INSECTS OF PANAMA AND MESOAMERICA

Selected Studies

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Review of the genera of Mayflies of Panama, with a checklist of Panamanian and Costa Rican species (*Ephemeroptera*)

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INTRODUCTION

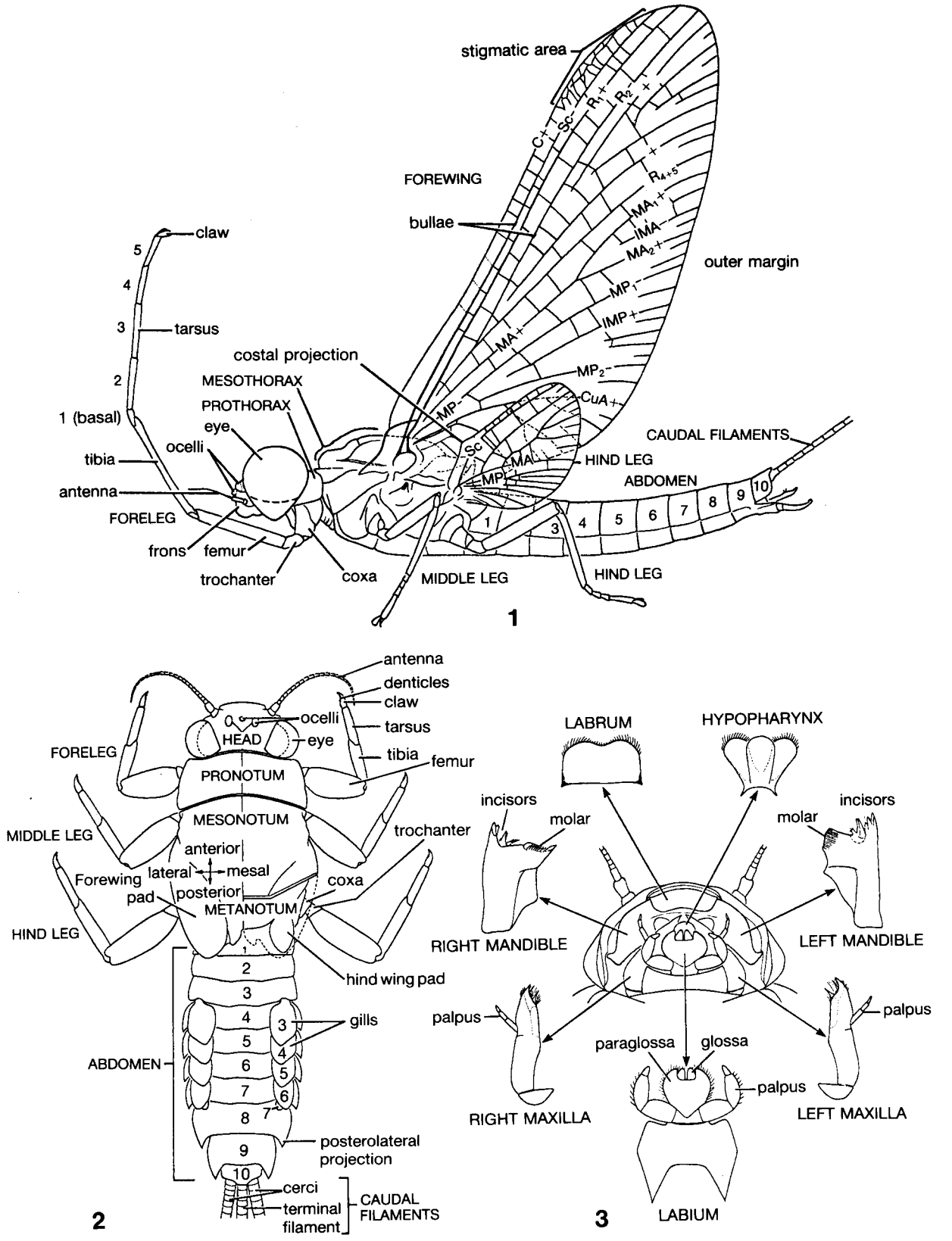
The ancient insect order of Ephemeroptera, or mayflies, is a major component of the invertebrate fauna of freshwater habitats. They are found in lakes, ponds, and streams on all continents except Antarctica, as well as on many islands. The aquatic immature stages, or nymphs, play an important role in freshwater ecosystems by feeding on detritus and algae, and by serving as prey for fish and other aquatic animals. Adults are short-lived and frequently swarm at dusk or dawn. During swarming activities they are preyed upon heavily by dragonflies, birds, and bats. Although the importance of mayflies in temperate stream ecology is well documented, a relative lack of studies on tropical aquatic insects has meant that the importance of mayflies in tropical streams has sometimes been underappreciated. Almost 5 months of field work in Panama (and many more in the United States) have convinced me that Panamanian and North American mayflies have comparable importance in their respective aquatic ecosystems.

Figure 4.1 is a diagram of a mayfly adult, or imago, illustrating morphological terms used in this and other taxonomic papers. The genus depicted is North American but the terms apply generally. A nymph of the same genus is shown in Figs 4.2 and 4.3, also labelled. The life cycle of mayflies contains a flying but sexually immature subadult stage called a subimago which is unique to the Ephemeroptera. After a short time, usually within a day, the subimago moults to the fully mature adult or imago stage. Subimagos closely resemble imagos in appearance but can be distinguished by the cloudy appearance of their wings, the presence of a fringe of hair on the hind margins of the wings and, in males, the undeveloped condition of the genitalia. (In a few groups, the female never moults to the imago but completes her reproductive activities as a subimago.) Because the taxonomy of adult mayflies depends heavily on the structure of the male genitalia, female imagos and subimagos of either sex frequently cannot be identified. Nymphs can be identified most reliably when they are mature (almost ready to moult to the subimago stage) but generic identifications can usually be made on nymphs that are half grown or older.

