreviations: an ppl, anal papilla; hyps plt, hypostomal plate; md, mandible; mx, maxilla.

75. Basal transverse section of  $CuA_1$  located before fork of M (Fig. 84); male hypopygium with outer gonostylus divided, one lobe with conspicuous fringe of long setae (Fig. 143) . . . . . *Austrolimnophila (Limnophilella)* Alexander
- Basal transverse section of  $CuA_1$  at or beyond fork of M (Fig. 83); male hypopygium with outer gonostylus not divided into two lobes with long setae (rarely with one gonostylus; Fig. 142). . . . . *Austrolimnophila (Austrolimnophila)* Alexander
76. Anteprepronotum with sides of anterior margin produced forward, overlapping head (Fig. 109a); wing usually with long and sinuous radial and medial veins beyond cord (Fig. 85);  $R_3$  and  $R_4$  usually parallel to one another; cell  $m_1$  present . . . . . *Pseudolimnophila* Alexander
- Anteprepronotum not produced along anterior margin (Figs. 109b, c); distal wing veins beyond cord straighter (Figs. 86, 87); cell  $r_3$  widened at margin; cell  $m_1$  present or absent. . . . . 77
77. Wing with basal margins of cells  $r_4$ ,  $r_5$ , and dm in transverse alignment (Fig. 86); wing usually with petiole of cell  $r_3$  (vein  $R_{2+3+4}$ ) as long as or longer than vein  $R_3$ ; cell  $r_3$  often small, triangular in outline; cell  $m_1$  absent; crossvein  $R_2$  at or close to the fork of  $R_{2+3+4}$  . . . . . *Shannonomyia (Shannonomyia)* Alexander
- Wing with inner ends of cells  $r_4$ ,  $r_5$ , and dm not in transverse alignment (Fig. 87), if so, then cell  $m_1$  present; cell  $r_3$  longer and usually much longer than its petiole; crossvein  $R_2$  usually beyond fork of  $R_{2+3+4}$  . . . . . *Limnophila (Limnophila)* Macquart

## Synopsis of the fauna

At present 629 species of crane flies are recorded from Central America, with only 123 species known from Costa Rica. This modest number, which is indicative of the poor sampling available for study, accounts for probably one-third to one-fourth of the true crane fly fauna. Crane flies are found in all terrestrial and some marine habitats, with the greatest species richness in the vicinity of aquatic habitats.

**Atarba Osten Sacken.** The typical subgenus *Atarba* (*Atarba*) is primarily a New World group, with 15 species in Central America, but only one species, *A. bifilosa* Alexander, recorded from Costa Rica. Two regional species can be identified in the key in Alexander (1926), and the genus was reviewed by Alexander (1948a). The larvae and pupae of the Nearctic *A. picticornis* Osten Sacken have been described (Rogers, 1927a); they were collected just below the surface of soft, wet logs in a temporary streambed. Oosterbroek & Theowald (1991) discussed probable phylogenetic relationships of *Atarba* as one of the more basal lineages of Limoniini (= Limoniinae sensu Oosterbroek & Theowald).

*Atarba (Ischnothrix)* Bigot contains a single Central American species, *A. (I.) patens* Alexander from Panama, although a number of other species are distributed from Colombia through Chile and Argentina, as well as Australia and New Zealand. The immature stages and habitat are undescribed, but are assumed to be similar to those known for *Atarba (Atarba)*.

**Atypophthalmus Brunetti.** This is an Old World genus with a single tropical cosmopolitan species, *A. umbratus* de Meijere, in Central America (Veracruz, Mexico). In the older

literature this genus is considered a subgenus of *Dicranomyia* or *Limonia* sensu lato. This species has been dispersed in the Neotropical Region presumably through commerce (Alexander, 1967b) but possibly through other mechanisms as well (Byers, 1966). The larvae are aquatic, living in silken tubes among moss or algae growing on wood or stones (Alexander, 1967b).

**Austrolimnophila Alexander.** *Austrolimnophila (Austrolimnophila)* is species rich and distributed worldwide, with only two species found in Central America. The genus appears closely related to *Epiphragma*; generic characters are summarized in Alexander (1948b). There are no keys available for identifying the species in this region. Adults rest with wings outstretched, as in *Epiphragma* (Alexander, 1943a). Of the few species reared (none Neotropical), the immatures have been recorded from decaying wood (Alexander, 1948b); adults of one Nearctic species are found on wet faces of vertical cliffs (Alexander, 1929a).

*Austrolimnophila (Limnophilella)* Alexander is a small Neotropical group, with two Central American species, one of which, *A. subvictor* (Alexander), is found in Costa Rica. There are no keys to identify the species. The group may represent a highly apomorphic lineage within the larger subgenus *Austrolimnophila*. There is nothing known of the biology of the species, although larvae presumably develop in rotting wood like others in the genus.

**Brachypremna Osten Sacken.** This is a mostly New World group, with four species recorded for Central America, two of which are from Costa Rica. Alexander (1912a, 1969a) reviewed the genus, and the earlier paper offered a

key that included all regional species. The adults have extremely long, slender legs, often with whitened tarsi, making it difficult to follow them in flight in shaded forests. *Brachyremna dispellens* (Walker), which occurs in Central America, is known as “the king of the dancing tipulids”, as it hovers up and down in densely shaded areas with a distinctive vertical dance over a height of 3–4 ft (0.9–1.2 m) (Johnson, 1909). The immature stages, habitat, and behavior of *B. dispellens* (Walker) and pupal description for a Peruvian species are given in Gelhaus & Young (1991); the larval habitat is damp humus soil along streams, seepage areas, and low grassy areas.

