Heptageniidae of the World. Part II: Key to the Genera

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Abstract. Keys and diagnoses illustrated with line drawings and colour photographs for the identification of larvae and adult males of the genera of Heptageniidae of the world and female adults of North American Heptageniidae genera are provided. *Siberionurus* McCafferty is recognized as a junior objective synonym of *Ecdyogymnurus* Kluge. *Epeiron* Demoulin is shown to be congeneric with *Rhithrogena* Eaton. All subgenera that have been proposed for *Rhithrogena*, *Compsoneuria* Eaton, and *Epeorus* Eaton are treated as junior synonyms (*Rhithrogena* = *Himalogena* Kluge, N.SYN.; = *Sibirigena* Kluge, N.SYN.; = *Tumungula* Zhou & Peters, N.SYN.; *Epeorus* = *Alpiron* Braasch, N.SYN.; = *Albertiron* Kluge, N.SYN.; = *Belovius* Tshernova; = *Caucasiron* Kluge, N.SYN.; = *Iron* Eaton; = *Ironopsis* Traver; = *Proepeorus* Kluge, N.SYN.; *Compsoneuria* = *Siamoneuria* Braasch, N.SYN.)

Introduction

In Part I of the Heptageniidae of the World (Ephemeroptera), Wang and McCafferty (2004) analyzed the generic relationships and presented a phylogenetic classification of the family. Three subfamilies, 12 tribes, and 29 genera were recognized. The present paper provides worldwide keys and diagnoses for larvae and male adults of the genera recognized in Part I as well as subsequently described genera and revisions of generic concepts, and a key for female adults of North American genera. The forthcoming Part III will be a catalog of the Heptageniidae with coverage of all valid names, nomenclatural history, and pertinent taxonomic literature (Webb and McCafferty in prep.).

Generic Changes

Kluge (2004) established *Ecdyogymnurus* Kluge as a subgenus of *Ecdyonurus* Eaton, designating *Ecdyonurus inversus* Kluge as the type species. Independently, McCafferty (2004) described *Siberionurus* McCafferty as a new genus, also designating *E. inversus* as the type species. Because *Ecdyogymnurus* was published shortly before *Siberionurus*, it is the senior name of the genus by priority (*Ecdyogymnurus* Kluge = *Siberionurus* McCafferty, N. OBJ. SYN.) and we treat it at the generic level herein.

Two genera were described subsequent to Wang and McCafferty's (2004) revision: *Parafronurus* Zhou & Braasch and *Darthus* Webb & McCafferty. These two genera were found to belong to a clade with *Afronurus* Lestage (Webb and McCafferty 2007) and, in accordance with sequencing conventions, the tribe Afronurini Webb & McCafferty was established in order to retain the generic status of *Atopopus* Eaton, *Thalerosphyrus* Eaton and *Asionurus* Braasch & Soldán.

Webb et al. (2006) showed that larvae Ulmer (1939) described as *Compsoneuria* Eaton are actually a species of *Trichogenia* Braasch & Soldán. Based on characteristics of adult males, Webb et al. (2006) furthermore showed *Compsoneuria* to be a member of the Ecdyonurinae and transferred the genus and the tribe Compsoneuriini to that subfamily, at the same time establishing the tribe Trichogeniini Webb & McCafferty in the Heptageniinae for the genus *Trichogenia*. Webb et al. (2006) additionally recognized the synonymy of *Compsoneuriella* Ulmer and *Notonurus* Crass with *Compsoneuria*, and restricted the concept of *Thalerosphyrus*.

Wang and McCafferty (2004) placed *Epeiron* Demoulin as a synonym of *Cinygmula* because they did not detect any significant difference in the male genitalia, tarsal segment ratios, or thoracic structure between the two genera. All species of *Cinygmula*

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possess median and usually ventral titillators, but no species described in *Epeiron*, including the type species *E. amseli* Demoulin, have either median or ventral titillators (Demoulin 1964, Kluge 2004). The lack of titillators indicates that *Epeiron* is equivalent to *Rhithrogena*, which always lack median titillators (ventral titillators may be present or absent). Although no species initially described in *Epeiron* are known as larvae, Kluge (2004) showed that several species described in *Rhithrogena* form a monophyletic group with *Epeiron* and many of these species are known in the larval stage, such as *R. binerve* Kluge, *R. eugeniae* Kluge, *R. paulinae* Sartori & Sowa, and *R. znojkoi* Tshernova. These larvae all possess gill lamellae that form a friction disc, characteristic of *Rhithrogena*. *Epeiron* was synonymized with *Rhithrogena* by Kluge (1988) and Sartori and Sowa (1992), and we follow that interpretation herein.

Kluge (2004) recognized five subgenera within *Rhithrogena*: *Himalogena* Kluge, *Tumungula* Zhou & Peters, *Sibirigena* Kluge, *Epeiron*, and *Rhithrogena*. *Tumungula*, *Sibirigena* and *Epeiron* each possess autapomorphies, but *Himalogena* and *Rhithrogena* are defined by plesiomorphic characteristics (Kluge 2004). Recognition of these groupings results in a paraphyletic classification and therefore, we do not recognize any of the subgenera of *Rhithrogena* (=*Himalogena* Kluge, N.SYN.; = *Sibirigena* Kluge, N.SYN.; = *Tumungula* Zhou & Peters, N.SYN.). For similar reasons, we do not recognize subgenera of *Epeorus* (= *Albertiron* Kluge, N.SYN.; = *Alpiron* Braasch, N.SYN.;= *Belovius* Tshernova; = *Caucasiron* Kluge, N.SYN.; = *Iron* Eaton; = *Ironopsis* Traver; = *Proepeorus* Kluge, N.SYN.) or *Compsoneuria* (=*Siamoneuria* Braasch, N.SYN.).

Kluge (2004) established several subgenera within *Ecdyonurus*, many of which are treated as genera by Wang and McCafferty (2004). One of these subgenera, *Thamnodontus* Kluge, is not defined by any apomorphies, but the three included species cannot be confidently placed in any other genus. *Thamnodontus* appears to be most similar to *Notacanthurus* as adults have slightly to greatly expanded head capsules (Kluge 1983). Larvae, however, lack the characteristic median ridge of spines on the abdomen. Even though the monophyly of *Thamnodontus* is not supported, we are tentatively recognizing it as a valid genus until further evidence becomes available.

Notes on the Keys

Most specimens of Heptageniinae and Rhithrogeninae should be readily identified using this key. Differentiation of some Ecdyonurinae genera, however, is more provisional, especially in the poorly known Oriental Region. For larvae of Ecdyonurinae, the relative development of the anterior margin of the head capsule is frequently useful, but may be difficult to interpret. The more primitive genera generally have the dorsal and ventral surfaces of the anterior margin distinctly differentiated (Fig. 34). *Afronurus*, *Darthus*, and *Parafronurus* differ in having a rounded anterior margin where the dorsal and ventral surfaces do not meet in a distinct edge (Fig. 30). *Thalerosphyrus* and *Atopopus* have the anterior margin distinctly thickened ventrally, and sometimes dorsally as well (Figs. 31, 36). Larvae of *Nixe* and the *Ecdyonurus simplicioides* group cannot reliably be distinguished except by examination of eggs from mature females. In North America, *Ecdyonurus simplicioides* (McDunnough, 1924a) is known to be sympatric with several *Nixe* spp. in central Canada, but can be distinguished by the colour pattern of the head capsule, as indicated in the key. *Nixe kennedyi* (McDunnough, 1924b) is sympatric with *Ecdyonurus* in far western North America, but the larva is unknown and so diagnostic characters cannot be provided. In the eastern Palearctic, *Nixe joernensis* (Bengtsson, 1909) is sympatric with several species of the *Ecdyonurus simplicioides* group, but there is insufficient information to provide characters that will consistently differentiate *Ecdyonurus* and *Nixe* in this region.

The key should correctly identify males of most genera, but some difficulties within the Ecdyonurinae may be encountered due to our lack of knowledge, particularly in the highly diverse and poorly known Oriental realm. The terminology used for the various spines, sclerites, and titillators of the penes are illustrated in Figure 163.

Most well marked North American females should be correctly identified using the key. Females of some of the Heptageniinae genera can be difficult to distinguish, but examination of eggs under magnifications of 400-1000X will confirm their identity.

Distribution maps are referenced when their use will aid identification; general biogeographic zones are as in Figure 246. The following genera, arranged alphabetically under their respective subfamilies, are included in the male and larval keys:

Ecdyonurinae

Afronurus Lestage, 1924
Asionurus Braasch & Soldán, 1986
Atopopus Eaton, 1881
Compsoneuria Eaton, 1881

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Darthus Webb & McCafferty, 2007 (Adult unknown)
Ecdyogymnurus Kluge, 2004
Ecdyonurus Eaton, 1868
Electrogena Zurwerra & Tomka, 1985
Leucrocuta Flowers, 1980
Nixe Flowers, 1980
Notacanthurus Tshernova, 1974
Parafronurus Zhou & Braasch, 2003
Thalerosphyrus Eaton, 1881
Thamnodontus Kluge, 2004

Heptageniinae
Dacnogenia Kluge, 1988
Heptagenia Walsh, 1863
Kageronia Matsumura, 1931
Maccaffertium Bednarik, 1979
Macdunnoa Lehmkuhl, 1979
Raptoheptagenia Whiting & Lehmkuhl, 1987
Stenacron Jensen, 1974
Stenonema Traver, 1933
Trichogenia Braasch & Soldán, 1988

Rhithrogeninae
Anepeorus McDunnough, 1925
Bleptus Eaton, 1885
Cinygma Eaton, 1885
Cinygmula McDunnough, 1933
Epeorus Eaton, 1881
Ironodes Traver, 1935
Paegnioides Eaton, 1881
Rhithrogena Eaton, 1881
Spinadis Edmunds & Jensen, 1974

Key to the Genera of Heptageniidae: Larvae

1 Median caudal filament vestigial (as in Figs. 9, 11, 29)....2
- Median caudal filament well developed (as in Figs. 1, 26)....6

2 Maxillary palps slender (as in Fig. 56); medial interfacing setae present on cerci (as in Fig. 11); Nearctic distribution (Figs. 215, 240)....3
- Maxillary palps enlarged (as in Figs. 52, 53); medial interfacing setae absent on cerci, although dorsal row of fine setae sometimes present (Fig. 104); widespread distribution....4

3. Head, pronotum, and mesonotum each with well-developed tubercles (Fig. 25); legs without long, fine setae; eastern Nearctic distribution (Fig. 240)....***Spinadis***
- Head without well-developed tubercles (Fig. 11), small thoracic tubercles sometimes present; legs with long, fine setae (Fig. 75); western Nearctic distribution (Fig. 215)....***Anepeorus***

4. Anterior margin of head capsule with dense fringe of setae (as in Fig. 38); glossae subtriangular (as in Fig. 70); Holarctic, northern Neotropical, Oriental distribution (Figs. 227, 229)....5
- Anterior margin of head capsule without dense fringe of setae (Fig. 35); glossae subquadrate (Fig. 67); eastern Palearctic distribution (Fig. 218)....***Bleptus***

5 Lamellae of gills 1 reduced, subequal to length of segment 2 (Fig. 99); galealaciniae with incisors not greatly enlarged (Fig. 53); abdominal terga with small paired tubercles (Fig. 29); caudal filaments without dorsal row of fine setae; western Nearctic distribution (Fig. 229)....***Ironodes***
- Lamellae of gills 1 well developed and longer than length of segment 2 (Fig. 10); galealaciniae with incisors greatly enlarged (Fig 52); abdominal tubercles present or absent (Fig. 9-10), western Nearctic species never with paired tubercles; caudal filaments with dorsal row of fine setae (Fig. 104); Holarctic, northern Neotropical, Oriental distribution (Fig. 227)....***Epeorus***