North American aquatic entomologists are fortunate in having available a choice of keys that cover all nearctic genera, not only of Ephemeroptera but most other aquatic orders. Also available are species revisions in many groups, and state and regional faunas. Most nearctic Ephemeroptera can now be identified to species using the present literature. This is not true for the neotropics. Until recently most of the literature on neotropical Ephemeroptera was widely scattered and consisted mostly of species descriptions. The first comprehensive guide to Central American Ephemeroptera was Edmunds *et al.* (1976), which included keys to the genera then known to occur in Panama. However, during the last decade a great deal of new information has become available on the mayfly fauna of Central America and northern South America. Studies of rainforest insect diversity have disclosed many new mayfly genera and added significant range extensions to many other genera. While relatively few insect studies in the neotropics have focused on aquatic habitats, those few have yielded many undescribed species and genera of mayflies (as well as other aquatic insects). Perhaps the most important development is that the study of mayflies – once nearly the exclusive domain of North American and European entomologists – has attracted Latin American scientists from Argentina to Mexico.

Edmunds (1982) reviewed the taxonomic knowledge of Central American mayflies and provided a complete bibliography of all literature pertaining to the Ephemeroptera fauna of Central America. Publications on or related to the Ephemeroptera of Panama that have appeared since 1982 include McCafferty (1981, 1984), Waltz and McCafferty (1984, 1987*a,b*), Dominguez (1984), Soldan (1984), Flowers (1985, 1987*a,b*), Wolda and Flowers (1985), Roldán (1985, 1988), Savage (1983). The biogeography of Central American Ephemeroptera was reviewed by Edmunds (1982) and more recently by McCafferty *et al.* (in press).

In this paper I present a key to the mayfly genera presently known or strongly suspected to occur in Panama. The latter



Figs 4.1–4.3 *Ephemerella* sp. (from Edmunds *et al.* 1976): **1,** lateral view of adult; **2,** dorsal view of nymph; **3,** ventral view of mouthparts of nymph.

category of genera refers to those collected in Central America outside of Panama *and* in northern South America. The key is based on a review of the literature cited above and on the following sources: several long-term light trap studies by Dr Henk Wolda (Colón, Chiriquí and Bocas del Toro Provinces); three field trips I made to Panama in 1977, 1982, and 1985 (Colón, Coclé, Chiriquí and Bocas del Toro Provinces); mayfly collections at Florida A&M University, the University of Utah, and the US National Museum. Following the key is a brief discussion of each family and its genera in Panama. This includes notes on habitats and biology of the genera as I and others have observed them in Panama. For a more general discussion of mayfly biology and morphology as well as additional information on the families and genera described in this paper, see Edmunds *et al.* (1976). A number of undescribed taxa from Panama are also discussed since many of these are common and are likely to be encountered by aquatic biologists. No undescribed mayflies are included in the key but most will key easily to one of the known genera and additional information will be found under the appropriate family discussion.

In the following key, terminology of Edmunds (1978) and Edmunds *et al.* (1976) is followed. Most terms are illustrated in Figs 4.1–4.3. Genera followed by an asterisk have not been collected in Panama but are likely to be found there.

Key to genera of *Ephemeroptera* of Panama

Mature Nymphs

1	Mandibles with large tusks (Figs 4.4, 4.6)	2
—	Mandibles without tusks	6
2	Foretibia and foretarsi modified for burrowing (Fig. 4.7)	3
—	Foretibia and foretarsi not as above (Figs 4.4, 4.8)	**Euthyplociidae** 5
3	Mandibular tusks curved upward at tip	**Ephemeridae** ***Hexagenia****
—	Mandibular tusks curved downward at tip	**Polymitarcyidae** 4
4	Mandibular tusks with prominent tooth near apex	***Tortopus****
—	Mandibular tusks with prominent tooth near base (Fig. 4.6)	***Campsurus***
5	Foretibia with apical extension one-half the length of foretarsus (Figs 4.4, 4.8)	***Euthyplocia***
—	Foretibia with apical extension at most one-fourth the length of foretarsus	***Campylocia***
6	Abdominal gills operculate on segment 2, covering gills on succeeding segments (Fig. 4.5)	7
—	Abdominal gills on segment 2 not as above	11
7	Operculate gills quadrate, meeting on mid-line of abdomen	**Caenidae** 8
—	Operculate gills oval or triangular, not meeting on mid-line of abdomen	**Tricorythidae** 9
8	Ocelli on small tubercles	***Cercobrachys***
—	Head without ocellar tubercles	***Caenis***
9	Femora with spines on dorsal surface, operculate gill oval (Fig. 4.5)	***Leptohyphes***
—	Femora with long setae on dorsal surface, operculate gills triangular or oval	10

10 Forefemora with spines on basal part of ventral edge; body elongate, base of abdomen only slightly wider than apex ***Haplohyphes***

— Forefemora lacking ventral spines; body robust, base of abdomen distinctly wider than apex; gills triangular or oval ***Tricorythodes***

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11 Forelegs with a double row of long setae on inner surfaces **Oligoneuriidae** 12

— Forelegs not as above 13

---

12 Two caudal filaments present ***Lachlania***

— Three caudal filaments present ***Homoeoneuria****

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13 Body flattened and mandibles not visible from above **Heptageniidae** 14

— Body either not flattened, or if flattened, mandibles visible from above 15

---

14 Two caudal filaments present ***Epeorus***

— Three caudal filaments present ***Stenonema***

---

15 Clypeus separated from frons by a distinct suture (Fig. 4.9) **Baetidae** 16

— Clypeus fused with frons (Figs 4.21–4.23) **Leptophlebiidae** 23

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16 Abdominal gills on segments 1–5 only; terminal filament less than one-fourth length of cerci ***Baetodes***

— Abdominal gills on segments 1–7 or 2–7 17

---

17 Claws spatulate (Fig. 4.14) ***Dactylobaetis***

— Claws pointed, with or without ventral denticles 18

---

18 Tibiae with a fan of fine setae just below articulation with femora (Fig. 4.18) ***Cloeodes***

— Tibiae not as above 19

---

19 Mandibles with inner and outer incisors completely separate (Fig. 4.15) 20

— Mandibles with inner and outer incisors partly or completely fused (Figs. 4.16, 4.17) 21

---

20 Labial palp with second segment expanded medially (Fig. 4.11); gills simple, platelike ***Paracloeodes***

— Labial palp not expanded on second segment; gills on anterior abdominal segments with recurved flaps ***Callibaetis***

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21 Claw with large tooth and small denticles (Fig. 4.12); labrum with broad median emargination and heavy spines on ventral side (Fig. 4.10) ***Guajirolus***