***Cheilotrichia* Rossi.** The subgenus *Cheilotrichia* (*Empeda*) Osten Sacken is a species-rich group in Central America with 17 species, 11 mostly from tropical Mexico, but only two recorded in Costa Rica. The species include some of the smallest crane flies (e.g., *C. stygia* Alexander with wing length of 2.5 mm). There are no keys for identifying Central

American species. Larvae are unknown for regional species, but two European species are known to inhabit rich organic earth or mud, in woods or edges of streams or ponds (Alexander, 1931; Brindle, 1967)

***Cryptolabis* Osten Sacken.** *Cryptolabis* (*Cryptolabis*) is primarily a Neotropical group, with 19 Central American species, five of which are found in Costa Rica. There are no keys available for identifying the species. It is difficult to discern the sexes without recourse to high magnification (Alexander, 1943b, 1947a). Adults emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993), and an undetermined troglobitic species was collected from a cave near a subterranean stream in Trinidad (Darlington & Gelhaus, 1994). The immature stages are described for one species, the Nearctic *C. magnistyla* (Hynes, 1963). Larvae and pupae are found in the sandy sediments of streams and rivers (Byers, 1996).

***Dicranomyia* Stephens.** *Dicranomyia* is a large genus of over 1000 species worldwide. In older literature, it was considered a subgenus of *Limonia*.

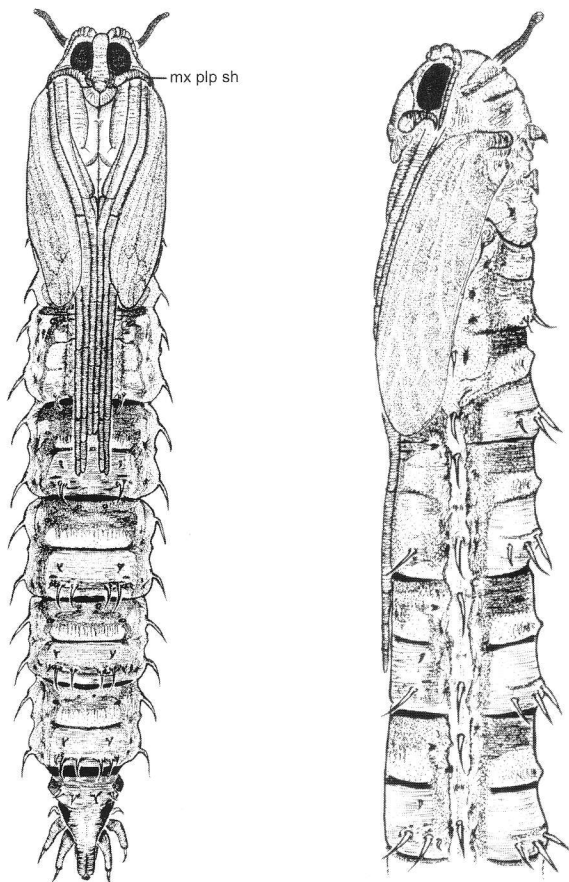
*Dicranomyia* (*Caenoglochina*) Alexander is a group restricted to subtropical and tropical America, with seven Central American species, and a single species, *D. paniculata* Byers, in Costa Rica (Isla del Coco). Species were formerly placed in *Limonia* (as the *L. apicata* (Alexander) species group). The larvae of one species, *D. subapicata* Alexander, have been found in damp wood powder under the bark of pines (*Pinus*) (Alexander, 1950). One species was one of the commonest crane flies emerging from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994).

*Dicranomyia* (*Caenolimonia*) Alexander is a Neotropical subgenus, with five species recorded from Central America and none from Costa Rica (all five are known from Panama). Species were formerly placed in *Limonia* (*L. neorepanda* species group) or *Neolimnobia*. Nothing is known of the biology of any of the species.

*Dicranomyia* (*Dicranomyia*) includes 28 Central American species, with only three recorded from Costa Rica. Larvae of *Dicranomyia* in other regions have been reared from a wide variety of aquatic and semiaquatic habitats, including hygroscopic areas, edges of streams and marshes, and even intertidal zones. Two species of *Dicranomyia* emerged from a small mountain stream in Puerto Rico, with the endemic species one of the commonest crane flies (Gelhaus et al., 1993; Livingston & Gelhaus, 1994).

*Dicranomyia* (*Neoglochina*) Alexander is an endemic Neotropical group, formerly treated as the *L. insularis* species group in *Limonia*. Six species are known from Central America, although none are yet recorded from Costa Rica. Nothing is known of the biology for any of the species.

*Dicranomyia* (*Neolimnobia*) Alexander is an endemic Neotropical group with only one species, *D. diva* (Schiner), recorded from Central America (Mexico). An identification key for many species of *Neolimnobia*, including *D. diva*, is



157 *Brachyremna*

158 *Brachyremna*

**Figs. 8.157–158.** Pupa: ventral view (157) and lateral view, terminal abdominal segments omitted, (158) of pupa of *Brachyremna dispellens* (Walker), (Nearctic, Gelhaus & Young, 1991, figs. 12, 13).

Abbreviation: mx plp sh, maxillary palpal sheath.



found in Alexander (1954). Nothing is known of the biology of any species of *Neolimnobia*, although *D. diva* adults emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994).

*Dicranomyia (Neolimonia)* Alexander includes five species in Central America, with none recorded as of yet from Costa Rica. Species were formerly placed in the *L. eiseni* species group in the genus *Limonia*, but some current authors treat this group as a separate genus. There are no comprehensive identification keys, but several species can be keyed in Alexander (1912b, as *Furcomyia*; 1954, as *Limonia*). The larvae of two north temperate species have been reared from damp rotting wood (Alexander, 1920a, for *D. dumetorum* (Meigen)), and adults of one species emerged from a small mountain stream in Puerto Rico (Livingston & Gelhaus, 1994).

*Dicranomyia (Peripheroptera)* Schiner is an endemic Neotropical group, with three species in Central America, and one, *D. nitens* Schiner, recorded from Costa Rica. Alexander (1913a) provided an identification key to species, including *D. nitens*. The biology of the subgenus is unknown.

***Dicranoptycha* Osten Sacken.** This genus includes only three species in Central America, with one in Costa Rica; the genus is more diverse in North America, Asia, and Madagascar. There are no keys to separate the three species. An excellent treatment of morphology, biology, and phylogeny of *Dicranoptycha* can be found in the review of Young (1987). Adults usually stand upright on upper leaf surfaces of understory plants. The larvae of three North American species have been reared from forest soil directly under leaf litter (Young, 1987).