6 Labrum longer than wide (Fig 47); glossae triangular and apically expanded (Fig 74); eastern Palearctic, western Nearctic distribution (Fig. 219)....***Cinygma***
- Labrum wider than long (as in Figs. 44, 46); glossae variable in shape (as in Fig. 71, 73); widespread distribution....7

7 First pair of gills meet or overlap ventrally to form friction disk (Fig 24); maxillary palps enlarged (Fig. 55); Holarctic, northern Neotropical, Oriental distribution (Fig.239)....***Rhithrogena***
- First pair of gills not meeting ventrally and not forming ventral friction disk; maxillary palps variable; widespread distribution....8

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8 Ventral surface of maxillae with scattered setae (as in Fig. 50); outer incisor of planate mandible with single terminal denticle (as in Fig. 42); lamellae of gills 1 usually banana shaped (as in Fig. 88), but sometimes absent, reduced, or cordate (as in Fig. 85); widespread distribution 9

- Ventral surface of maxillae with setae in row (as in Fig. 58); outer incisor of planate mandible usually with three terminal denticles (as in Figs. 40, 41); lamellae of gills 1 variable, but never banana shaped; widespread distribution 24

9 Abdominal terga with median ridge (as in Fig. 7, 18); southern Palearctic (Himalayas to Korea) and Oriental distribution (Figs. 223, 235) 10

- Abdominal terga without median ridge; widespread distribution 11

10 Lamellae of gills 2-6 sickle shaped (Fig. 87); lamellae of gills 1 absent; hindtibiae with two rows of long fine setae and row of long robust setae (Fig. 78); tarsal claws with denticles; anterior margin of head capsule slightly thickened (as in Fig. 30); endemic to Borneo (Fig. 223)..... ***Darthus***

- Lamellae of gills 2-6 rounded or with small apical extension, never sickle shaped; lamellae of gills 1 present and banana shaped (as in Fig. 88); hindtibiae with only one well-developed row of long, fine setae and no row of long, robust setae; tarsal claws without denticles; anterior margin of head capsule not thickened; southern part of eastern Palearctic (Fig. 235) ..... ***Notacanthurus***

11 Supercoxal projections acutely pointed (as in Fig. 79); Afrotropical and Oriental distribution (Figs. 221, 243) 23

- Supercoxal projections rounded or bluntly pointed (as in Fig. 80); widespread distribution 12

12 Lamellae of gills 1 highly reduced; posterolateral margins of head capsule emarginate (Fig. 4); anterior margin of head capsule distinctly thickened (Fig. 31); posterolateral spines of abdomen relatively wide basally (Fig. 105); Borneo, Philippines (Fig. 217) ..... ***Atopopus***

- Lamellae of gills 1 well developed; posterolateral margins of head capsule rounded; anterior margin of head capsule slightly thickened or not thickened (as in Figs. 30, 34); posterolateral spines of abdomen relatively small or narrow basally (as in Fig. 14); widespread distribution..... 13

13 Gills 7 slender and pointed (Fig. 86); posterolateral margin of pronotum usually expanded posteriorly; superlinguae bent posteriorly and distinctly pointed (Fig. 59); lamellae of gills 1 cordate (Fig. 85); gills with distinct trachaea; robust setae on inner surface of hindtarsi pectinate (Fig. 77); southeast Asia (Fig. 216)..... ***Asionurus***

- Gills 7 usually rounded apically, never as long and narrow as above (as in Fig. 89); pronotum variable; superlinguae never sharply pointed (as in Fig. 61); lamellae of gills 1 usually banana shaped (as in Fig. 88), tracheation variable; setae on inner surface of tarsi either simple or fimbriate, never pectinate; widespread distribution 14

14 Hindtibiae with two dense rows of long, fine setae and usually with row of long, stout somewhat clavate setae present on lateral ridge of tibiae (as in Figs. 76, 78); head capsule slightly thickened anteriorly (as in Fig. 30); Afrotropical, Oriental, and eastern Palearctic distribution (Figs. 214, 237) 15

- Hindtibiae with single row of long, fine setae (second, sparse row of short, fine setae with short robust setae may be present on lateral ridge) and usually without row of long stout setae; head capsule usually with distinct edge anteriorly and not thickened (as in Fig. 34); widespread distribution 16

15 Caudal filaments with spines and whorls of long, fine setae at articulations (Fig. 103); China (Fig. 237) ..... ***Parafronurus***

- Caudal filaments without whorls of long, fine setae at articulations (Fig. 100); Afrotropical, Oriental, eastern Palearctic distribution (Fig. 214)..... ***Afronurus, in part***

16 Terminal segment of labial palps with patch of long setae projecting medially (Fig. 66); head capsule slightly thickened anteriorly (Fig. 30); Borneo, Celebes, Philippines..... ***Afronurus, in part***

- Terminal segment of labial palps never with patch of long setae projecting medially (as in Fig. 69); head capsule not thickened anteriorly; Holarctic, Oriental distribution 17

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17 Posterolateral margins of pronotum expanded posteriorly (Fig. 8); Palearctic distribution (Fig. 225) ..... ***Ecdyonurus*, *in part***

- Posterolateral margins of pronotum not expanded posteriorly; Holarctic, Oriental distribution 18

18 Scattered setae on ventral surface of galealaciniae simple (as in Fig. 49); distal dentisetae of maxillae divided into several branches (as in Fig. 49); southern and western Palearctic distribution (Fig. 226, 244) 36

- Scattered setae on ventral surface of galealaciniae fimbriate (as in Fig. 51); distal dentisetae of maxillae simple or distally bifurcate (as in Fig. 51); Holarctic, northern Neotropical, Oriental distribution (Figs. 224, 225, 231, 234) 19

19 Western Hemisphere 20

- Eastern Hemisphere 22

20 Caudal filaments without interfacing setae (Fig. 101); abdomen usually with well-developed posterolateral spines (Fig. 14); Nearctic distribution (Fig. 231) ..... ***Leucrocuta***

- Caudal filaments with numerous interfacing setae (as in Fig 102); abdomen with small posterolateral spines (as in Fig. 17); Nearctic, Central American distribution 21

21 Western Nearctic and Central American distribution (Fig. 225); labrum usually >2X wider than long and expanded laterally; (Fig. 44); if labrum <2X wider than long, (Fig. 45), then median pair of pale spots on head capsule separated by distance greater than distance between bases of antennae (Fig. 33); eggs from mature female larvae with knob terminated coiled threads and small tubercles or longitudinal ridges with small granules (Figs. 108, 109), never with meshlike ridges surrounding knob terminated coiled threads ..... ***Ecdyonurus, in part***

- Widespread Nearctic distribution (Fig.234); labrum not greatly expanded laterally, usually <2X wider than long (Fig. 43); median pair of pale spots on head capsule separated by distance less than distance between bases of antennae (Fig. 32); eggs from mature female larvae with meshlike ridges surrounding knob terminated coiled threads (Fig. 110) ..... ***Nixe, in part***

22 Caudal filaments without interfacing setae (as in Fig. 101); eastern Palearctic distribution (Fig. 224) ..... ***Ecdyogymnurus***

- Caudal filaments with numerous interfacing setae (Fig 102); Palearctic, Oriental distribution (Figs. 225, 234) 34

23 Anterior margin of head capsule not thickened (Fig. 34); posterolateral spines of abdomen small; glossae apically narrowed, not subquadrate (Fig. 68); posterolateral margin of head capsule rounded; femora and head capsule usually stippled with black spots (Fig. 6); Oriental, Afrotropical distribution (Fig. 221) ..... ***Compsoneuria***

- Anterior margin of head capsule distinctly thickened (Fig. 36, 37); posterolateral spines of abdomen usually large (Fig. 106); glossae subquadrate (Fig. 73); posterolateral margin of head capsule often emarginate (Fig. 37); femora and head capsule without numerous black dots; Oriental distribution (Fig. 243) ..... ***Thalerosphyrus***

24 Gills inserted laterally, lamellae usually well developed; labial palps never spinelike and sharply pointed (as in Fig. 71); widespread distribution 25

- Gills inserted ventrally, lamellae reduced to slender filaments (Figs. 21, 22); labial palps spinelike and sharply pointed (Fig. 72); Nearctic distribution (Fig. 238) ..... ***Raptoheptagenia***

25 Lamellae of gills 1-6 with anal rib submarginal and costal rib absent (as in Figs. 94, 96, 97); gills 7 slender and without fibrils (as in Figs. 95, 98), or vestigial; superlinguae of hypopharynx with large lateral projections (as in Fig. 64); Nearctic, Central American distribution 30

- Lamellae of gills 1-6 with anal and costal ribs marginal (as in Figs. 91, 92); gills 7 similar in shape to other gills, usually with fibrils; superlinguae without large lateral projections (as in Figs. 62-63, 65); Holarctic, Oriental distribution 26

26 Apices of forefemora with dorsal process projected and narrower than ventral process (as in Fig. 81); maxillary palps enlarged (as in Fig. 55) 33

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- Apices of forefemora with dorsal process not projected (as in Fig.82); maxillary palps narrow (as in Fig. 58) 27

27 Lamellae of gills 1 reduced in size (Fig. 12); abdominal terga with branched fan-shaped setae and fine setae (Fig. 107); gill lamellae distally pointed or very long and slender (Fig. 12); labrum much wider than long (Fig. 48); southeast Asia (Fig. 245) ..... ***Trichogenia***

- Lamellae of gills 1 similar in shape and size to other gills; abdominal terga with fine setae only; gill lamellae usually not as above; labrum usually less than 4X wider than long; Holarctic distribution 28

28 Mandibles with stout incisors (Fig. 39); gill lamellae all long and slender (Fig. 90); hypopharynx with superlinguae much longer than lingua (Fig. 60); western Palearctic distribution (Fig. 222)..... ***Dacnogenia***

- Mandibles with slender incisors (as in Fig. 40); lamellae of gills variable, usually somewhat ovate with apex rounded or pointed (Figs. 91, 92), never as long and slender as above; superlingua only slightly longer than lingua (Figs. 62, 63); Holarctic distribution (Figs. 228, 230) 29

29 Superlinguae of hypopharynx not lyre-shape (Fig. 63); tarsal claws with serrate ridge (Fig. 83); gills 1-6 as in Fig. 91; gills 7 without fibrils; dorsal margin of femora with only short setae; Palearctic distribution (Fig. 230) ..... ***Kageronia***

- Superlinguae of hypopharynx lyre-shaped (Fig. 62); tarsal claws usually with only single basal denticle, occasionally small submarginal teeth present (Fig. 84); gills 1-6 not acutely pointed apically (Fig. 92); gills 7 with fibrils; dorsal margin of femora with long setae (as in Figs. 1-2); Holarctic distribution (Fig. 228) ..... ***Heptagenia***

30 Apex of gill lamellae 1-6 rounded or truncate (as in Figs. 93, 94, 97); maxillae with or without comb setae on crown of galea lacinia (Fig. 54); Nearctic, Central American distribution..... 31

- Apex of gill lamellae 1-6 acutely pointed (Fig. 96); maxillae with comb setae on crown of galea lacinia (Fig. 57); Nearctic distribution ..... ***Stenacron***

31 Gills 7 vestigial, gills 6 much smaller than gills 1-5 (Fig. 93); Nearctic distribution (Fig. 233) ..... ***Macdunnoa***

- Gills 7 slender (as in Figs. 95, 98), gills 6 subequal in size to gills 1-5; Nearctic, Central American distribution (Fig. 232, 242)..... 32

32 Apex of lamellae of gills 1-6 rounded (Fig. 97); lamellae of gills 7 with trachea present (Fig. 98); abdominal sterna each with pair of lateral dark, round spots (Fig. 27); central and eastern Nearctic distribution (Fig. 242) ..... ***Stenonema***