— Claw with small denticles only, seta may be present (Fig. 4.13); labrum not as above 22

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22 Large species, 9–12 mm; hindwing pads always present; osmobranchia (thick membraneous gills) present on inner margin of procoxae (Fig. 4.20) *or* scape of antennae broad and strongly flattened (Fig. 4.19) ***Moribaetis***

— Smaller species; hindwing pads present or absent; osmobranchia lacking and scape of antennae not flattened ***Baetis***

---

23 Labrum greater than 25 per cent wider than clypeus; a row of long setae on basal third of labrum (Fig. 23) **24**

— Labrum less than 25 per cent wider than clypeus or not wider than clypeus; row or setae on labrum, if present, near apical margin (Figs 4.21, 4.22) **25**

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24 Maxilla with short apical tooth (Fig. 4.25); clypeus often with median projection (Fig. 4.23); gills fringed ***Traverella***

— Maxilla with a very long apical tooth (Fig. 24); clypeus without median projection; gills with single apical filament ***Hermanella***

---

25 Gills fringed (Figs 4.26, 4.27) **26**

— Gills not fringed (Figs 4.28, 4.29) **27**

---

26 Gills with fringe around entire outer margin (Fig. 4.26) ***Ulmeritus***

— Gills with fringe on one side only (Fig. 4.27) ***Atopophlebia***

---

27 Gills on abdominal segment 1 different in structure from those on succeeding segments ***Choroterpes****

— Gills on abdominal segment 1 similar to those on succeeding segments **28**

---

28 Labrum distinctly wider than clypeus (Fig. 4.22) ***Thraulodes***

— Labrum at most slightly wider than clypeus (Fig. 4.21) **29**

---

29 Hindwing pads absent ***Hagenulopsis***

— Hindwing pads present **30**

---

30 Abdomen somewhat flattened; gills moderately broad, tracheae with a few lateral branches (Fig. 4.28) ***Terpides***

— Abdomen not as above; gills narrow, tracheae unbranched (Fig. 4.29) ***Farrodes***

Adults

1 Wing venation reduced to seven or fewer longitudinal veins **Oligoneuriidae** 2

— Wing with ten or more longitudinal veins **3**

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2 Three caudal filaments present ***Homoeoneuria****

— Two caudal filaments present ***Lachlania***

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3 Base of veins MP_2 and CuA strongly divergent from base of MP_1 (Fig. 4.30) **4**

— Base of MP_2 and CuA not as above (Figs 4.31–4.33) **8**

---

4 Middle- and hindlegs weakly developed, non-functional **Polymitarcyidae** 5

— Middle- and hindlegs well developed, functional **6**

---

5 Middle- and hindlegs with all segments present ***Tortopus****

— Middle- and hindlegs reduced to femora only ***Campsurus***

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6 Genital forceps of male with one or two segments (Fig. 4.41) **Euthyplociidae** 7

— Genital forceps of male with four segments **Ephemeridae** ***Hexagenia****

7 Genital forceps of male with one segment ***Campylocia***

— Genital forceps of male with two segments (Fig. 4.41) ***Euthyplocia***

8 Hindwings absent 9

— Hindwings present 13

9 Wings with cross-veins reduced and single or double intercalary veins present on outer margin (Fig. 8.31) **Baetidae** 16

— Wings lacking intercalary veins; cross-veins variable 10

10 Cross-veins present near outer margin of wing **Leptophlebiidae** ***Hagenulopsis***

— Cross-veins absent near outer margin of wing 11

11 Vein MA_1 and MA_2 forming a symmetrical fork (Fig. 4.33); genital forceps of male with two or three segments **Tricorythidae** 31

— Vein MA_2 attached to MA_1 by a crossvein (Fig. 4.32); genital forceps of male with one segment **Caenidae** 12

12 Forecoxae widely separated (Fig. 4.40) ***Cercobrachys***

— Forecoxae narrowly separated (Fig. 4.39) ***Caenis***

13 Three well-developed caudal filaments present 14

— Two well-developed caudal filaments present 15

14 Hindwings with very prominent costal projection (Fig. 4.35) **Tricorythidae** 31

— Hindwings not as above **Leptophlebiidae** 24

15 Forewing with cross-veins reduced in number, single or paired intercalary veins along outer margin (Fig. 4.31) **Baetidae** 20

— Numerous cross-veins present in forewing **Heptageniidae** 23

16 Genital forceps of male with patch of prominent setae on inner apical angle of first segment (Fig. 4.43); body white with black markings ***Cloeodes***

— Genitalia of male and body colour not as above 17

17 Metanotum in lateral view with scutellum projecting dorsally or posteriorly (Figs 4.36, 4.37) 18

— Metascutellum not or scarcely projecting above metanotum (Fig. 4.38) ***Baetodes***

18 Genital forceps with prominent mesal notch on second segment (Fig. 4.42) ***Guajirolus***

— Genital forceps without mesal notch 19

19 Metascutellum projecting dorsally above notum ***Paracloeodes***
— Metascutellum projecting posteriorly (Fig. 4.37) ***Baetis***

20 Hindwings with numerous cross-veins ***Callibaetis***
— Hindwings with few or no cross-veins **21**

21 Metascutellum not or scarcely projecting above metanotum (as in Fig. 4.38) ***Dactylobaetis***
— Metascutellum projecting posteriorly above metanotum (Fig. 4.37) **22**

22 Large species, body length 10–12 mm ***Moribaetis***
— Medium to small species, body length less than 10 mm ***Baetis***

23 Foreleg of male with basal tarsal segment equal to or longer than segment 2 ***Epeorus***
— Foreleg of male with basal tarsal segment shorter than segment 2 ***Stenonema***

24 Genital forceps inserted near centre of subgenital plate, which is narrowed and elongated to form a median projection beyond insertion of forceps (Fig. 4.44) ***Thraulodes***
— Genital forceps not as above **25**

25 Subgenital plate with large blunt projections above forceps (Fig. 4.45) ***Farrodes***
— Subgenital plate not as above **26**

26 Penes fused in basal third, widely separated and narrow in apical two-thirds (Fig. 4.47); body yellow with a few black maculae ***Atopophlebia***
— Penes and body colour not as above **27**