***Elephantomyia* Osten Sacken.** The genus *Elephantomyia* has 13 species in Central America, although none are recorded as of yet from Costa Rica. There are no keys to species for this area; reviews of the genus in the Neotropical Region can be found in Alexander (1948a) and Ribreiro & Amorim (2002). The phylogenetic position of the genus is problematic, and two distinct larval types are described (Oosterbroek & Theowald, 1991). Larvae of four species have been found in damp to saturated, rotting branches, logs, or palm fronds (Alexander, 1920a; Hynes, 1997). Larvae of two African species have been reared from moss cushions along streams and waterfalls (Wood, 1952; but see Hynes, 1997). The long proboscis of the adult is undoubtedly used for nectar feeding, but its function is not well documented (Alexander, 1924). Adults of one species appear to be associated with spider webs (Alexander, 1930).

***Ellipteroides* Becker.** *Ellipteroides (Progonomyia)* Alexander includes six Central American species, with none yet recorded from Costa Rica. A key is available for identifying species in the *E. (P.) quinqueplagiata* species group, including two Central American species (Alexander, 1941). Adults of an undetermined species emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston &

Gelhaus, 1994). The immature stages are known for a single South African species, *E. (P.) nigrobimbo* Alexander (Wood, 1952), found developing in saturated organic mud on the margins of a small forest stream. Adults of *E. nigrobimbo* crawled over exposed rocks in the stream and were reluctant to fly.

***Epiphragma* Osten Sacken.** *Epiphragma (Epiphragma)* is a diverse group worldwide, with the Neotropical Region supporting about half the species. Twelve species are known from Central America, two of these are from Costa Rica. Adults are some of the most beautiful crane flies, with strongly patterned wings and legs. Available keys to New World adults identify few Central American species (Alexander, 1913a, 1916a, 1943a, 1953a). Adults of Nearctic species rest, with wings outstretched, on upper surfaces of understory vegetation; at least one species, *E. fasciapenne* (Say), forms mating swarms (Alexander, 1919a). The immatures, where known, are found in decaying wood, often in or adjacent to ponds or streams (Alexander, 1920a). Bruch (1939) reared and described the egg, larval, and pupal stages of *E. (E.) imitans* Alexander from saturated, soft poplar wood along the edge of a river and river delta in Argentina. The larvae of the Nearctic *E. solatrix* (Osten Sacken), known also from Mexico, have been reared from damp to sodden logs or limbs in streams or forest floor (Rogers, 1933b; Young, 1978).

***Erioptera* Meigen.** The subgenus *Erioptera (Erioptera)* has four Central American species, with none recorded from Costa Rica. There are no keys available for identifying the species. The similarities in the male genitalia and wing and leg patterning between species of *Mesocyphona* and the Neotropical species of subgenus *Erioptera* indicate that these species might be consubgeneric, as noted by Alexander (1947a). Bruch (1939) described the eggs, larval, and pupal stages of *Erioptera (E.) cladophoroides* Alexander collected along a drainage ditch and river bank in Argentina. Two immature larval and pupal types are known for Holarctic species (Alexander, 1920a), including a pupal form with spinous thoracic horns for piercing roots for oxygen in anoxic mud (Houlihan, 1969).

*Erioptera (Mesocyphona)* Osten Sacken is primarily a Neotropical group, with 25 Central American species, only three of which are recorded from Costa Rica. Adults are small, attractive flies with patterned wings and banded legs, and are one of the commonest groups encountered. A key for identifying adults of seven of the Central American species is found in Alexander (1913a). Some or all of the Neotropical species of *Erioptera (Erioptera)* may be better placed in *Mesocyphona* (Alexander, 1947a). The pupa of only a single species, *E. (M.) knabi* Alexander, has been described, from muddy sand along a creek in Kansas, USA (Alexander, 1920a), although other species are known to develop in similar muddy situations along streams or other water bodies. Adults of two species of *Erioptera (Mesocyphona)* emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). Bruch (1939) ob-

served large accumulations of adults of a species of *Mesocyphona* along a drainage ditch and river bank in Argentina. A troglophilic species, *Erioptera (Mesocyphona) troglodyta* Edwards, has been recorded from a cave in Trinidad (Darlington & Gelhaus, 1994).

***Eriopterodes* Alexander.** This Neotropical genus includes only two species, one of which, *E. latipleura* (Alexander), occurs in Mexico. These species may represent a specialized clade of *Mesocyphona*. The biology of the genus is unknown, and immature stages are not described.

***Eugnophomyia* Alexander.** The genus *Eugnophomyia* includes four species in Central America (a fifth, the type species *E. luctuosa* Osten Sacken, is a doubtful record), with two species in Costa Rica. The genus is distributed in the New World and eastern and southern Africa. There are no keys for identifying the regional species. Species lacking macrotrichia on the wing membrane may be confused with *Gnophomyia* (e.g., *G. rubicundula* Alexander), and the male genitalia indicate that the monotypic Andean genus *Aymaramyia* Alexander may be an autapomorphic *Eugnophomyia* (Alexander, 1947b). The adults of many Neotropical species have black and orange patterned bodies and resemble pleciine bibionid flies in collections. The immature stages have been described only for *E. luctuosa*; they were collected in the wet, waxy rotten wood caused by bacterial decay in the heartwood of standing, apparently healthy hardwood trees (Rogers, 1928). Adults were found on the lower trunks of trees, and females were observed ovipositing in the rotting interior wood or in fissures of the outer bark.

***Geranomyia* Haliday.** Thirty-eight species of *Geranomyia* are recorded for Central America, with eight from Costa Rica. They form one of the commonest groups of crane flies in the tropics. Identification keys that include Central American species can be found in Alexander (1932 for Puerto Rico, 1953b for Ecuador, 1970a for Dominica). Adults, when resting, quickly bob up and down (like many other Limoniinae, such as *Dicranomyia*) and use the lengthened mouthparts for probing tubular flowers for nectar, most commonly those of Lauraceae, Umbelliferae, and Compositae (Alexander, 1953b; Rogers, 1926a). Larvae are best known from aquatic habitats, particularly hygropetric situations, where they form silken, gelatinous tubes among the algae they feed on; others live in saturated mats of mosses and liverworts (Alexander, 1950). A Nearctic species was found in a hot spring, although not in the hottest region (Bartow, 1994). Several species were the commonest crane flies emerging from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). A few species are found in the marine intertidal zone. The immature stages of one species, *G. recondita* Alexander, have been found in globules of clear gelatinous material suspended from the end or underside of leaves (Edwards, 1934; Grimaldi & Young, 1992).