- Apex of lamellae of gills 1-6 truncate (Fig. 94); lamellae of gills 7 without trachea (Fig. 95); maculation of abdominal sterna variable; Nearctic and Central American distribution (Fig. 232) ..... ***Maccaffertium***

33 Caudal filaments with interfacing setae; lamellae of gills 1 reduced in size, much shorter than fibrils; southeast Asia (Fig. 236)..... ***Paegnioides***

- Caudal filaments without interfacing setae; lamellae of gills 1 well developed, nearly as long as or longer than fibrils or fibrils absent; Holarctic, Oriental distribution (Fig. 220) ..... ***Cinygmula***

34 Western Palearctic..... ***Nixe, in part***

- Eastern Palearctic, Oriental 35

35 Eggs from mature female larvae with meshlike ridges surrounding knob terminated coiled threads (Fig. 110) ..... ***Nixe, in part***

- Eggs from mature female larvae with knob terminated coiled threads not surrounded by meshlike ridges but with small, scattered tubercles or irregular ridges (Figs. 108, 109)..... ***Ecdyonurus, in part***

36 Far eastern Russia, Japan, and Korea (Fig. 244) ..... ***Thamnodontus***

- Western and southern Palearctic (Fig. 226)..... ***Electrogena***

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Key to the Genera of Heptageniidae: Male Adults

1 Mesonotum without apparent transverse suture (Fig. 114); foretarsi with segment 1 subequal in length to segment 2 (Fig. 124); Holarctic, Oriental, northern Neotropical distribution 2

- Mesonotum with apparent transverse suture (Fig. 115); foretarsi variable, but usually with segment 1 shorter than segment 2; widespread distribution 4

2 Hindwings relatively narrow, darkly stained distally (Fig 174); forewings with brown staining medially and apically (Fig. 173); bases of forceps greatly expanded, meeting medially (Fig 139); prosternum with transverse crest (Fig. 120); Japan, Korea (Fig. 218)..... ***Bleptus***

- Hindwings broad (Fig. 176), without dark staining distally; forewings variable; bases of forceps not, or only slightly, expanded, and never meeting medially (Figs 150-154); prosternum rounded, without transverse crest (as in Fig. 121); Holarctic, Oriental, northern Neotropical distribution (Figs. 227, 229) 3

3. Penes separated to base, not apically expanded, and often widely divergent; titillators absent (Fig. 158); basal crossveins of forewings well developed (Fig. 197); abdominal terga without large pale spots or dark median line but with transverse black line on posterior margins (Fig. 197); western Nearctic distribution (Fig. 229) ..... ***Ironodes***

- Penes usually apically expanded or fused in basal half (Figs 150-154); titillators present or absent; for western Nearctic species that lack titillators: basal crossveins of forewings less well developed (Fig. 175) and abdominal terga with large pale spots and dark median line (Fig.194); Holarctic, northern Neotropical, Oriental distribution (Fig. 227)..... ***Epeorus***

4. Foretarsi shorter than foretibiae in combination with Nearctic distribution..... 5

- Foretarsi longer than tibiae and widespread distribution, or foretarsi shorter than foretibiae in combination with Oriental or Afrotropical distribution..... 6

5 Hindtibiae shorter than hindfemora; head capsule pointed (Fig. 128); western Neactic distribution (Fig. 215)..... ***Anepeorus***

- Hindtibiae longer than hindfemora; head capsule truncate (Fig. 129); eastern Nearctic distribution (Fig. 240) ..... ***Spinadis***

6 Medial depression of furcasternum of mesothorax narrowed anteriorly (as in Fig. 119); Holarctic, northern Neotropical, Oriental distribution 15

- Medial depression of furcasternum of mesothorax subparallel or slightly divergent anteriorly (Fig. 118); widespread distribution..... 7

7 Penes triangular with well-developed lateral and apical sclerites (Fig. 148); dorsolateral spines absent or minute; Palearctic distribution ..... ***Ecdyonurus, in part***

- Penes not as above; dorsolateral spines variable; widespread distribution..... 8

8 Hindtarsi distinctly longer than hindtibiae (Fig. 125); fore- and hindwings with dark staining at margins (Fig. 177); Borneo, Philippines (Fig. 217)..... ***Atopopus***

- Hindtarsi subequal to, or shorter than, hindtibiae; forewings coloration variable; hindwings never with marginal brown staining; widespread distribution 9

9 Titillators widely separated or absent (Figs. 135-137); Oriental, Afrotropical, eastern Palearctic distribution (Fig. 214) ..... ***Afronurus***

- Titillators present and closely situated medially (as in Fig. 144); widespread distribution..... 10

10 Anterior margin of head distinctly produced (Fig. 131); abdomen sometimes with dorsal ridge; southern and eastern Palearctic distribution (Fig. 235, 244) 32

- Anterior margin of head only slightly produced (Fig. 130); widespread distribution 11

11 Penes with ventral spines (as in Figs. 144, 163); widespread distribution 12

- Penes without ventral spines 29

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12 Titillators thickened, spindle shaped, and usually denticulate apically (Figs. 163-164); Holarctic and Oriental distribution (Fig. 234)..... ***Nixe***

- Titillators slender (Figs. 144, 147, 160); widespread distribution.....13

13 Penes with dorsolateral spines large and distinctly projected dorsally (Figs. 146, 160); Holarctic distribution 28

- Penes with dorsolateral spines absent or small and only slightly projected dorsally; (Figs. 144, 145, 147); Holarctic, northern Neotropical, Oriental, Afrotropical distribution.....14

14 Crossveins of forewings usually reduced in number and bordered with dark staining (Fig 178); femora usually with distinct black spots (Fig. 126); tibiae usually with three dark bands (Fig. 126); Afrotropical, Oriental distribution (Fig. 221)..... ***Compsoneuria***

- Crossveins well developed and not surrounded by dark staining (Fig. 183); femora without distinct black spots; tibiae without 3 dark bands; Holarctic, northern Neotropical, Oriental distribution (Fig. 225) ..... ***Ecdyonurus, in part***

15 Mesonotum with lateroparapsidal sutures strongly bent laterally (Fig. 116); Holarctic, Oriental, northern Neotropical distribution 26

- Mesonotum with lateroparapsidal sutures not bent laterally (Fig. 117); Holarctic, northern Neotropical distribution 16

16 Stigmatic area of forewings divided in two by longitudinal vein between costa and subcosta, usually with numerous small cellules (Fig. 179); segment 1 of foretarsi 2/3-7/8 length of segment 2; eastern Palearctic, western Nearctic distribution (Fig. 219)..... ***Cinygma***

- Stigmatic area of forewings not divided into two rows of cellules (as in Figs. 185, 189); segment 1 of foretarsi usually less than 2/3 length of segment 1; Holarctic, northern Neotropical distribution 17

17 Western Hemisphere 18

- Eastern Hemisphere.....23

18 Penes usually with large spines laterally (Fig. 171); forewings with two or three crossveins below bullae between veins R_1 and R_2 connected or nearly connected by black staining (Fig.193); central and eastern Nearctic distribution (Fig. 241)..... ***Stenacron***

- Penes without large spines laterally (minute spines may be present); crossveins below bullae never as above; Nearctic, northern Neotropical distribution 19

19 Penes 'L' shaped, with angle between medial and apical margins approximately 90° (Fig. 161), or somewhat subquadrate (similar in shape to Fig. 162, but with slender titillators and pair of spines on dorsal surface); Nearctic, northern Neotropical distribution 20

- Penes variable, but never 'L' shaped or described as above (as in Figs. 155-157, 162, 167); Nearctic distribtution 21

20 Abdominal terga 3-8 each with median dark spot and pair of transverse black lines along posterior margin (Fig. 195); forewings with distinct cluster of crossveins in first three interspaces below bullae (Fig. 191); eastern and central Nearctic distribution (Fig. 242) ..... ***Stenonema***

- Abdominal terga variable, but never as above; forewings variable; widespread Nearctic and northern Neotropical distribution (Fig. 232)..... ***Maccaffertium***

21 Penes somewhat subquadrate, titillators thickened (Fig. 162); distribution as in Fig. 233..... ..... ***Macdunnoa***

- Penes variable, usually subquadrate or apically divergent and with large dorsolateral spines (Figs. 155-157, 167) 22

22 Dorsolateral spines present, penes variable in shape (Figs. 155-157)..... ***Heptagenia, in part***

- Dorsolateral spines absent (Fig. 167) ..... ***Raptoheptagenia***

23 Oriental distribution (Fig. 245); forewings with violet staining..... ***Trichogenia***

- Palearctic distribution; forewings never with violet staining 24

24 Base of penes with small spines laterally (Fig. 159); prosternum without distinct longitudinal keel ..... ***Kageronia***

- Base of penes never with small spines laterally; prosternum with longitudinal keel (as in Figs. 122, 123) 25

25 Penes with V-shaped emargination apically, nearly contiguous medially, and with well-developed dorsomedial spines; small brown dot near the midpoint of femora; western Palearctic distribution (Fig. 222) ..... ***Dacnogenia***

- Not with above combination of characters; eastern and western Palearctic (Fig. 228) ..... ***Heptagenia, in part***

26 Penes widely separated and apically broad, median titillators present (arising from median part of penes) and bent laterally, ventral titillators absent (Fig. 165); southeastern Oriental distribution (Fig. 236) ..... ***Paegniodes***

- Penes variable, but never as above; ventral titillators usually present; Holarctic, northern Neotropical, Oriental distribution 27

27 Median titillators absent (Figs. 168-170) ..... ***Rhithrogena***

- Median titillators present (Figs. 140-143) ..... ***Cinygmula***

28 Eyes contiguous or nearly contiguous dorsally; Palearctic distribution (Fig. 224) ..... ***Ecdyogymnurus***

- Eyes separated dorsally by width greater than diameter of median ocellus; Nearctic distribution (Fig. 231) ..... ***Leucrocuta***

29 Western and southern Palearctic distribution (Fig. 226); penes tear-drop shaped, lobes narrowly seperated for most of length (Fig. 149); hindtarsi < 0.5X length of hindtibiae; apical and lateral sclerite of penes largely contiguous such that no groove is present between sclerites apicolaterally (Fig. 149) ..... ***Electrogena***

- Oriental distribution; penes not tear-drop shaped or only slightly so and contiguous medially (Figs. 138, 166, 172); hindtarsi ≥ 0.5X length of hindtibiae; apical sclerite either absent or distinct from lateral sclerite (Figs. 138, 166, 172) 30

30 Penes with apical sclerites distinctly separate from lateral sclerites (Fig. 166); hindtarsi 0.5X length of hindtibiae; southern China distribution (Fig. 237) ..... ***Parafronurus***

- Penes without apical sclerites (Figs. 138, 172); hindtarsi usually greater than 0.5X length of hindtibiae; Oriental distribution (Figs. 216, 243) 31

31 Forewings with red staining between costa and subcosta; penes without distinct lateral sclerites and not expanded apicolaterally (Fig. 138); southeast Asia distribution (Fig. 216) ..... ***Asionurus***

- Forewings with brown or no staining between costa and subcosta; penes with distinct lateral sclerites and expanded apicolaterally (Fig. 172); widespread Oriental distribution (Fig. 243) ..... ***Thalerosphyrus***

32 Far east Russia, Japan, Korea (Fig. 244) ..... ***Thamnodontus***

- Southern eastern Palearctic, including Korea (Fig. 235) ..... ***Notacanthurus***

Key to the Genera of Heptageniidae: Female Adults

1 Mesonotum without apparent transverse suture (Fig. 114) 13

- Mesonotum with transverse suture (Fig. 115) 2

2 Medial depression of furcasternum of mesothorax narrowed anteriorly (as in Fig. 119) 3

- Medial depression of furcasternum of mesothorax subparallel or slightly divergent anteriorly (as in Fig. 118) 14