27 Wings marked with dark spots **28**
— Wings unmarked or with dark pigment at base only **29**

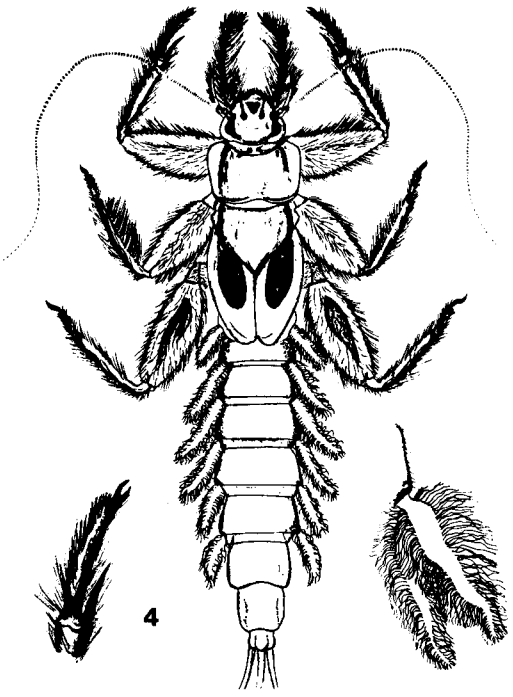
28 Penes forming a small cone-like structure (Fig. 4.48) ***Terpides***
— Penes not as above ***Ulmeritus***

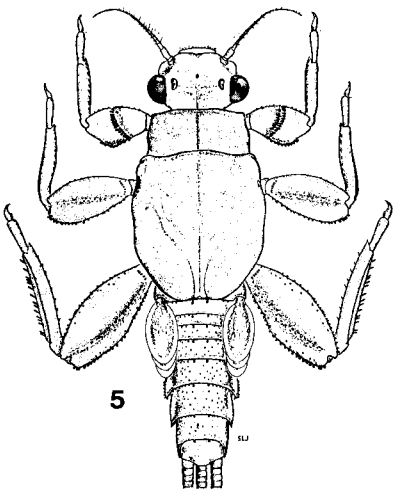
29 Forewings with vein MA symmetrically forked; costal projection of hindwings rounded ***Choroterpes****
— Forewings with vein MA asymmetrically forked; costal projection of hindwings sharp (Fig. 4.34) **30**

30 Subgenital plate with a pair of long, thin, sublateral spines (Fig. 4.46) ***Traverella***
— Subgenital plate with a median pair of short, curved spines ***Hermanella***

31 Forewings of male greatly expanded in cubito-anal area, vein CuP evenly recurved (Fig. 4.33); hindwings absent ***Tricorythodes***
— Forewings not expanded in cubito-anal area; hindwings present or absent **32**

32 Hindwings present in both sexes; males with penes as long as forceps ***Haplohyphes***
— Hindwings lacking in female; males with forceps distinctly longer than penes ***Leptohyphes***





Figs 4.4–4.5 Ephemeroptera nymphs, dorsal views: **4,** *Euthyplocia hecuba*, including detail of fore tarsus and gill (from Roldán 1986); **5,** *Leptohyphes* sp. (from Edmunds *et al.* 1963).

OLIGONEURIIDAE

This is a small family of mayflies found in all continents except Australia. The nymphs are filter feeders, using the long setae on their front legs to collect particulate food from the stream current. In western Panama I have collected *Lachlania* in large, clean rivers at low altitudes. A second genus, *Homoeoneuria*, has been found in Brazil and Honduras to North America. *Homoeoneuria* is known only from streams with sand bottoms (Pescador and Peters 1980) and if it occurs in Panama it will most likely be found in such a habitat.

HEPTAGENIIDAE

This family is most diverse in the Holarctic with a few genera in Africa and South-east Asia. No Heptageniidae are known from South America; a single specimen of *Stenonema mexicanum* (Ulmer) from the Canal area of Panama represents this family's closest known approach to that continent (Flowers and Peters 1980). In western Panama, *Epeorus metlacensis* Traver is common in rocky streams at high altitudes.