***Gnophomyia* Osten Sacken.** This genus is diverse, with 17 species in Central America, eight of which are from Costa Rica. The Andean monotypic genus *Quechuamyia* Alexander appears closely related based on male genitalia and may just contain autapomorphic species of *Gnophomyia* (Alexander, 1947a). Edwards (1938) reviewed the genus, and Alexander (1947b) provided a brief review of the tropical American species. Keys available for indentifying species are out of date. For example, Alexander (1913a) keys six New World species, only two Central American, and the key includes species now transferred to four other genera. An undetermined troglophilic species was found in a cave in Trinidad (Darlington & Gelhaus, 1994). The immature stages of several species have been described, none Neotropical. Larvae and pupae of the Nearctic *G. tristissima* Osten Sacken are found in the rotting, moist inner layer of bark from dead hardwood trees and stumps (Alexander, 1920a), and a similar habitat was described for the Palearctic *G. lugubris* Zetterstedt (Brindle, 1967). Rogers (1927c) described from Sumatra the larvae and pupae of *G. jacobsoni* Alexander collected from "slimy putrefaction" in the flower bracts of *Hornstedtia* sp. (Zingiberaceae).

***Gonomyia* Meigen.** *Gonomyia (Gonomyia)* is a species-rich Neotropical group with 35 Central American species, yet only a single species has been recorded from Costa Rica. This group is particularly rich in Mexico, which boasts 20 species found mostly in tropical areas (Contreras-Ramos & Gelhaus, 2002). The taxonomy of adults is difficult, with many species having no illustrations of the critically important male genitalia. The only available key for identifying adults is of limited use, as it employs color features (Alexander, 1913a). Almost nothing is known of the biology of the species of this subgenus. Adults are found in the vicinity of wet areas, such as streams and marshes (Alexander, 1943a) and emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). Nearctic *G. kansensis* (Alexander) was reared from the wet sand near rivers, and *G. subcinerea* Osten Sacken was reared from muddy edges of ponds and small streams (Alexander, 1920a).

Subgenus *Gonomyia (Neolipophleps)* Alexander is a New World group with three species in Central America, two of which are known from Costa Rica. The subgenus was described by Alexander (1947b) for the *Gonomyia cinerea* Doane species group. No comprehensive keys are available for identifying species, but Alexander (1916b, c) keys two species. The identification of the widespread *G. helophila* Alexander has been confused as a result of mistaken illustrations (Alexander, 1937). The immature stages of only the Nearctic *G. alexanderi* (Johnson) are illustrated (Alexander, 1920a); larvae were collected from coarse wet sand near pools along a river. Alexander (1920a) described the resting position of adults.

*Gonomyia (Paralipophleps)* Alexander is almost entirely Neotropical, with nine species in Central America and three

known from Costa Rica. The subgenus was described by Alexander (1947b) for the *Gonomyia pleuralis* species group. There are no keys for Central America, but five species, including *G. pleuralis* (Williston), are keyed in Alexander (1970a). Rogers (1926b) described the immature stages, habitat, larval food, and adult dispersal of *G. pleuralis*; the immature stages were abundant in black mud at the edges of marshes, where they fed on filamentous algae.

*Gonomyia (Leiponeura)* Skuse is a species-rich group in Central America with 25 species, with eight known from Costa Rica. The subgenus is known as *Lipophleps* Bergroth in much of the older literature (see Alexander, 1964a: 381). Central American species are keyed in part (as the *Gonomyia manca* species group) in Alexander (1913a, 1916c), and five Caribbean species are keyed in Alexander (1970a). Surprisingly, the immature stages of few species are known, though none Neotropical. Nearctic *G. sulphurella* Osten Sacken larvae inhabit sandy mud along streams and ponds (Alexander, 1920a), and African *G. sulphurelloides* Alexander larvae were taken from saturated gravelly sand near the water margin (Wood, 1952).

***Helius* Lepelletier & Serville.** This genus is diverse in the Neotropical Region, with 13 Central American species, four of which are found in Costa Rica (including Isla del Coco). There are no keys for identifying Central America species. The troglobyte *H. (H.) darlingtonae* Welch & Gelhaus was found in the Aripo cave system in Trinidad (Darlington & Gelhaus, 1994); it has the fewest antennal segments of any Tipuloidea (Welch & Gelhaus, 1994). Adults of an undetermined species in Peru were commonly associated with the underside of spider webs extending over small streams, where they would hang from the middle pair of legs (J.K. Gelhaus, personal observation). Zalom (1979) discusses the mating aggregation of the Nearctic species *H. flavipes* (Macquart). Larvae of several temperate species are known from open marshy areas, in mud rich with organic material, or in decaying plant material (Alexander, 1920a). Larvae were collected from the water inside living bamboo internodes (*Guadua weberbaueri* Pilger) in Peru; the openings to some internodes were no more than 1 mm wide (Louton et al., 1996). Adults of *H. albitarsis* (Osten Sacken) emerged from a small mountain stream in Puerto Rico (Livingston & Gelhaus, 1994) and were reared from the wet fibrous layer under the bark of a dead tree in Costa Rica (Hancock et al., 2000).