3. Prosternum with distinct longitudinal and transverse prosternal crests (Fig. 122-123) 4

- Prosternum evenly rounded or with only slight transverse crest (Fig. 121) 16

4. Forewings with distinct black spot joining or nearly joining some crossveins below bullae between R_1 and R_2 (Fig. 193); eggs with large coiled thread around each pole (Fig. 112) ..... ***Stenacron***

- Forewings never with distinct black spot joining or nearly joining some crossveins below bullae; eggs with or without scattered knob-terminated coiled threads and/or tubercles, never with large coiled thread around each pole 5

5 Forewings with crossveins crowded in first 2-3 interspaces below bullae (Fig. 191); posterior margins of abdominal terga with median black dot and pair of transverse dashes (Fig. 195)..... ***Stenonema***

- Forewings with crossveins below bullae variable; abdomen variable, but never as above 6

6 Forewings with crossveins in first 3-6 interspaces below bullae crowded (Fig. 188-189) or hindwings with brown margins (as in Fig. 190); sperm guide of eggs formed by elongate break in adhesive layer (Fig. 111); knob-terminated coiled threads absent on eggs ..... ***Maccaffertium, in part***

- Forewings with crossveins in interspaces below bullae not crowded (Fig. 185); eggs variable..... 7

7 Abdomen with distinct posterolateral spines on segments 2-9 (Fig. 206); subanal plate deeply cleft (Fig. 206); abdominal terga with pair of triangular brown markings on posterior margins (Fig. 199) ..... ***Heptagenia culacantha***

- Abdomen without posterolateral spines or with small spines only on terminal segments; subanal plate variable; abdominal terga variable 8

8 Head capsule greatly expanded anteriorly, extending for length greater than length of eye (Fig. 132); abdomen pale or tan colored with pale median marks; basal crossveins in forewings brown or black (Fig. 187); subgenital plate rounded (Fig. 205)..... ***Raptoheptagenia***

- Head capsule not extended for length greater than length of eye (Fig. 133-134); abdomen variable, but if tan with pale median markings, then basal crossveins uncolored and poorly developed (Fig. 186) and subgenital plate truncate (Fig. 207) 9

9 Abdominal terga tan, light brown or reddish dorsally, usually with pale median markings (Fig. 200, 202); if tan or light brown with pale markings, then basal crossveins between costa and subcosta poorly developed and colorless (Fig. 186); subgenital plate truncate or evenly rounded (Fig. 207-208) ..... ***Heptagenia, in part***

- Without the above combination of characteristics..... 10

10 Abdominal terga with large reddish brown triangles posterolaterally (Fig. 198) or black sublateral oblique lines (Fig. 201) ..... ***Heptagenia, in part***

- Abdomen variable, but as above 11

11 Abdominal terga with any combination of spiracular dark spots, median longitudinal dark stripe, wide brown band on posterior margins, or thin black transverse line slightly anterior of posterior margins (line sometimes broken medially)(Fig. 204) ..... ***Maccaffertium, in part***

- Abdomen without dark markings laterally or medially, posterior margin sometimes darkly colored... 12

12 a) Posterior margins of abdominal terga either uncolored or with thin black transverse line; caudal filaments white, articulations usually not darkened; eggs with knob-terminated coiled threads (Fig. 113), sperm guides oval..... ***Heptagenia, in part***

- b) Posterior margins of abdominal terga with thin black line or uncolored (Fig. 204); caudal filaments with or without articulations darkened; eggs without knob-terminated coiled threads, sperm guides formed by elongate break in adhesive layer (as in Fig. 111), chorion without longitudinal grooves at poles ..... ***Maccaffertium, in part***

- c) Abdominal terga without any dark markings; eggs without knob-terminated coiled threads, sperm guides small, crescent shaped; chorion with deep grooves near poles ..... ***Macdunnoa***

13 Forewings with basal crossveins well developed (Fig. 197); western North America (Fig. 229) ..... ***Ironodes***

- Forewings with basal crossveins poorly developed (Fig. 175); widespread (Fig. 227)..... ***Epeorus***

14 Forewings with black or brown staining around some crossveins (Fig. 184) or abdomen hyaline with large, dark brown lateral markings and black crossveins in the forewings ..... ***Leucrocuta***

- Forewings without brown staining around crossveins (Fig. 183)..... 15

15 Eggs with meshlike ridges surrounding knob-terminated coiled threads (Fig. 110); subgenital plate with marginal lip (Fig. 209-210); abdominal terga often reddish brown medially, although may be reddish brown laterally or without dark markings; mostly found east of Rocky Mountains (Fig. 234).... ..... ***Nixe***

- Eggs with only tubercles or longitudinal ridges, never meshlike (Fig. 108, 109); abdominal terga often reddish brown laterally; if abdomen completely pale, then apical margin of subgenital plate not thickened ventrally (Fig. 211); western North America, but *E. simplicioides* also found east to Manitoba in Boreal Forest (Fig. 225) ..... ***Ecdyonurus***

16 Hindwings with very small, rounded costal process (Fig. 192); hindtibiae longer than femora 17

- Hindwings with well-developed costal process (Fig. 181); hindtibiae subequal to or shorter than femora 18

17 Anterior margin of head capsule truncate (as in Fig.129); eastern distribution (Fig. 240)..... ***Spinadis***

- Anterior margin of head capsule pointed (as in Fig. 128); western distribution (Fig. 215)..... ..... ***Anepeorus***

18 Lateral parapsidal sutures strongly bent laterally (Fig. 116); stigmatic area of forewings variable, but usually not divided into two rows cellules; widespread distribution..... 19

- Lateral parapsidal sutures not strongly bent laterally (as in Fig. 117); stigmatic area of forewings divided into two rows of cellules (Fig. 179); western distribution (Fig. 219) ..... ***Cinygma***

19 Subanal plate truncate or rounded, not distinctly emarginate (Fig. 212); stigmatic area of forewings usually with crossveins anastomosed (Fig. 182); wing membranes usually colorless, without brown staining; femora usually with dark streak (Fig. 127)..... ***Rhithrogena***

- Subanal plate distinctly emarginate (Fig. 213); stigmatic area of forewings usually without crossveins anastomosed (Fig. 180); wing membranes frequently stained yellow or brown; femora usually without dark streak ..... ***Cinygmula***

Diagnoses

Ecdyonurinae

Larval Diagnosis: All known Ecdyonurinae are easily identified by the unique scattered setae on the ventral surface of the maxillae (Figs. 49-51). Additionally, the planate mandible has a single terminal denticle (Fig. 42) and the anal margin of the lamellae of gills 1 are usually concave, giving them a banana shape, allowing them to curve over the abdomen (Fig. 88). In some genera, however, the lamellae of gills one are reduced, absent, or lack the banana shape.

Kluge (2004) indicated that the shape of the distal dentisetae on the maxillae varies among the genera (dentisetae are the thickened, enlarged setae on the medial margin of the maxillae posterior to the incisors and between the dorsal and ventral rows of setae). The shape of the setae on the ventral surface of the maxillae parallels differences in the dentisetae, but is easier to observe as there are no other setae obscuring them. Those groups Kluge (2004) indicated as having a simple distal dentisetae have fimbriate setae on the ventral surface (Fig. 51), whereas the groups with branched distal dentisetae have simple setae on the ventral surface (Fig. 49). Because they are more easily observed, in the following diagnoses we only refer to the shape of the ventral setae.

Adult Diagnosis: Adults of Ecdyonurinae can be identified by having the medial depression of mesothoracic furcasternum parallel sided or divergent anteriorly (Fig. 118). The shape of the penes in Ecdyonurinae varies, but are generally distinctive in having both the lateral and apical sclerites curve over the dorsal surface.

Distribution: Holarctic; northern Neotropical; Afrotroptical; Oriental.

Afronurus

Figures: 1, 30, 66, 76, 80, 100, 135-137, 214

Larval Diagnosis: The combination of a slightly thickened anterior margin of the head capsule (Fig. 30), simple scattered setae on the ventral surface of the maxillae (as in Fig. 49), the absence of whorls of long, fine setae on the caudal filaments (Fig. 100), the absence of a dorsal ridge

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on the abdominal terga, and the presence of two rows of long, fine setae on the mid- and hindtibiae (Fig. 76) should differentiate larvae of *Afronurus* from other Ecdyonruinae genera. Additionally, mature female larvae can be identified by the presence of large, equatorial knob terminated coiled threads on the eggs. Larvae are most similar to those of *Parafronurus* and *Darthus* but lack whorls of fine setae on the caudal filaments and a dorsal abdominal ridge. At least one species of *Afronurus* has long posterolateral abdominal spines, similar to those of *Thalerosphyrus*, but otherwise the two should be readily differentiated by the other characteristics listed above.

Adult Diagnosis: Adult male *Afronurus* differ from all other known Ecdyonurinae males by having either no titillators or titillators that are widely separated (Figs. 135-137).

Distribution: Afrotroptical; Oriental; southern Palearctic (Fig. 214).

Asionurus

Figures: 3, 42, 59, 77, 85-86, 138, 216

Larval Diagnosis: Larvae of *Asionurus* are easily differentiated from those of all other Ecdyonurinae genera by the extremely long, narrow lamellae on gills 7 (Fig. 86). The acutely pointed posterolateral extensions of the superlinguae (Fig. 59) will also separate *Asionurus* from all other genera except *Atopopus*. The pectinate setae present on the tarsi of *Asionurus* (Fig. 77) appear to be unique. Larvae are superficially similar to those of *Compsoneuria* in their overall appearance and the presence of apically pointed, narrow glossae and convex anal margins on the lamellae of gills 1, but the characteristics listed above should separate the two.

Adult Diagnosis: The combination of the presence of medially situated titillators, red staining between the costa and subcosta of the forewings, and the lack of distinct lateral sclerites on the penes (Fig. 138) should identify males of *Asionurus.*

Distribution: Southeast Asia (Fig. 216).

Atopopus

Figures: 4, 31, 105, 125, 177, 217

Larval Diagnosis: *Atopopus* are distinctive in appearance because the head capsule is emarginate posterolaterally (as in Fig. 37) and has an extremely thickened anterior margin (Fig. 31), the lamellae on gills 1 are minute, and the posterolateral spines of the abdomen have a wide base (Fig. 105). *Atopopus* is most similar to, and most closely related to, *Thalerosphyrus*, but all species of *Thalerosphyrus* have well developed lamellae on gills 1. Additionally, most species of *Thalerosphyrus* have long, acutely pointed posterolateral spines on the abdominal segments and sharply pointed supracoxal spurs.

Adult Diagnosis: *Atopopus* males are distinguished by having hindtarsi ~1.5X the length of the hindtibiae (Fig. 125) and by having both the fore- and hindwings with brown staining near the margins (Fig. 177). Other genera may have brown staining between the costa and subcosta or around crossveins, but no other Ecdyonurinae genus has brown staining on the hindwings.

Distribution: Borneo and Philippines (Fig. 217).

Compsoneuria

Figures: 6, 34, 49, 68, 118, 126, 144-145, 178, 221

Larval Diagnosis: Larvae of *Compsoneuria* are distinct from all other Ecdyonurinae genera by having the combination of long, sharply pointed supracoxal spurs (as in Fig. 79), black spotting on the head capsule and femora, and narrow, apically pointed glossae (Fig. 68). *Leucrocuta* larvae also have black spotting on the head capsule but the glossae are subquadrate rather than narrow and apically pointed, and the setae on the ventral surface of the maxillae are fimbriate, whereas those of *Compsonuria* are simple (Fig. 49). Additionally, *Compsonueuria* is found in the Afrotropical and Oriental realms, whereas *Leucrocuta* occurs in the Nearctic realms.