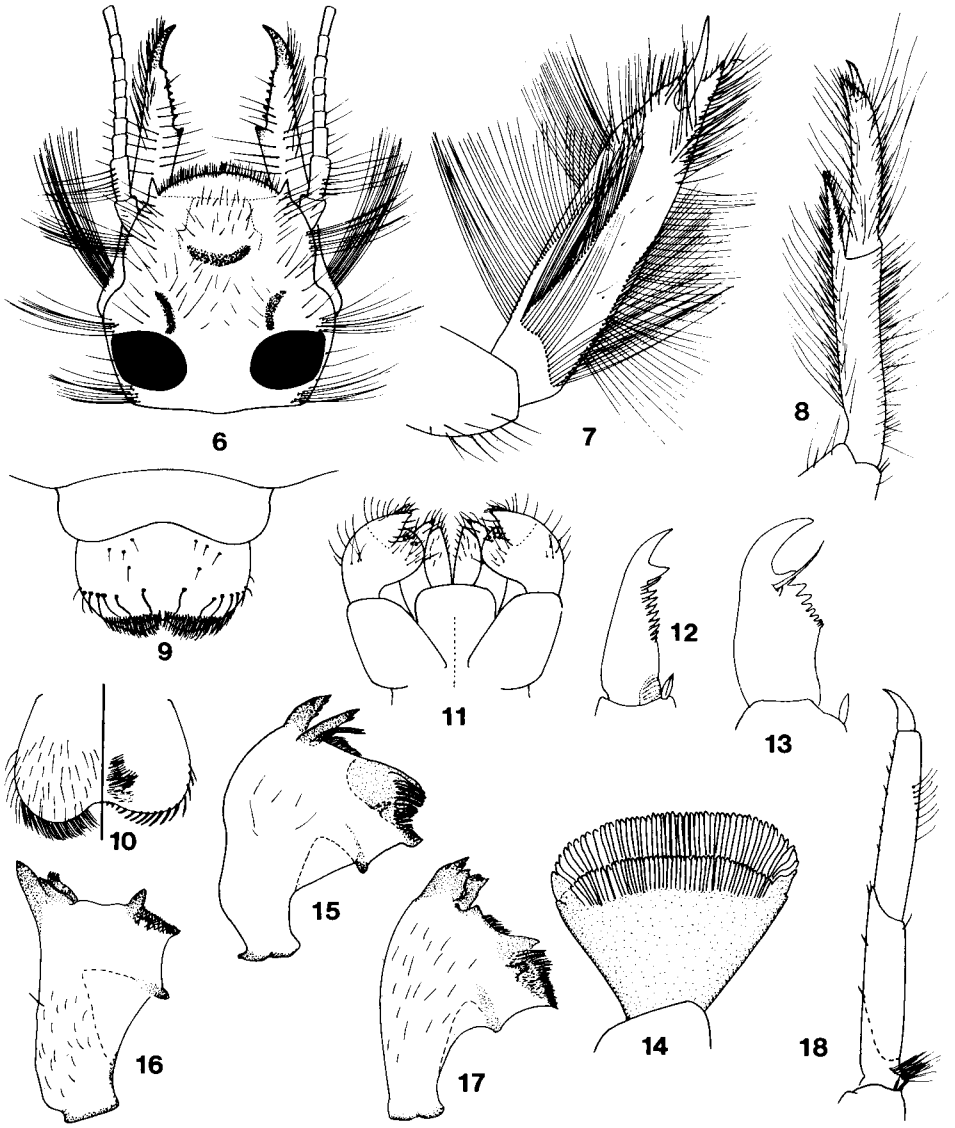
BAETIDAE

This family is found on all continents and many oceanic islands. In Central America and the neotropics it is especially diverse, including many undescribed or poorly known genera. In Panama, the most distinctive genera are *Baetodes*, *Dactylobaetis*, and *Moribaetis*, which also are very abundant (sometimes even dominant) in mountain streams. At low altitudes these genera are much less common, being replaced by *Guajirolus*, *Paracloeodes* and a variety of small *Baetis* species. *Callibaetis* is found in ponds and lakes and is the dominant mayfly in Lake Gatun.

Except for *Moribaetis* (recently revised by Waltz and McCafferty 1984), and *Guajirolus* (one species, *ektrapeloglossa* Flowers, is known from Panama), the baetid fauna of Panama is poorly known at the species level even for *Baetodes* and *Dactylobaetis* which have had some revisionary work. *Baetis*, as treated in this key, includes a number of two-tailed nymphs and two-winged adults that key to *Pseudocloeon* in Edmunds *et al.* (1976) and other keys. Work by Müller-Liebenau (1973, 1981) indicates that true *Pseudocloeon* may be confined to south-east Asia and that many valid *Baetis* species in the tropics lack hindwings. Pending further clarification, I am including a number of two-winged Panamanian species in *Baetis*.

LEPTOPHLEBIIDAE

This family is the dominant family of mayflies in Central America as well as the most ecologically and morphologically diverse. *Thraulodes*, the most common genus in Panama, occurs in streams of all sizes in both low and high elevations. Adults are attractively marked mayflies and most can be recognized by colour pattern. (In spite of this, most of the species I have collected in Panama have not yet been described.) Nymphs of different species, on the other hand, are difficult to tell apart. In the forested areas of western Panama is found an undescribed

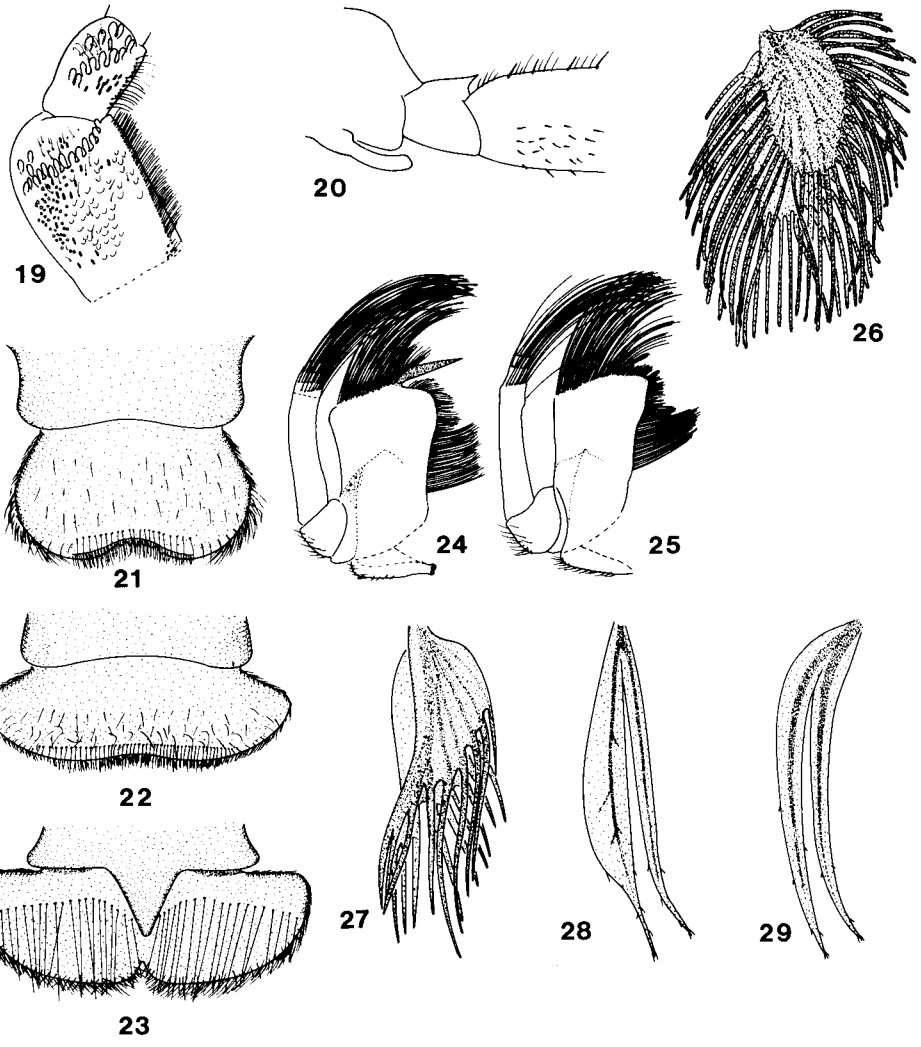


Figs 4.6–4.7 *Campsurus*: **6,** dorsal view of head; **7,** foretibia and tarsus. **Fig. 4.8** *Euthyplocia*, foretibia and tarsus. **Fig. 4.9** *Dactylobaetis*, labrum and clypeus. **Fig. 4.10** *Guajirolus*, labrum (left, dorsal: right, ventral). **Fig. 4.11** *Paracloeodes*, ventral view of labium. **Figs 4.12–14** claws: **12,** *Guajirolus*; **13,** *Moribaetis*; **14,** *Dactylobaetis*. **Figs 4.15–4.17** left mandible: **15,** *Callibaetis*; **16,** *Baetodes*; **17,** *Guajirolus*. **Fig. 4.18** *Cloeodes*, fore tibia and tarsus.

genus closely related to *Thraulodes*. Both adults and nymphs of this genus will key to *Thraulodes*.