***Hexatoma* Latreille.** The subgenus *Hexatoma (Eriocera)* Macquart is species rich in Central America, with 31 species recorded, six of these from Costa Rica. The species of the Neotropical Region were most recently reviewed by Alexander (1948a). Adults are often medium to large species, commonly with brightly contrasted body colors and with wings often banded. Unlike adult descriptions in many crane fly groups, almost no attention has been paid to the male genitalia in the numerous papers by Alexander, with species distinctions based on body coloration and wing venation dif-

ferences alone. Edwards (1921), however, gave a detailed discussion of the male genitalia in this group. Alexander (1914a) provided the only keys for identifying regional species, including 15 Central American species, in two separate keys for *Eriocera* and *Penthoptera* Schiner. The larvae of several Nearctic species have been described (Alexander, 1920a). They were collected in sandy or gravelly bottoms of streams, and migrated to pupate in sediments along the stream edge. A single species formerly placed in *Penthoptera* was reared from organic mud in shaded situations (Alexander, 1920a). Where known, larvae are predaceous. The larvae of all Neotropical species remain undescribed, but adults of two species emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). Adults of several Nearctic species form mating swarms, sometimes 5–6 m high (Alexander 1967a), along streams or rivers, in open areas (Alexander, 1919a), or under trees.

***Ischnotoma* Skuse.** The subgenus *Ischnotoma (Neotipula)* Alexander comprises only four Neotropical species, two of which are Central American; none have been recorded from Costa Rica. The placement of this group within *Ischnotoma* is not definitive, the genus otherwise being distributed in southern South America, Australia, and Tasmania (Vane-Wright, 1967). There are no keys for identifying the species. The adults are some of the largest Central American species, with body length of around 30 mm and strongly patterned wings. The immature stages for the subgenus are unknown. Immature stages of *I. (Icriomastix) jujuyensis* (Alexander) occurred in Argentina among wet mats of plants growing along stream margins; Bruch (1939) described egg, larval, and pupal stages. A Chilean species in the typical subgenus of *Ischnotoma*, *I. fagorum* (Alexander), was reared from a pupa found “in wet moss in a small mountain stream” (Alexander, 1929b). An Australian species, *I. eburnea* (Walker) (as *I. serricornis* (Macquart)), was reared from “thick wet moss” in a creek, and larvae were observed eating “the green shoots of the moss” (Alexander, 1944a).

***Lecteria* Osten Sacken.** *Lecteria (Lecteria)* comprises a single species in Central America, *L. acanthosoma* Alexander, which was recorded from Panama. The Neotropical species were reviewed and keyed by Alexander (1969b). Adults are moderately sized, with femora and tibiae having conspicuous black bands and strong and erect setae. Since the original description of the group (Osten Sacken, 1887), its relationships within the Limoniinae have been debated, with contention centering on placement in the tribes Chioneini or Limnophilini. Alexander (1948b) considered the distribution of the subgenus in the Neotropical Region and Africa to be strong evidence of Wegener’s hypothesis of continental drift. The immature stages are undescribed.

***Leptotarsus* Guérin-Méneville.** This doubtfully monophyletic genus comprises 11 New World subgenera of sometimes questionable validity. The genus is reviewed by Alexander (1969a) and Dobrotworsky (1968). Subgenus *Pe-*



*hlkea* Enderlein includes several species with large, greenish-tinged adults; none are recorded in Central America, but two species occur in neighboring Colombia, and the genus will likely be found in Central America. The two Colombian species are keyed in Alexander (1914b, as *Tanypremna*). Gelhaus and Young (1995) described the pupae of several *Leptotarsus*, including *L. (P.) regina* Alexander. Pupae were collected in fast, moderate-sized forested streams, and the larvae are presumably aquatic. Pupal characters do not support monophyly of *Leptotarsus*, but indicate a close association between subgenera *Pehlkea* Enderlein and *Longurio* Loew (based on a North American species; Gelhaus and Young, 1995).

The subgenus *Tanypremna* Osten Sacken includes three species in Central America, with two occurring in Costa Rica. Adults are usually large, generally over 25 mm long, with much of this length made up by the abdomen. The legs are also extremely long and slender. The subgenus was reviewed by Alexander (1914b), and the key therein will identify four species, one of which, *L. opilio* (Osten Sacken), is from Central America. Young (2001) provided a discussion of the biogeography of Antillean *Tanypremna*. The immature stages of the subgenus are unknown, but immatures of *Leptotarsus* sensu lato range from fully terrestrial to fully aquatic (Alexander 1969a). The larvae of more closely related groups (such as *Pehlkea* and North American *Longurio*) are found in aquatic habitats.

***Limnophila* Macquart.** *Limnophila* (*Limnophila*) comprises four species in Central America, with two from Costa Rica. There are no keys available for identifying the regional species. It is unclear whether these species are all congeneric. Alexander (1948a) suggests that some species may be better placed in *Shannonomyia*, but states that members of the *L. undulata* group, including at least two regional species, are the Neotropical species most similar to the type species, *L. pictipennis* (Meigen). Larvae are described for Palearctic species only. They are predators in wet soil, sand, or leaves along bog or stream margins (Alexander, 1920a; Brindle, 1967).

***Lipsothrix* Loew.** A single species, *L. neotropica* Alexander, occurs in Central America (Panama). Immature stages are found in sodden wood in small streams (Alexander, 1967a). Hynes (1965) published a key to larvae and pupae of five Nearctic species. Rogers & Byers (1956) and Hinton (1955) also described immatures and discussed biology.

***Megistocera* Wiedemann.** This genus includes a single New World species, *M. longipennis* (Macquart), which occurs in the southeastern United States, Caribbean islands, and parts of South America. Although not yet found in Central America, it should be looked for in coastal lowland areas. Alexander (1914b, 1969a) reviewed the species. Rogers (1949) provided a detailed biology of the species in Florida and described the larval and pupal stages. Immatures occur in the neuston (water surface) of vegetated ponds and inhabit floating hollow pieces of stem. The larva feeds on filamentous algae and leaves of floating macrophytes. Adults

are gregarious; groups of one to several dozen can be found resting, with their legs overlapping, on upper surfaces of low vegetation. When disturbed, adults arise all at once, each flying an elliptical path until resettling.