Adult Diagnosis: The presence of ventral spines on the penes (Fig. 144) distinguishes *Compsoneuria* males from all other Ecdyonurinae genera except the *simplicioides* group of *Ecdyonurus*, *Nixe*, *Leucrocuta*, and *Ecdyogymnurus*. *Compsoneuria* is distinguished from these genera by the presence of black spotting on the femora (Fig. 126), a reduction in the number of crossveins in the forewings (Fig. 178), and an Oriental and Afrotropical distribution. Most males of *Compsoneuria* have three dark bands on the tibiae (Fig. 126), although these are absent in several Afrotropical species.

Distribution: Afrotropical; Oriental (Fig. 221).

Darthus

Figures: 7, 50, 61, 69, 78, 87, 223

Larval Diagnosis: Larvae of *Darthus* differ from all other Ecdyonurinae genera except *Notacanthurus* by the presence of a dorsal ridge on the abdomen (Fig. 7). *Darthus* differs from *Notacanthurus* by the slightly thickened anterior margin of the head capsule (as in Fig. 30) and the sickle shaped gill lamellae on segments 2-7 (Fig. 87). Additionally, *Darthus* is known only from the

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island of Borneo, whereas *Notacanthurus* is not known from southeast Asia.
Adult Diagnosis: Unknown.
Distribution: Borneo (Fig. 223).

Ecdyogymnurus
Figure: 146, 224

Larval Diagnosis: Larvae of *Edcyogymnurus* differ from all other genera of Ecdyonurinae except *Leucrocuta* by the combination of having fimbriate setae on the ventral surface of the maxillae (as in Fig. 51) and no interfacing setae on the caudal filaments (as in Fig. 101). Female larvae of *Ecdyogymnurus* and *Leucrocuta* cannot be differentiated morphologically, but mature male larvae of *Ecdyogymnurus* have well-developed eyes, separated by a distance less than the width of the median ocellus, whereas male larvae of *Leucrocuta* have small eyes that are widely separated. Also, *Leucrocuta is* exclusively Nearctic, whereas *Ecdyogymnurus* is only found in the eastern Palearctic.

Adult Diagnosis: In males the combination of ventral spines, well-developed dorsolateral spines on the penes (Fig. 146), and eyes separated by a distance less than the width of the median ocellus will differentiate *Ecdyogymnurus* from all other Ecdyonurinae genera.
Distribution: Eastern Palaearctic (Fig. 224).

Ecdyonurus
Figures: 8, 33, 44-45, 51, 108-109, 147-148, 183, 211, 225

Larval Diagnosis: Larvae of all *Ecdyonurus*, except the *simplicioides* species group may be diagnosed by the combination of the presence of interfacing setae on the caudal filaments (as in Fig. 102) and large, posteriorly projecting pronotal extensions (Fig. 8). Other Ecdyonurinae genera that may posses pronotal extenstions (i.e. *Thalerosphyrus*) differ in having simple scattered setae on the ventral surface of the maxillae (as in Fig. 49), as opposed to fimbriate setae (as in Fig. 51), and they lack interfacing setae on the caudal filaments. Larvae of the *simplicioides* group cannot be differentiated from those of *Nixe* except on a species by species basis. In North America, the *simplicioides* group has a western distribution, whereas *Nixe* are mostly eastern. In central North America, *Nixe* and *E. simplicioides* (McDunnough) are sympatric but *E. simplicioides* differs from *Nixe* in having the pair of pale spots on the anterior margin of the head capsule separated by a distance subequal to or slightly greater than the distance between the bases of the antennae (Fig. 33), whereas the pale spots in sympatric *Nixe* are closer together than the bases of the antennae (Fig. 32). *Nixe kennedyi* (McDunnough) occurs in western North America, but the larvae are unknown. In mature female larvae of Nearctic *Ecdyonurus*, the eggs have scattered knob terminated coiled threads with either scattered tubercles (Fig. 109) or ridges covered with small granules (Fig. 108). In contrast, all known *Nixe* have a distinctive meshlike pattern of ridges surrounding the knob terminated coiled threads (Fig. 110).

Adult Diagnosis: Males of *Ecdyonurus* typically have penes that are somewhat triangular in shape with well-developed lateral sclerites and apical sclerites that extend over the medial surface (Fig. 147). Dorsolateral spines are absent or minute and ventral spines are absent on the penes. Males of the *simplicioides* group differ in that the penes have ventral spines (as in Figs. 144, 163), small dorsolateral spines, and less developed sclerites. Males of the *simplicioides* group are similar to those of *Nixe*, but differ in that the titillators are not thickened and denticulate. Males of *Leucrocuta* and *Ecdyogymnurus* are also similar to the *simplicioides* group but differ in having well-developed dorsolateral spines and apical sclerites that distinctly extend dorsally.

North American females can be differentiated from other Ecdyonurinae by the combination of the absence of dark staining on the wings and by having eggs with only small tubercles or ridges on the chorion (Figs. 108-109) that are never arranged in a mesh-like pattern.
Distribution: Holarctic; Oriental (Fig. 225).

Electrogena
Figure: 149, 226

Larval Diagnosis: There are no unique characteristics for *Electrogena* larvae. They can be identified, however, by the combination of having simple setae on the ventral surface of the maxillae (as in Fig. 49), only one row of long, fine setae on the mid- and hindtibiae, rounded supracoxal sclerites (as in Fig. 80), an unthickened anterior margin of the head capsule (as in Fig. 34), no dorsal ridge on the abdomen, tarsal claws with at least one denticle, well-developed lamellae on all gills, gills 1 with a concave anal margin (as in Fig. 88), and rounded posterolateral projections on the superlinguae. Larvae of *Thamnodontus* are similar, but the two genera are not sympatric.

Adult Diagnosis: The teardrop shaped penes with partially fused apical and lateral sclerites (Fig. 149) will distinguish *Electrogena* from all other Ecdyonurinae genera.
Distribution: Western and southern Palearctic (Fig. 226).

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Leucrocuta

Figures: 13-14, 101, 160, 184, 231

Larval Diagnosis: Larvae of *Leucrocuta* can be distinguished from all other Ecdyonurinae genera except *Ecdyogymnurus* by the combination of having fimbriate setae on the ventral surface of the maxillae (as in Fig. 51) and no interfacing setae on the caudal filaments (Fig. 101). *Leucrocuta* is Nearctic, and *Ecdyogymnurus* is Palearctic. Additionally, mature male larvae of *Leucrocuta* have widely separated eyes, whereas those of male *Ecdyogymnurus* are separated by a distance less than the width of the median ocellus. The presence of black spotting on the head capsule of *Leucrocuta* larvae is not a good characteristic for separating *Leucrocuta* from *Nixe* as nearly all North American *Nixe* have black spotting on the head capsule, although it is generally not as well developed as it in *Leucrocuta*, and larvae of some *Leucrocuta* lack the black spots.

Adult Diagnosis: The combination of the presence of ventral spines (as in Fig. 144) and large dorsolateral projections on the penes (Fig. 160, as in Fig. 146) and eyes separated by a distince much greater than the width of the medial ocellus will distinguish males of *Leucrocuta*. Females of all species except *L. umbratica* (McDunnough) differ from other North American Ecdyonurinae by having dark staining around the crossveins of the forewings (Fig. 184). Although we have not examined specimens, females of *L. umbratica* should differ from those of other Ecdyonurinae by having hyaline abdominal terga with large, very dark sublateral markings and black crossveins in the forewings.

Distribution: Nearctic (Fig. 231).

Nixe

Figures: 16-17, 32, 43, 102, 110, 163-164, 209-210, 234

Larval Diagnosis: Larvae of *Nixe* are differentiated from those of other Ecdyonurinae genera, except the *simplicioides* group of *Ecdyonurus,* by the presence of interfacing setae on the caudal filaments (Fig. 102), fimbriate setae on the ventral surface of the maxillae (as in Fig. 51), and the absence of posterolateral projections on the pronotum (Fig. 16). In North America, *Nixe* can be differentiated from larvae of *Ecdyonurus simplicioides*, which is sympatric with *Nixe* in the central part of the continent, by having the median pair of pale spots on the anterior margin of the head capsule separated by a distance less than the distance between the bases of the antennae (Fig. 35).

Adult Diagnosis: Males of *Nixe* are characterized by having ventral spines on the penes (Fig. 163), titillators that are robust, spindle shaped and usually apically denticulate (Fig. 164), and eyes that are contiguous dorsally or separated by distance less than diameter of median ocellus. The *simplicioides* group of *Ecdyonurus* are similar but have slender titillators. Females of North American *Nixe* differ from other Ecdyonurinae by having eggs with a distinct mesh-like pattern of ridges surrounding the knob-terminated coiled threads (Fig. 110). The subgenital plate of females has the posterior margin thickened, forming a ridge (Figs. 209-210), which is absent in *Ecdyonurus simplicioides*, but present in *E. criddlei*.

Distribution: Holarctic; Oriental (Fig. 234).

Notacanthurus

Figures: 18, 131, 235

Larval Diagnosis: Larvae of *Notacanthurus* are easily identified by having a dorsal median abdominal ridge and well-developted gill lamellae (Fig. 18). Larvae of the Indian species *N. edentatus* Braasch do not have a well-developed dorsal ridge on the abdomen (Braasch, 1986), so they are similar to *Electrogena* but can be differentiated from by the absence of denticles on the claws.

Adult Diagnosis: Adults of *Notacanthurus* have a greatly expanded anterior margin of head capsule (Fig. 131), a characteristic not found in any other Ecdyonurinae genus except *Thamnodontus*. In Korea, a species of *Notacanthurus* is sympatric with *Thamnodontus* but the adults are unknown so differentiating characters cannot be specified.

Distribution: Southern Eastern Palearctic (Fig. 235).

Parafronurus

Figures: 20, 103, 166, 237

Larval Diagnosis: The combination of having a slightly thickened anterior margin of the head capsule (as in Fig. 30), two rows of long setae on the mid- and hindtibiae (as in Figs. 76, 78), and whorls of fine setae on the articulations of the caudal filaments (Fig. 103) will distinguish *Parafronurus* from all other Ecdyonurinae genera. Larvae of *Parafronurus* are similar to those of *Afronurus* but, in addition to the above combination of characters, the eggs from mature female larvae of *Parafronurus* have scattered knob terminated coiled threads with scattered granules, whereas those of *Afronurus* have large, equatorial knob terminated coiled threads.

Adult Diagnosis: *Parafronurus* males may be distinguished from those of other Ecdyonurinae genera by the combination of having penes (Fig.

166) that lack both ventral and dorsolateral spines, have well-developed titillators that are located medially, the presence of both apical and lateral sclerites, and hindtarsi that are 0.5X the length of the hindtibiae.
Distribution: China (Fig. 237).

Thalerosphyrus
Figures: 28, 36-37, 73, 79, 106, 172, 243

Larval Diagnosis: The combination of having a distinctly thickened anterior margin of the head capsule (Figs. 36-37), long posterolateral spines on the abdomen (Fig. 106), acutely pointed supracoxal spurs (Fig. 79), and well-developed lamellae on gills 1 will distinguish *Thalerosphyrus* from other Ecdyonurinae genera. Larvae of *Thalerosphyrus* are most similar to larvae of *Atopopus*. *Atopopus* differs in having rounded supracoxal spurs and minute lamellae on gills 1. Larvae of *Compsoneuria* had previously been confused with those of *Thalerosphyrus* because they also have acutely pointed supracoxal spurs, but *Compsoneuria* larvae do not have a thickened anterior margin of the head capsule or long posterolateral spines on the abdomen, and have narrowed glossae and black spotting on the head capsule and femora. Unlike other species in *Thalerosphyrus*, larvae of the type species, *T. determinatus* (Walker) have only slightly produced supracoxal sclerites, although they are still acutely pointed. Wang and McCafferty (2004) noted that Ulmer (1939) possibly misassociated the larvae and adults of *T. determinatus* but we have recently obtained reared specimens that show Ulmer's (1939) association was correct.