Morphologically, the most distinctive leptophlebiids of Panama belong to the *Hermanella* complex, a group of mayflies whose nymphs have mouthparts adapted for filter feeding. Labrum, maxillae, and labium all have rows of long setae which together form a large seine at the front of the nymph's head. Other genera of Leptophlebiidae in the Old World and the Caribbean islands are also filter feeders; the *Hermanella* complex is unique among these in having the setae on the maxillary palpi arranged in well-defined rows (Sivaramakrishnan and Peters 1984). In South America the *Hermanella* complex is abundant and very diverse; in Panama this group includes two described and one undescribed genera. The described genera are *Traverella*, which ranges from Argentina to Canada, and *Hermanella*, which occurs from Argentina to Honduras. In 1985 I collected a third genus from Bocas del Toro Province which is undescribed but apparently related to *Travellera*. In the key the nymphs will come out as *Traverella* and adults will run as far as couplet 30 in the adult key. They can be distinguished from both *Traverella* and *Hermanella* by a lack of spines on the subgenital plate. Mayflies in the *Hermanella* complex are found at both low and high elevations but they are much more common in large lowland rivers.

Another widespread polytypic group of genera in Panama is the *Farrodes* complex. Most species can be assigned to *Farrodes* but specimens belonging to two other undescribed genera have also been found in western Panama. This group of lep-



Figs 4.19–4.20 *Moribaetis*: **19,** base of antenna; **20,** forecoxa showing osmobranch. **Figs 4.21–4.23** labrum and clypeus: **21,** *Farrodes*; **22,** *Thraulodes*; **23,** *Traverella*. **Figs 4.24–4.25** left maxilla. **24,** *Hermanella*; **25,** *Traverella*. **Figs 4.26–4.29** 4th abdominal gill. **26,** *Ulmeritus*; **27,** *Atopophlebia;* **28,** *Terpides*; **29,** *Farrodes*.

tophlebiids is almost ubiquitous in running-water habitats, from the lowlands to very high elevations – they appear to be the dominant mayfly group at the Smithsonian station at Guadelupe Arriba at 2200 m – and from large rivers to the smallest streams. In Cuenca Fortuna, I found adult females and nymphs of one of these mayflies living in leaf litter through which water was percolating on the forest floor. *Farrodes* adults fly both after dusk and before dawn.

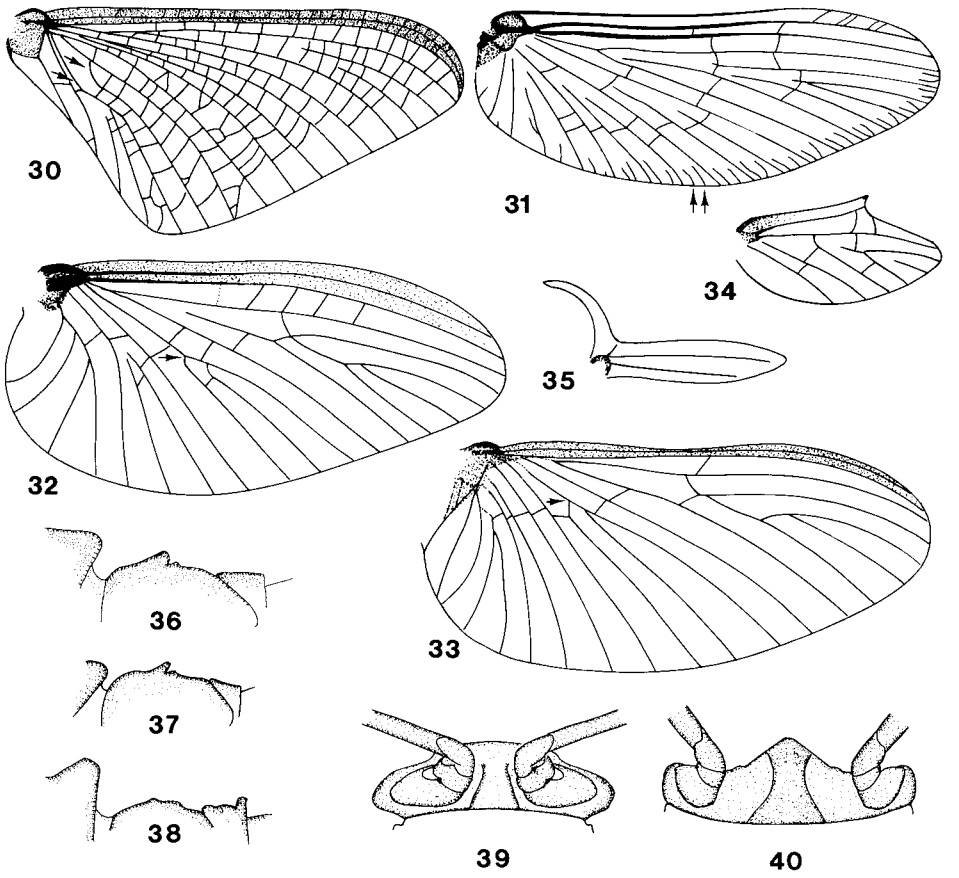
Hagenulopsis is the only leptophlebiid in Panama that lacks hindwings. It has been collected in both western Panama and the Canal area. Nymphs apparently burrow in the upper level of substrate of rocky streams. Subimagos emerge in the evening but mating swarms apparently occur in the morning. At Miramar I encountered a swarm at 9.00 a.m. on an overcast day.

Terpides is a widespread but uncommon polytypic genus in Panama. Some adults have wings marked with dark spots. Nymphs appear to be active swimmers like many Baetidae, instead of crawlers like most other Leptophlebiidae. Savage (1983) reviewed this group and found that Panamanian species belong either to true *Terpides* or to an undescribed related genus.