***Molophilus* Curtis.** This is one of the most diverse crane fly groups worldwide. In Central America only the subgenus *Molophilus* occurs with 29 species recorded; only five of these are found in Costa Rica, but 18 are from mostly tropical areas of Mexico. There are no keys for identifying the Central American species. Alexander (1927) discusses the species groups based on male genitalic differences, with most tropical American species occurring in the *M. plagiatus* group, and a few species in the *M. gracilis* group (Alexander, 1947a). Most adults are dark flies. Males of some species have lengthened nodulose antennae, and in the subgenera *Eumolophilus* Alexander and *Trichomolophilus* Alexander (Amazonian region), males have long, dark fanlike clusters of setae on the hind tibia, which resemble those of *Sabethes* mosquitoes (Alexander, 1921; Edwards, 1927). Adults are found in shaded woods, and often males will form small aerial swarms (Alexander, 1919a). Larvae of few species are known, and of these, none are Neotropical, but the immature stages of the Nearctic species *M. hirtipennis* (Osten Sacken) are found in wet organic mud in woods near streams or springs (Alexander, 1920a).

***Neognophomyia* Alexander.** The genus *Neognophomyia* is endemic to tropical America, with four species known in Central America, two of which are found in Costa Rica. There are no keys for identifying the species. Alexander (1947b) provided a brief review of the genus, but there is nothing known of the biology of any of the species, and the immature stages are not described.

***Nephrotoma* Meigen.** *Nephrotoma* includes over 500 species worldwide, with 12 species known from Central America, four of which are from Costa Rica. Oosterbroek (1984) provided a key for identifying two species that occur in Mexico. The discussion of generic and species phylogenetics and morphology (for Holarctic species) in Tangelder (1985) is recommended. Numerous species, mostly European, have been reared; all were taken from damp soil under leaf litter or mosses, often in forests (Alexander, 1920a; Brindle, 1960). Several species are known to damage crops, including one, *N. ferruginea* (Fabricius), which occurs in Central America (Alexander, 1920a; Rao & Gelhaus, 2003).

***Orimarga* Osten Sacken.** Subgenus *Diotrepha* Osten Sacken has five species in Central America, only one of which, *O. flavescens* Byers, has been recorded from Costa Rica (Isla del Coco). No immatures of Neotropical species are described but an undetermined species was reared from a well-rotted branch on wet gravel near a stream in Peru (J.K. Gelhaus, personal observation). Larvae and pupae of the Nearctic *O. mirabilis* (Osten Sacken) have been taken from well-rotted, saturated wood found along small streams, marshes, and wet

ravines. The diaphanous larvae live in shallow, lined burrows, feeding on wood and associated algae (Rogers, 1927b).

*Orimarga* (*Orimarga*) contains eight species in Central America, only one of which, *O. nigroapicalis* Alexander, is recorded from Costa Rica. A key to species, including two Central American species, is found in Alexander (1916a). No immatures of Neotropical species are described. Larvae and pupae of the European *O. attenuata* (Walker) (as *O. hygropetrica* Vaillant) are described as being hygropetric, occurring on wet calcareous rocks (Vaillant, 1950, as quoted in Alexander, 1967b).

**Ozodicera Macquart.** *Ozodicera* is restricted to the New World tropics with over 50 known species. The typical subgenus has a single Central American species, *O. (O.) septemtrionis* Alexander from Mexico. There are no keys available for identifying the species; Alexander (1969a) reviewed the genus. Although the two subgenera of *Ozodicera* are distinguished solely on branching of the antenna in the adult, Alexander (1969a) notes that not all species can be easily assigned to a group. There are no observations on behavior, and the immature stages are undescribed.

*Ozodicera* (*Dihexaclonus*) Enderlein includes a single Central American species, *O. panamensis* Alexander from Panama. The immature stages remain undescribed.

**Paradelphomyia Alexander.** The subgenus *Paradelphomyia* (*Oxyrhiza*) de Meijere includes six Central American species, two of which occur in Costa Rica. The group was reviewed in Alexander (1948b), but no keys are available for identifying the regional species. Adults are small, and the weak tibial spurs and indistinct  $R_2$  vein can cause them to be confused with other groups, including *Gonomyia*. Although Alexander (1920a) considered the genus related to other Pediciini based on larval characters, Oosterbroek & Theowald (1991) placed it as a sister group to the rest of the Limnophilini, albeit without cladistic support. Larvae of three Nearctic species were reared from organic mud (Alexander, 1920a).

**Polymera Wiedemann.** *Polymera* (*Polymera*) is a diverse, almost entirely New World group with 12 Central American species, only one of which is recorded from Costa Rica. Alexander (1913a) provided the only key, identifying two Central American species, and the genus was reviewed by Alexander (1948b). Rogers described the immature stages of two species of *Polymera* (*P.*) from the southeastern United States (Rogers, 1933a); larvae were found in fine, black organic mud at margins of small pools and shores of swamp bordered lakes. Larvae are predaceous, feeding on chironomid and crane fly larvae and lumbricid worms. Adults of these USA species spend the day among lower vegetation near where the larvae occur and will fly readily toward lights far removed from any larval habitat. Adults of *Polymera* (*P.*) emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). Alexan-

der (1920a) reported that adults of *P. geniculata* Alexander were found in crabholes in Puerto Rico.

The subgenus *Polymera* (*Polymerodes*) Alexander is a New World group, with only a single species, *P. conjuncta* Alexander, in Central America (Panama). The subgenus is of doubtful validity; its only difference with the typical subgenus is the lack of tibial spurs and cell  $m_1$ . Alexander (1920b) provided a key for identifying three species, including the Central American species. Nothing is known of the biology of any included species.

**Pselliophora Osten Sacken.** *Pselliophora* includes just three Neotropical species, two occurring in Central America and none recorded from Costa Rica. The genus is diverse and otherwise distributed in the eastern Palearctic and Oriental Regions. Alexander (1969a) reviewed the genus. Two of the three species can be identified using the key in Alexander (1944b). Larvae of *Pselliophora* are undescribed, but those of related genera (e.g., *Ctenophora* Meigen) feed in dead, often solid hardwood logs or trunks. Alexander (1969a) noted for Oriental species of *Pselliophora* a record of oviposition into a tree hollow, and an adult reared from a larva damaging orchid roots.