Adult Diagnosis: Males of *Thalerosphyrus* are unique among the Ecdyonurinae in lacking apical sclerites on the penes (Fig. 172).
Distribution: Oriental (Fig. 243).

Thamnodontus
Figure: 244

Larval Diagnosis: We do not know of any unique diagnostic characters for larvae of *Thamnodontus*. They can be identified, however, by the combination of having simple setae on the ventral surface of the maxillae (as in Fig. 49), only one row of long, fine setae on the mid- and hindtibiae, rounded supracoxal sclerites (as in Fig. 80), an unthickened anterior margin of the head capsule (as in Fig. 34), no dorsal ridge on the abdomen, tarsal claws with at least one denticle, well-developed lamellae on all gills, gills 1 with a concave anal margin (as in Fig. 88), and rounded posterolateral projections on the superlinguae. Larvae of *Electrogena* are similar, but the two genera are not sympatric.

Adult Diagnosis: Adults of *Thamnodontus* have anteriorly expanded head capsules, as is found in *Notacanthurus*. The two genera are not sympatric except in Korea. The Korean species of *Notacanthurus* is not known in the adult stage, so differentiating characters cannot be provided at this time.
Distribution: Palearctic in far eastern Russia, Korea, and Japan (Fig. 244).

Heptageniinae

Larval Diagnosis: The combination of having a row of setae on the ventral surface of maxillae (Fig. 58) and forefemora without a dorsal projection (Fig. 82) will distinguish larvae of Heptageniinae from the Ecdyonurinae and the Rhithrogeninae.

Adult Diagnosis: Adults of Heptageniinae are characterized by the presence of distinct longitudinal and transverse ridges on the prosternum (Figs. 122-123) and the medial depression of the mesothoracic furcasternum is convergent anteriorly (as in Fig. 119).

Dacnogenia
Figures: 39, 60, 90, 222

Larval Diagnosis: The short, wide mandibular incisors (Fig. 39) of *Dacnogenia* are unique in the Heptageniinae. Additionally, the superlinguae are much longer than the lingua (Fig. 60) and the gill lamellae are narrow (Fig. 90).

Diagnosis: Males of *Dacnogenia* cannot be separated from those of *Heptagenia* except on a species by species basis. In the Palearctic, where both genera occur, the combination of having V-shaped penes that are nearly contiguous medially, well-developed dorsomedial spines, and a small brown dot near the midpoint of the femora will separate *Dacnogenia* from most *Heptagenia*.
Distribution: Palearctic (Fig. 222).

Heptagenia
Figures: 2, 41, 46, 62, 71, 84, 92, 113, 133-134, 155-157, 185-186, 198-202, 206-208, 228

Larval Diagnosis: Larvae of *Heptagenia* are characterized by having gills that are inserted laterally, gill lamellae that are somewhat rounded (only rarely slender) with a marginal anal rib (Fig. 92), fibrils present on gills 1-7, a lyre shaped hypopharynx (Fig. 62), and no fan shaped robust setae on the tergum. The shape of the hypopharynx will separate larvae of *Heptagenia* from all other Heptageniinae except the southeast Asian genus *Trichogenia*. *Heptagenia* can be differentiated from

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Trichogenia by the absence of fan shaped robust setae on the terga, and Holarctic distribution.

Adult Diagnosis: Males of *Heptagenia* are characterized by having well-developed dorsolateral spines on the penes, no lateral spines on the base of the penes, and relatively slender titillators. The penes of *Heptagenia* are variable in shape (Figs. 155-157), but they are never 'L' shaped, as in *Stenonema* and *Maccaffertium*, or subquadrate with robust titillators, as in *Macdunnoa*. Males of *Dacnogenia* and some *Heptagenia* are similar and can only be separated on a species by species basis. In the Palearctic, where both genera occur, no *Heptagenia* will have the combination of medially contiguous penes lobes with a V shaped emargination apically, and a small brown dot near the midpoint of the femora. North American females cannot always be distinguished from those of *Maccaffertium* and *Macdunnoa*, except by the presence of knob-terminated coiled threads on the eggs (Fig. 113).
Distribution: Holarctic (Fig. 228).

Kageronia
Figures: 63, 83, 91, 159, 230

Larval Diagnosis: Larvae of *Kageronia* are diagnosed by having serrated tarsal claws (Fig. 83). Additional diagnostic characteristics include pointed gill lamellae (Fig. 91), gills 7 without fibrils, and marginal anal and costal ribs on the gill lamellae (Fig. 91).

Adult Diagnosis: The lack of a distinct longitudinal ridge on the prosternum will separate male and female adults of *Kageronia* from all other Heptageniinae. Adults of *K. orbiticola* (Kluge) are similar to those of *Arthroplea* Bengtsson (Arthropleidae) in having an unforked vein MA in the hindwings.
Distribution: Palearctic (Fig. 230).

Maccaffertium
Figures: 15, 54, 94-95, 117, 123, 134, 161, 188-190, 204, 232

Larval Diagnosis: Larvae of *Maccaffertium* are characterized by the combination of having long, narrow lamellae without tracheation or fibrils on gills 7 (Fig. 95) and a submarginal anal rib on gill lamellae 1-6 (Fig. 94). Furthermore, the lamellae of gills 1-6 are truncate apically and the costal rib is absent (Fig. 94).

Adult Diagnosis: The 'L' shaped penes (Fig. 161) will separate *Maccaffertium* from all other Nearctic genera except *Stenonema*. Males of *Stenonema* have a median dark spot and a pair of transverse dark lines on the posterior margin of the abdominal terga (Fig. 195), whereas the terga of *Maccaffertium* are variable, but never like those of *Stenonema* (Fig. 204). Many species have the crossveins in the first 2-6 interspaces below the bullae crowded (Fig. 189), unlike any other North American genus except *Stenonema*. The eggs differ from those of all other North American genera except *Stenonema* by having an elongate sperm guide formed by a break in the adhesive layer (as in Fig. 111).
Distribution: Nearctic (Fig. 232).

Macdunnoa
Figures: 93, 162, 233

Larval Diagnosis: The combination of submarginal anal ribs on the gill lamellae, vestigial gills 7, and minute gills 6 (Fig. 93) will differentiate *Macdunnoa* from all other Heptageniidae.

Adult Diagnosis: The combination of subquadrate penes and titillators that are thickened and abruptly narrowed apically (Fig. 162) will differentiate males of *Macdunnoa* from all other Heptageniinae genera. Females can be differentiated from those of other North American Heptageniiane by having eggs with a crescent-shaped sperm guide and longitudinal grooves near the poles.
Distribution: Nearctic (Fig. 233).

Raptoheptagenia
Figures: 21-22, 72, 132, 167, 187, 203, 205, 238

Larval Diagnosis: The ventrally inserted gills (Fig. 21) will differentiate *Raptoheptagenia* from all other Heptageniidae genera. Furthermore, it is the only three-tailed Heptageniinae with raptorial mouthparts (Fig. 72).

Adult Diagnosis: Males of *Raptoheptagenia* are differentiated from other Nearctic Heptageniinae by the 'V' shaped penes that lack dorsolateral spines (Fig. 167). Females differ from other North American genera by having a head capsule that extends beyond the anterior margin of the eyes by a distance greater than the length of the eye (Fig. 132).
Distribution: Nearctic (Fig. 238).

Stenacron
Figures: 26, 57, 64, 82, 96, 112, 171, 193, 241

Larval Diagnosis: Larvae of *Stenacron* are differentiated from all other Nearctic genera by having gill lamellae 1-6 with a submarginal anal rib and a pointed apex (Fig. 96).

Adult Diagnosis: The presence of a black spot joining two or three crossveins below the bullae of the forewings (Fig. 193) will differentiate adults of *Stenacron* from other Heptageniinae. The well-developed spines on the lateral margins of the base

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of the penes (Fig. 171) will differentiate males of *Stenacron* from all other Nearctic genera. *Stenacron carolina* (Banks) and *S. candidum* (Traver) may lack the lateral spines on the base of the penes. *Maccdunnoa* and *Maccaffertium* may have minute lateral spines, but their penes will be either subquadrate or 'L' shaped. The eggs of *Stenacron* are unique in having a large coiled thread around each pole (Fig. 112).
Distribution: Nearctic (Fig. 241).

Stenonema
Figures: 27, 97-98, 111, 191, 195, 242

Larval Diagnosis: Larvae of *Stenonema* are characterized by the combination of having long, narrow lamellae with tracheation but no fibrils on gills 7 (Fig. 98) and a submarginal anal rib on gill lamellae 1-6. Furthermore, the lamellae of gills 1-6 are rounded apically and the costal rib is absent (Fig. 97).

Adult Diagnosis: Adults of *Stenonema* are differentiated from those of other Nearctic Heptageniinae by having abdominal terga 3-8 each with a median black dot and a pair of dark transverse dashes on the posterior margin (Fig. 195).
Distribution: Nearctic (Fig. 242).

Trichogenia
Figures: 12, 40, 48, 58, 65, 107, 245

Larval Diagnosis: The fan shaped robust setae on the abdominal terga are unique to *Trichogenia* (Fig. 107). Additionally, combination of minute lamellae of gills 1, narrow, pointed lamellae of gills 2-7, and an Oriental distribution will differentiate *Trichogenia* from other Heptageniinae larvae (some Palearctic species of *Heptagenia* have gill lamellae similar to those of *Trichogenia*, but lack the fan shaped robust setae).

Adult Diagnosis: The combination of a long pair of spines on ventral surface of penes and forewings with violet coloration should differentiate males of *Trichogenia* from other Heptageniinae genera. Only one species, tentatively placed in *Trichogenia*, is known in the adult stage. Because *Trichogenia* is the only Heptageniinae genus known from southeast Asia, identification should not be a problem.
Distribution: Southeast Asia (Fig. 245).

Rhithrogeninae

Larval Diagnosis: Larvae of Rhithrogeninae are identified by having the apices of the forefemora with a dorsal process that is projected and is narrower than the ventral process (as in Fig. 81). The mouthparts tend to be adapted for scraping diatoms as seen by the enlarged maxillary palps in most genera (as in Fig. 52), although in some less common genera the mouthparts are adapted for carnivory. Some Rhithrogeninae have a vestigial median caudal filament (as in Fig. 9).

Adult Diagnosis: Adults of Rhithrogeninae are differentiated from those of Ecdyonurinae by having the medial depression of mesothoracic furcasternum convergent anteriorly (as in Fig. 119). The rounded prosternum that lacks a transverse and longitudinal ridge will differentiate adults from those of Heptageniinae (Fig. 121).

Anepeorus
Figures: 11, 75, 128, 215

Larval Diagnosis: Larvae of *Anepeorus* are identified by the combination of having a vestigial median caudal filament (Fig. 11), interfacing setae on the caudal filaments (Fig. 11), mouthparts modified for predation, legs with numerous long, fine setae (Fig. 75), and no well-developed tubercles on the head capsule.

Adult Diagnosis: The combination of the presence of a transverse suture on the mesonotum (as in Fig. 115), foretarsi that are shorter than the foretibiae, hindtibiae that are shorter than the hindfemora, and a distinctly produced head capsule (Fig. 128) will differentiate *Anepeorus* from all other Nearctic Rhithrogeninae. The females of *Anepeorus* are unknown, but the produced head capsule, in combination with a rounded costal process on the hindwings (as in Fig. 192), should be present in this stage.
Distribution: Western Nearctic (Fig. 215).