Atopophlebia fortunensis Flowers was described from adults collected in western Panama (Flowers 1980). In 1985 I collected a nymph of this species from Bocas del Toro Province. The morphology of this nymph shows that *Atopophlebia* is related to *Thraulodes*. *Atopophlebia fortunensis* also occurs in Costa Rica (its gill is figured in Edmunds *et al.* 1976 as 'Ulmeritus ally') and other species are found in South America as far south as Peru (Flowers 1987*b*).

Ulmeritus is a South American genus that occurs in Central America as far north as Costa Rica. In Panama it has been collected in the Canal area and Bocas del Toro, both collections coming from pools. Adults have spotted wings.

Choroterpes is distributed worldwide and is widespread in



Figs 4.30–4.33 forewings: **30,** *Tortopus*; **31,** *Guajirolus*; **32,** *Caenis*; **33,** *Tricorythodes*. **Figs 4.34–35** hindwings: **34,** *Traverella*; **35,** *Leptohyphes*. **Figs 4.36–4.38** metanotum, lateral view: **36,** *Guajirolus*; **37,** *Baetis*; **38,** *Baetodes*. **Figs 4.39–40** prosternum: **39,** *Caenis*; **40;** *Cercobrachys*.

North America and northern Central America. Recently, nymphs were collected in northern Colombia, raising the possibility that this genus also occurs in Panama (several South American species reported in older literature have been shown to belong to other genera).

EUTHYPLOCIIDAE

This family contains Panama's largest mayflies. *Euthyplocia hecuba* (Hagen) (Fig. 4.4) is relatively common. The nymphs have long tusks covered with setae and are found in rocky streams and rivers, usually at low elevations. The purpose of the tusks is not known. *Campylocia* has been recorded from northern South America and Costa Rica; I have seen a single badly damaged female from Miramar that may be a Panamanian record for this genus.

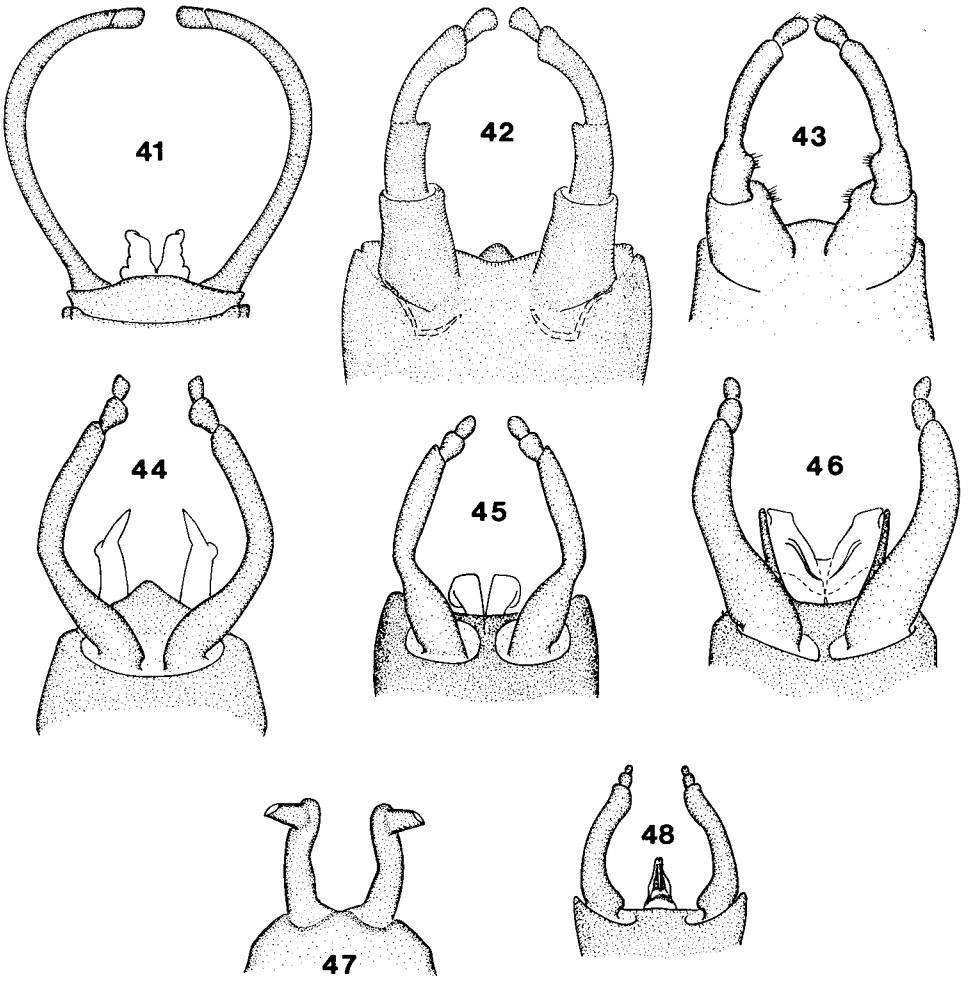
POLYMITARCYIDAE and EPHEMERIDAE

Nymphs of mayflies in both these families live in U-shaped burrows in mud or clay. They can be found in any low elevation rivers or streams where the substrate is suitable. Adults, which readily come to light, are often collected but nymphs, because of their burrowing habits, are relatively rare in aquatic insect collections. *Campsurus* (Polymitarcyidae) is abundant in Panama as well as throughout the Neotropics. Although over 30 species have been described, the genus is in need of revision. I have collected two species in Panama: *C. emersoni* Traver from Parque Nacional Soberania and a second species from both the Canal area and Bocas del Toro. Females are much more common at light than males.

Two other genera, *Tortopus* (Polymitarcyidae) and *Hexagenia* (Ephemeridae) are known from regions on both sides of Panama and probably occur in Panama also. Both genera are very abundant locally in North America but seem to be much less common in the neotropical parts of their ranges.