**Pseudolimnophila Alexander.** This genus comprises only a few Neotropical species, with only one doubtfully recorded for Central America, *P. luteipennis* (Osten Sacken), a widespread Nearctic species. A useful summary of the genus is found in Alexander (1948b); the species can be keyed in Alexander (1943a). Adults of *P. luteipennis* can be abundant along swamp and pond edges (Rogers, 1933b; Young, 1978), where the larvae develop on detritus. Alexander (1920a) described the larval and pupal stages.

**Rhabdomastix Skuse.** The subgenus *Rhabdomastix* (*Rhabdomastix*) has five Central American species, one of these is Costa Rican. There are no keys to identify the regional species. Alexander (1947a) notes the overall similarity between the species of this group and those of *Atarba* (*Ischnothrix*), except for the presence of tibial spurs in *Atarba*. Hynes (1969) described the immature stages of eight Nearctic species, including the regional *R. californiensis* Alexander. Larvae develop in sandy sediments in clear streams and along stream margins (Byers, 1996).

**Rhipidia Meigen.** Thirty species of *Rhipidia* (*Rhipidia*) occur in Central America; nine of these are recorded from Costa Rica. Alexander (1950) provided a discussion of the subgeneric characters. Species keys that include Central American species are found in Alexander (1912c for the general Neotropical Region, 1964b for Jamaica; 1970a for Dominica). Larvae of a few species have been reared from organic soil at edges of streams or ponds, wet forest soil, decaying vegetable matter, fermenting sap, and under the bark of dead trees (Alexander, 1950). Three species emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Liv-

ingston & Gelhaus, 1994). Adults of two species were collected in a cave in Trinidad (Darlington & Gelhaus, 1994).

**Shannonomyia Alexander.** *Shannonomyia* (*Shannonomyia*) is a diverse, mostly Neotropical group, with 17 species in Central America, although none have been recorded from Costa Rica. There are no keys for identifying the regional species. The genus was reviewed by Alexander (1948a). The limits of this genus and Neotropical *Limnophila* are not understood. Adults of two species emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). Adults of the Nearctic *S. lenta* (Osten Sacken) occur on vegetation in open shaded situations, usually near water (Alexander 1943a). The immature stages remain unknown (the statements of Alexander (1948a: 519) are apparently unsupported).

**Sigmatomera Osten Sacken.** Species of *Sigmatomera* are large flies, strikingly colored in orange and black.

Two species of *Sigmatomera* (*Sigmatomera*) occur in Central America, and one of these, *S. seguyi* Alexander, is known from Costa Rica. The Neotropical species are keyed in Alexander (1929c). Oosterbroek & Theowald (1991) suggest that *Sigmatomera* may represent one of the basal lineages of Pediciini, based on fragmentary information available on immature morphology and biology. The immatures of several species are known from aquatic tanks in tree holes, where they live in U-shaped silken tubes and feed on detritus, microinvertebrates, and mosquito larvae (Yanoviak, 2001). Mosquito larva are strongly attracted to the silken tube material, where they become ensnared (Alexander, 1929c). Alexander (1945a) noted a species reared from bromeliads.

Only one species of *Sigmatomera* (*Austrolimnobia*) Alexander, *S. magnifica* (Alexander), occurs in Central America, known only from Mexico. This species is keyed in Alexander (1913a, as a species of *Gnophomyia*). The only species of *Austrolimnobia* reared, *S. rufa* (Hudson) from New Zealand, was found as larvae feeding on the semiliquid plant debris accumulating at the leaf bases of an epiphyte in undisturbed forests (Hudson, 1920). The pupa was found enclosed in a tough silken tube. Alexander (1929b) suggests a Chilean species may develop in bromeliads.

**Styringomyia Loew.** Only one species of *Styringomyia* is known from Central America, including Costa Rica, *S. maya* Ribeiro. The genus is reviewed and all Neotropical species are keyed in Ribeiro (2003). The immature stages are known for one Austropacific species, developing in damp to wet decaying plant material, such as mats of leaf accumulations on soil, rotted interior sections of tree trunks, and rotting palm fronds (Hynes, 1990). Adults rest in a characteristic posture with legs closely appressed to the body (Fig. 112, Hynes, 1990).

**Symplecta Meigen.** A single species of *Symplecta* (*Symplecta*) occurs in Central America, *S. cana* (Walker), and is widespread through North America south to Guatemala (Al-

exander, 1913a, as *Helobia*). The subgenus is most diverse in the Northern Hemisphere, with scattered species also along the Andes (Alexander, 1947a). No keys are available to separate the Neotropical species. The immature stages of several species have been described, including *S. cana* (Alexander, 1920a) and the South American *S. macroptera* (Philippi) (Bruch, 1939). Immature stages inhabit moist earth, usually near water (Alexander, 1947a).

*Symplecta* (*Trimicra*) *pilipes* (Fabricius) from tropical Mexico is the only species of this subgenus recorded for Central America (Alexander, 1913a). The species is cosmopolitan and varies in size, pilosity, coloration, wing development, and venation, which has brought about a bewildering number of synonyms and doubtful subspecies (Alexander, 1962b; see also Andrew, 2000). The subgenus was previously considered to be an *Erioptera* or a full genus, and its current placement in *Symplecta* does not seem well supported. The immature stages are described and illustrated (Bruch, 1939; Valliant, 1953, as *T. hirsutipes*). Larvae develop in mud and wet earth usually at the margin of water, including brackish and marine conditions (Alexander, 1967a).

**Teucholabis Osten Sacken.** Adults of the genus *Teucholabis* are distinctive with highly polished bodies, often colored black and yellow, and the pleura often displays a pruinose or silvery stripe. The pronotum and cervical regions are prolonged and narrowed into a slender necklike region. Males are unique among Tipulidae in possessing depressions (sternal pockets) on abdominal sternites 5 and 6 (Figs. 111a–d). These pockets are bordered with various modified setae, and their function is unknown.

One species of *Teucholabis* (*Euparatropesa*) Alexander is known from Costa Rica, *T. (E.) invenusta* Alexander. Keys to the species are found in those for *T. (Paratropesa)* (Alexander, 1913b, 1933). The immature stages are unknown.