Bleptus
Figures: 35, 62, 120, 139, 173-174, 196, 218

Larval Diagnosis: The combination of a vestigial median caudal filament (as in Fig. 9), absence of a dense fringe of setae on the anterior margin of the head capsule (Fig. 35), and reduced lamellae on gills 1 will differentiate larvae of *Bleptus* from other Rhithrogeninae.

Adult Diagnosis: The presence of a transverse ridge on the prosternum (Fig. 120), long, narrow hindwings (Fig. 174), and the absence of a transverse suture on the mesonotum (as in Fig. 114) will differentiate adults of *Bleptus* from all other Rhithrogeninae genera. Additionally, the bases of the forceps are expanded so that they meet medially (Fig. 139), and segment 1 of the foretarsi is longer than second 2 (as in Fig. 124).
Distribution: Japan, Korea (Fig. 218).

Cinygma
Figures: 5, 47, 74, 179, 219

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Larval Diagnosis: Larvae of *Cinygma* can be identified by a labrum is that longer than wide (Fig. 47) and glossae that are narrow at the base and expanded distally (Fig. 74).

Adult Diagnosis: The presence of a transverse suture on the mesonotum (as in Fig. 115), lateroparapsidal sutures that are not distinctly bent laterally (as in Fig. 117), and two rows of cellules in the stigmatic region of the forewings (Fig. 179) will differentiate adults of *Cinygma* from all other Rhithrogeninae genera. Many *Rhithrogena* and *Cinygmula* have anastomosed veins in the stigmatic region that resemble the two rows of cellules in *Cinygma*, but differ in having the lateroparapsidal sutures of the mesothorax bent laterally.

Distribution: Western Nearctic; eastern Palearctic (Fig. 219).

Cingymula

Figures: 81, 140-143, 180-181, 213, 220

Larval Diagnosis: Larvae of *Cinygmula* can be identified by the combination of having the anterior margin of head capsule emarginate, lacking interfacing setae on the caudal filaments, and lacking a ventral friction disk formed by the gill lamellae. In most species, the maxillary palps protrude beyond the lateral margins of the head capsule in dorsal view. Many *Rhithrogena* larvae also have a median excavation on the anterior margin of the head capsule, but differ from larvae of *Cinygmula* in having a ventral friction disk formed by the gill lamellae.

Adult Diagnosis: Males of *Cinygmula* are differentiated from other Rhithrogeninae by the combination of having a transverse suture on the mesonotum (as in Fig. 115), median titillators on the penes that are not strongly bent laterally (Figs. 140-143), and lateroparapsidal sutures that are bent laterally (as in Fig. 116). The laterally bent lateroparapsidal sutures distinguish North American females of *Cinymula* from all othe Rhithrogeninae except *Rhithrogena*, but they can be differentiated from that genus by the distinctly emarginate subanal plate (Fig. 213).

Distribution: Holarctic; Oriental (Fig. 220).

Epeorus

Figures: 9-10, 38, 52, 70, 104, 114, 119, 124, 150-154, 175-176, 194, 227

Larval Diagnosis: Larvae of *Epeorus* are identified by the enlarged incisors on the galealaciniae (Fig. 52), the vestigial median caudal filament (Fig. 9), and the dense row of setae on the anterior margin of the head capsule (Fig. 38).

Adult Diagnosis: The combination of the absence of a transverse suture on the mesonotum (Fig. 114), segment 1 of the foretarsi equal to or longer than segment 2 (Fig. 124), and relatively broad hindwings without distal dark staining (Fig. 176) will differentiate adults of *Epeorus* from other Rhithrogeninae genera, except the Nearctic *Ironodes*. Some Nearctic species of *Epeorus* have penes that are separated nearly to the base and lack titillators (Fig. 152), such as in *Ironodes*, but can be differentiated by the poorly developed basal crossveins in the forewings (Fig. 175) and the reddish abdominal terga with pale median spots (Fig. 194).

Distribution: Holarctic; Oriental; Neotropical south to northern Columbia (Fig. 227).

Ironodes

Figures: 29, 53, 99, 158, 197, 229

Larval Diagnosis: Larvae of *Ironodes* are differentiated from other Nearctic Rhithrogeninae by the combination of a vestigial median caudal filament (Fig. 29), small lamellae on gills 1 (Fig. 99), a dense fringe of setae on the anterior margin of the head capsule (as in Fig. 38), and incisors on the galealaciniae that are not greatly enlarged (Fig. 53). Additionally, gills 7 lack fibrils, and all known species have small paired dorsal tubercles on the abdomen.

Adult Diagnosis: The absence of a transverse suture on the mesonotum (as in Fig. 114) will differentiate *Ironodes* adults from all other Nearctic Heptageniidae except *Epeorus*. All *Ironodes* males have penes that are widely separated and lack titillators. Some Nearctic *Epeorus* have similar penes, but differ in having poorly developed crossveins in the basal area of the forewings. The well-developed basal crossveins (fig. 197) will also separate females of *Ironodes* from those of *Epeorus* in North America.

Distribution: Western Nearctic (Fig. 229).

Paegnioides

Figures: 19, 165, 236

Larval Diagnosis: The combination of having reduced lamellae on gills 1, caudal filaments with interfacing setae, three well-developed caudal filaments (Fig. 19), and a labrum that is wider than long will differentiate larvae of *Paegnioides* from all other Rhithrogeninae genera. Unlike the relatively similar *Cinygmula*, the row of setae on ventral surface of maxillae is straight rather than curved, and the caudal filaments have interfacing setae.

Adult Diagnosis: Males of *Paegnioides* are unique in having widely separated penes with median titillators that are strongly bent laterally

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(Fig. 165). Additionally, the mesonotum has a transverse suture (as in Fig. 115).
Distribution: Southeast Asia (Fig. 236).

Rhithrogena
Figures: 23-24, 55, 115, 116, 121, 127, 168-170, 182, 212, 239

Larval Diagnosis: The presence of a well-developed median caudal filament and a ventral friction disk formed by the gills (Fig. 24) will differentiate larvae of *Rhithrogena* from all other Rhithrogeninae.

Adult Diagnosis: Males of *Rhithrogena* are identified by the combination of having a transverse suture on the mesonotum (Fig. 115), penes without median titillators (Fig. 168-170), and lateroparapsidal sutures that are strongly bent laterally (Fig. 116). North American females differ from all other genera by having strongly bent lateroparapsidal sutures and a rounded or truncate subanal plate (Fig. 212).
Distribution: Holarctic; Oriental (Fig. 239).

Spinadis
Figures: 25, 56, 129, 192, 240

Larval Diagnosis: Larvae of *Spinadis* are differentiated from all other Nearctic genera by the combination of having only two well-developed caudal filaments, interfacing setae on the caudal filaments, sparse setae on the legs, and well-developed paired submedian tubercles on the head and thorax (Fig. 25). The relatively long, narrow legs of these predatory larvae are atypical of the family in general. The closely related *Anepeorus* lacks well-developed tubercles on the head and has numerous long, fine setae on the legs.

Adult Diagnosis: Males of *Spinadis* are identified by having foretarsi that are shorter than the foretibiae and an anteriorly truncate head capsule (Fig. 129). Females differ from other North American Rhithrogeninae by the combination of having a transverse suture (as in Fig. 115), a rounded costal process on the hindwings (Fig. 192), and a truncate head capsule (Fig. 129).
Distribution: Eastern Nearctic (Fig. 240).

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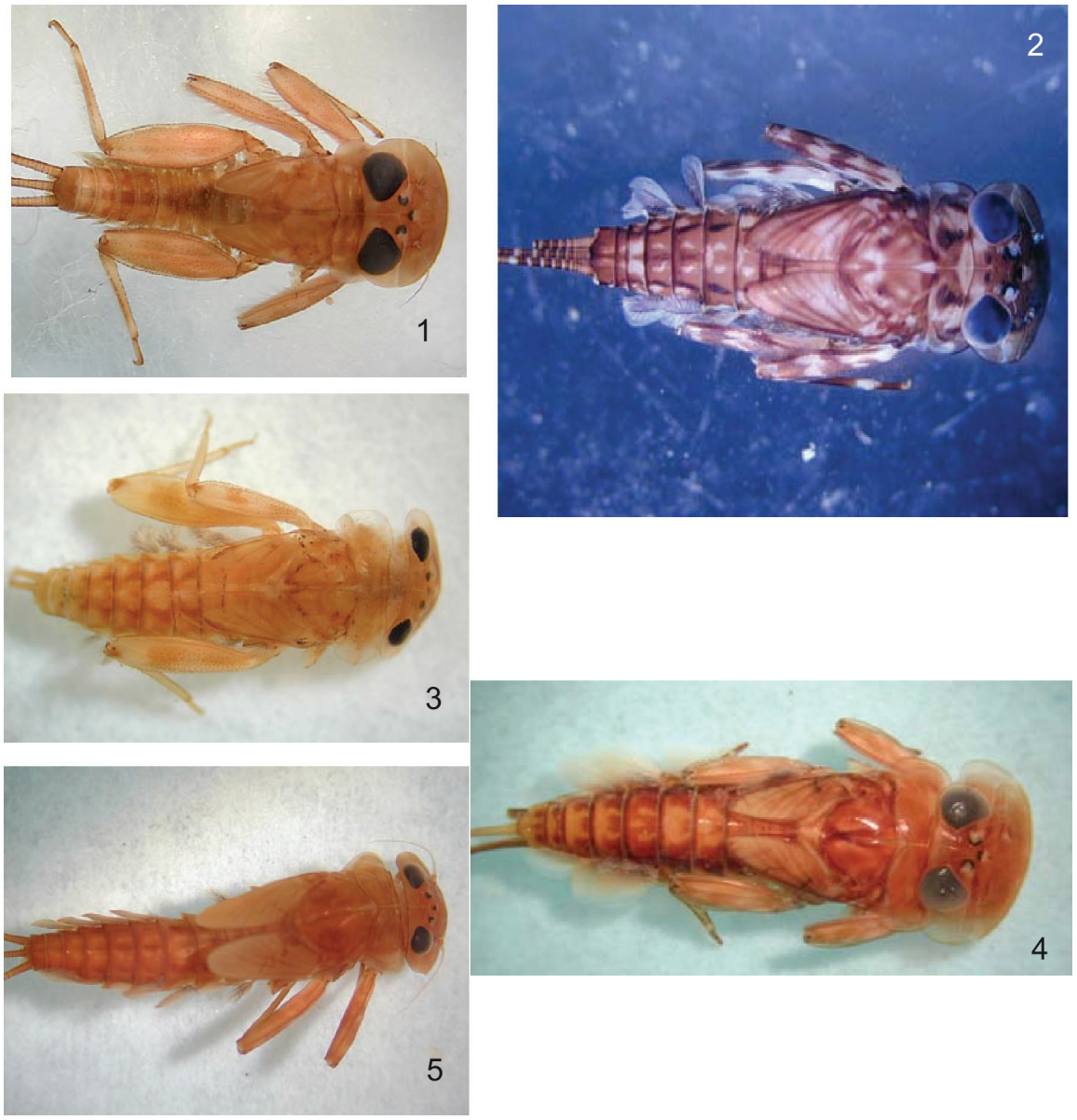

Figs. 1-5: larval habitus. 1 *Afronurus scotti*, 2 *Heptagenia marginalis*, 3 *Asionurus primus*, 4 *Atopopus tarsalis*, 5 *Cinygma integrum*.