TRICORYTHIDAE

Members of this family have the widest habitat preferences among Panamanian mayflies. They range from first-order forest streams to large rivers; from streams in primary rainforest to streams in pastures and near villages. The common genera are *Leptohyphes* and *Tricorythodes*, which often occur together in the same stream. The number of Panamanian species in these genera is unknown and may be large but *Leptohyphes*



Figs 4.41–4.48 male genitalia: **41**, *Euthyplocia*; **42**, *Guajirolus*; **43**, *Cloeodes*; **44**, *Thraulodes*; **45**, *Farrodes*; **46**, *Traverella*; **47**, *Atopophlebia* (penes only); **48**, *Terpides*.

appears to be the more abundant. At Miramar *Leptohyphes* numbers exceeded those of all other mayflies by several orders of magnitude (Wolda and Flowers 1985). Both genera emerge in the evening as subimagos but adults are rarely seen at this time. Most adult mating probably takes place just before dawn; I have encountered large swarms of both genera at this time on the Río Changuinola. The third Panamanian tricorythid, *Haplohyphes*, is much less common although *Haplohyphes mithras* (Traver) has been collected at several localities. The nymph of *Haplohyphes* has just been described by Dominguez (1984) and I have collected it in rainforest first-order streams in western Panama.

CAENIDAE

Caenis is poorly known from Panama but appears to be widespread at low elevations. I have collected it in large rivers and in streams in disturbed areas. Nymphs are often in muddy parts of streams with very little current. They are frequently covered with silt and difficult to see, which probably explains much of their rarity in collections of Neotropical mayflies. Adults have been taken at light traps on Barro Colorado Island (Wolda, personal communication). *Cercobrachys* is a second caenid genus that is known from North and South America. I have collected a few adults at the Río Teribe (Bocas del Toro Province) before dawn. This genus was recently established by Soldan (1984) for a number of species formerly placed in *Brachycercus*. Nymphs of *Cercobrachys* are often overlooked since they are covered with silt and are very slow moving. Some species may burrow in mud. The Río Teribe collection is the first record of this genus from Central America.

Biogeography

McCafferty *et al.* (in press) divide the Central American Ephemeroptera according to presumed origin in neotropical or nearctic centres of dispersal. At present no genera are known to be endemic to Central America. The neotropical component is

dominant and many genera penetrate through Central America and well into North America, some even into Canada. Proportionally fewer North American genera have penetrated all the way to South America.

Panama in its present form has been in existence only since the Pliocene (Pielou 1979). Because of this and because of Panama's location it is hardly surprising that most of Panama's mayfly fauna is closely related to northern South American forms. Three of the 27 Panamanian genera, *Stenonema*, *Epeorus*, and *Cercobrachys*, are North American or Holarctic in their affinities. Of these only *Cercobrachys* has been found in South America. If *Hexagenia* and *Choroterpes* are found in Panama, they would represent additional Nearctic components in the fauna.

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Checklist of described species of Ephemeroptera of Panama and Costa Rica

The following checklist enumerates all valid mayfly species that have been recorded from the fauna of Panama and Costa Rica. I have had the opportunity to examine some large mayfly collections from Costa Rica, and the mayfly fauna is almost identical to the fauna I have studied in western Panama. Hence, no attempt is made to differentiate between Panamanian and Costa Rican records in this list. No undescribed species or genera without published species records from Panama and Costa Rica are included but several species designed by letter only are listed, as they have been formally described although not named. Besides the records associated with original descriptions, additional records for Costa Rica are in McCafferty (1970, 1985).

Suborder **Pannota**

Family **TRICORYTHIDAE**

Haplohyphes
- ***mithras*** (Traver, 1958)

Leptohyphes
- ***costaricanus*** Ulmer, 1920
- ***murdocki*** Allen, 1967
- ***nanus*** Allen, 1967
- ***priapus*** Traver, 1958

Tricorythodes
- ***explicatus*** (Eaton, 1892)
- ***sordidus*** Allen, 1967

Suborder **Schistonota**

Family **BAETIDAE**

Baetis
- ***quilleri*** Dodds, 1923

Baetodes
- ***adustus*** Cohen & Allen, 1972
- ***caritus*** Cohen & Allen, 1972
- ***deficiens*** Cohen & Allen, 1972
- ***tritus*** Cohen & Allen, 1972
- ***velmae*** Cohen & Allen, 1972

Callibaetis
- ***paulinus*** (Navás, 1924)
- ***undatus*** (Pictet, 1843)

Guajirolus
- ***ektrapeloglossa*** Flowers, 1985

Moribaetis
- Subgenus ***Mayobaetis***
- ***ellenae*** (Mayo, 1973)
- Subgenus ***Moribaetis***
- ***macaferti*** Waltz, 1985
- ***maculipennis*** (Flowers, 1979)
- ***salvini*** (Eaton, 1883)

Family **EPHEMERIDAE**

Hexagenia
- Subgenus ***Pseudeatonica***
- ***albivitta*** (Walker, 1853)
- ***mexicana*** Eaton, 1883

Family **EUTHYPLOCIIDAE**

Campylocia
- ***anceps*** (Eaton, 1883)

Euthyplocia
hecuba (Hagen, 1861)

Family **HEPTAGENIIDAE**

Epeorus
metlacensis Traver, 1964
packeri Allen & Cohen, 1977
Stenonema
mexicanum (Ulmer, 1920)

Family **LEPTOPHLEBIIDAE**

Subfamily **ATALOPHLEBIINAE**

Atopophlebia
fortunensis Flowers, 1980
Choroterpes
atramentum Traver, 1947*a*
vinculum Traver, 1947*a*
Terpides
jessiae Peters & Harrison, 1974
Thraulodes
centralis Traver, 1946
hilaris (Eaton, 1892)
hilaroides Traver, 1946
irretitus Navás, 1924
lepidus (Eaton, 1883)
prolongatus Traver, 1946
spangleri Traver & Edmunds, 1967
valens (Eaton, 1892)
zonalis Traver & Edmunds, 1967
sp. C; Allen & Brusca, 1978
sp. E; Allen & Brusca, 1978
Thraulus (?)
roundsi Traver, 1947*a*
Traverella
primana (Eaton, 1892)
versicolor (Eaton, 1892)
sp. B; Allen, 1973

Family **OLIGONEURIIDAE**

Lachlania
fusca (Navás, 1924)

Family **POLYMITARCYIDAE**

Campsurus
emersoni Traver, 1947*b*
Tortopus
unguiculatus (Ulmer, 1920)

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