*Teucholabis* (*Paratropesa*) Schiner contains two Central American species, with one described from Costa Rica. The subgenus is being reviewed by E. Amat and J. Gelhaus for Colombia, where numerous new species have been discovered. Keys to species are found in Alexander (1913b, 1933). The immatures are unknown for the subgenus.

*Teucholabis* (*Teucholabis*) is a large subgenus of 50 species in Central America, with 13 of these in Costa Rica. The only specific keys for the Neotropical Region are found in Alexander (1913c, 1914c). Adults of an undetermined species were collected in a bat- and oilbird-inhabited cave in Trinidad (Darlington & Gelhaus, 1994) and emerged from a small mountain stream in Puerto Rico (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). The immature stages of only one (Nearctic) species are described, from under the bark of a log (Alexander, 1920a).

**Tipula Linnaeus.** The genus *Tipula* is the largest in Tipulidae, comprising approximately 2500 species worldwide in over 40 subgenera. The genus is doubtfully monophyletic as presently constituted. Although the Neotropical Region is rich in species, these fall in few subgeneric groups.



*Tipula (Bellardina)* Edwards is a New World group with large, showy adults with strongly patterned wings. There are 10 species in Central America; none have been recorded from Costa Rica, but eight species are found in Mexico. Contreras-Ramos & Gelhaus (2002) discussed the zoogeography of the genus in Mexico. Alexander (1951, 1965) and Edwards (1931) briefly characterized the subgenus. The larval stages of two species are known from the central and western United States (Gelhaus, 1986). Larvae are aquatic and found in or along springs or spring-fed streams in mud or among roots of aquatic plants or mosses.

*Tipula (Eumicrotipula)* Alexander is one of the most prominent of the Neotropical groups. The subgenus is endemic to Central and South America with over 260 species, 19 of which are found in Central America, but only one of these, *T. balloui* Alexander, is found in Costa Rica. There are no keys for identifying the Central American species. Many of these Central American species are found only in Mexico, and most of these belong to the *T. virgulata* species group, which is endemic. Females of some species are subapterous and flightless, particularly species at higher elevations in Mexico and the Andes. Alexander (1946a) discussed the subgenus and divided it into four species groups, all of which have representatives in Central America. Contreras-Ramos & Gelhaus (2002) discussed the biogeography of the *T. virgulata* group. The immature stages remain undescribed.

*Tipula (Microtipula)* Alexander is endemic to the tropical and subtropical New World, with 160 species; 23 species are found in Central America, with six in Costa Rica. There are no keys for identifying any of the species. The group is notable for the diverse range of structures of the male genitalia, making the subgenus hard to characterize. Alexander (1945b) reviewed the subgenus and suggested some species groupings. The subgenus *Nephrotomodes* Alexander, now considered a synonym, was described to include the large grouping of species in the *T. smilodon* group (Alexander, 1946b), with *Microtipula* referring to the *T. amazonica* group (Alexander, 1912d). At least one species, *T. armatipennis* Alexander, possesses costal spurs on the wings, a trait that is rare in the family (seen also in two species of the Oriental genus *Brithura* Edwards) and of unknown function (Alexander, 1912d). There have been no descriptions of adult behavior, and the immature stages are unknown.

**Toxorhina Loew.** *Toxorhina (Ceratocheilus)* Wesche has three species in Central America, one of which, *T. americana* (Alexander), is recorded from Costa Rica. There are no keys for identifying the Neotropical species. Tjeder (1981) presented an excellent discussion of adult morphology. The immature stages are known for a single Austropacific species,

*T. caledonica* Alexander. They were found in slimy, well-rotted branches under leaf litter and in the liquid between fibers in petioles of rotting palm fronds (Hynes, 1997).

*Toxorhina (Toxorhina)* has three species in Central America, with two from Costa Rica. Two regional species can be keyed in Alexander (1913c, 1970a). The immature stages of the typical subgenus are unknown, although immatures of the Nearctic species *T. muliebris* (Osten Sacken) apparently develop in saturated soil of swampy areas, possibly in buried decaying wood (Alexander, 1920a; see also subgenus *Ceratocheilus*). The long adult mouthparts are used to probe a variety of flowering plants for nectar (Alexander & McAtee, 1920; Alexander, 1964a).

**Trentepohlia Bigot.** *Trentepohlia (Paramongoma)* Brunetti includes 10 species from Central America, two of these are found in Costa Rica. Keys for identifying some of the Central American species can be found in Alexander (1913a, 1914c). Larvae and pupae of several Central American species have been found in the water and debris that collect at the base of bromeliads (Picado, 1913; Alexander, 1919a, 1969c), although a species in Puerto Rico was found emerging from a small mountain stream (Gelhaus et al., 1993; Livingston & Gelhaus, 1994). The larvae of other species of *Trentepohlia* have been found in the water inside living bamboo internodes in Peru (Louton et al., 1996) and have been reared from decaying plant material (cited in Alexander, 1920a). Adults of *Trentepohlia (Mongoma) pennipes* (Osten Sacken) (Old World tropical) and others rest in chains on spider webs, often performing up-and-down movements similar to those of the spiders in the web (Edwards, 1928; Alexander, 1920a, 1936, 1972).

**Zelandotipula Alexander.** This is a diverse group in the Neotropical Region, with four species in Central America, with one, *Z. furcifera* (Alexander), occurring in Costa Rica. Although once considered a subgenus of *Holorusia* Loew, Vane-Wright (1967) considered the two groups not closely related. He presented a preliminary phylogenetic and zoogeographic discussion of the group along with a review of the generic characters. All Central American species belong in the *Z. sinuosa* species group (sensu Vane-Wright). There are no keys to the Central American species, although Alexander (1962a) presented a key to species from Bolivia (as *Holorusia*). The immature stages of Neotropical species remain undescribed. Larvae of *Zelandotipula* are common invertebrates in New Zealand streams, and the larval stage has been briefly characterized and illustrated. The large larvae are found in seepages (Winterbourn et al., 2000).

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