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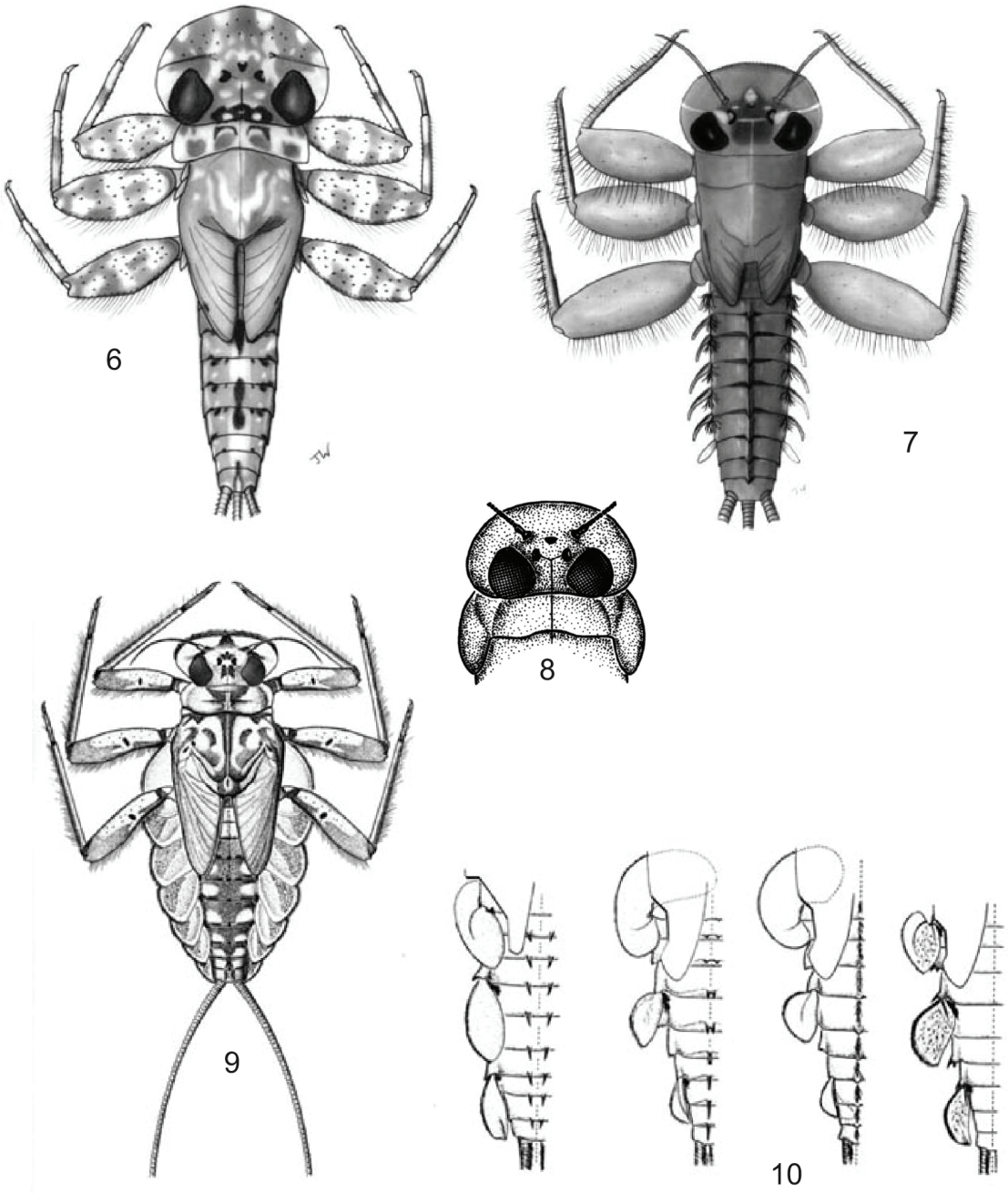

Figs. 6-10: larval habitus. 6 *Compsoneuria* sp (gills removed), 7 *Darthus vadorus*, 8 *Ecdyonurus* sp, 9 *Epeorus longimanus*, 10 *Epeorus* spp.

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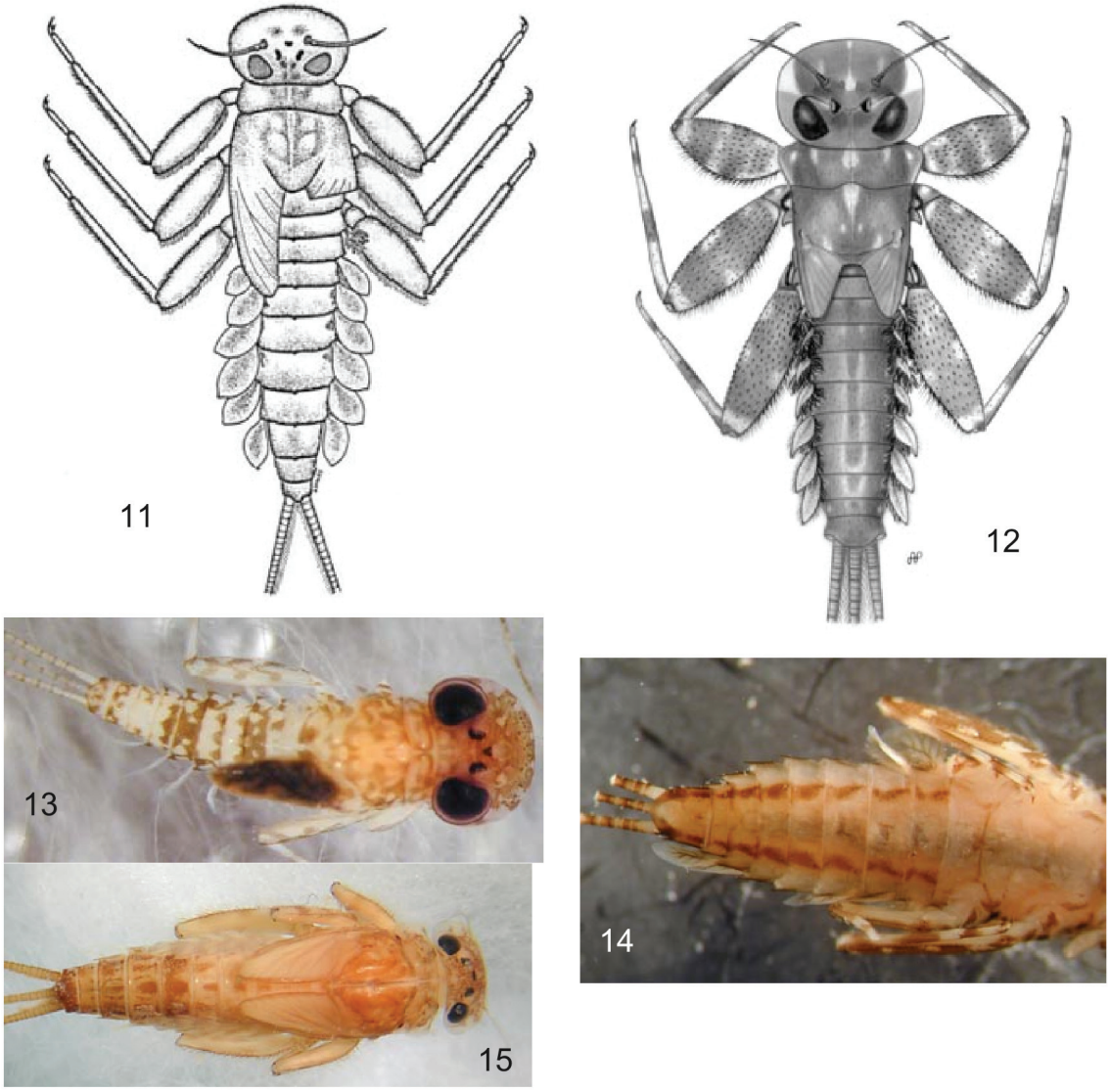
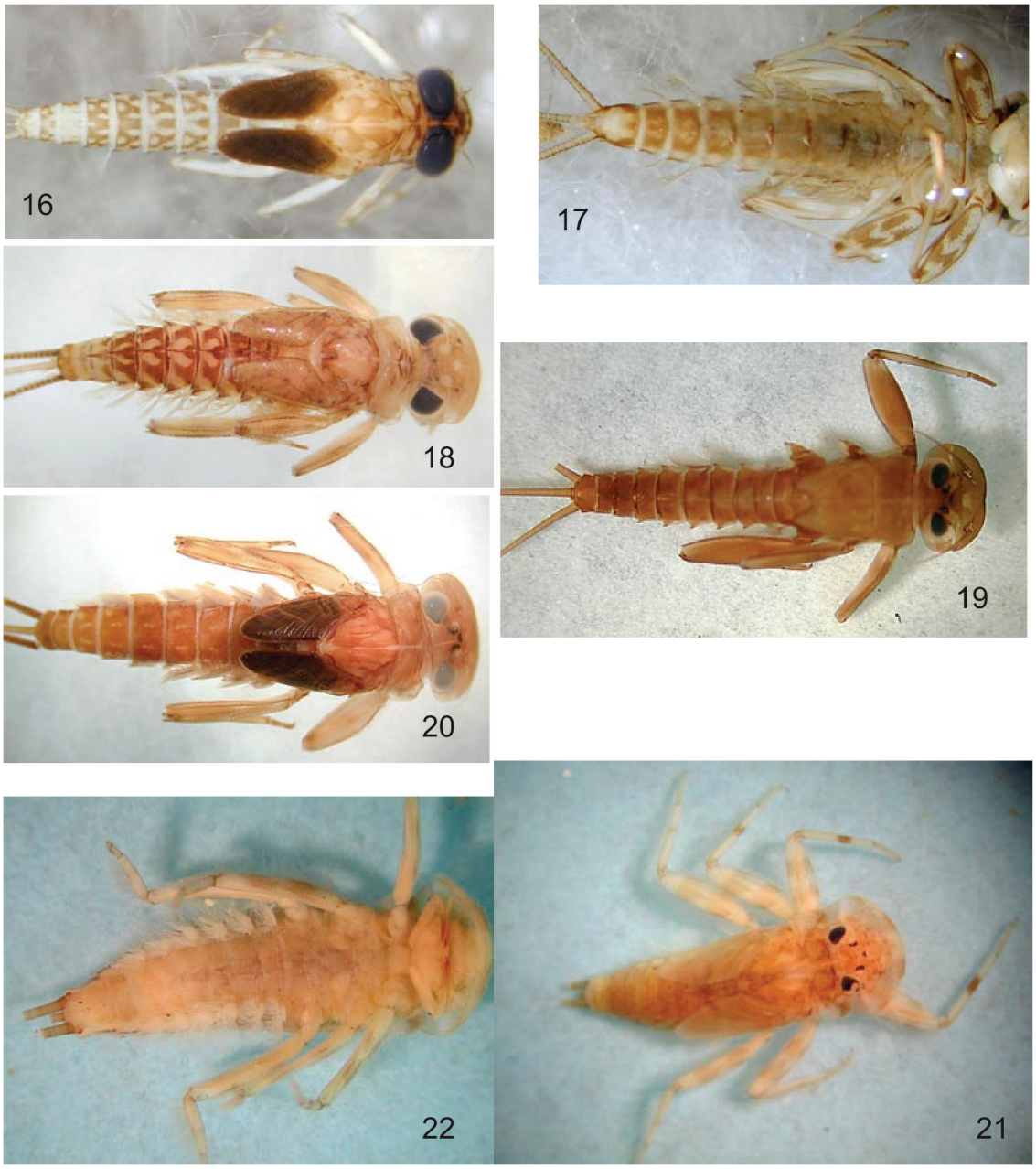


Figs. 11-15: larval habitus. 11 *Anepeorus rusticus* (modified from Whiting and Lehmkuhl, 1987), 12 *Trichogenia hubleyi*, 13 *Leucrocuta maculipennis* (left wingpads removed), 14 *Leucrocuta hebe*, ventral view of abdomen, 15 *Maccaffertium terminatum*.

doi: 10.3752/cjai.2008.07



Figs. 16-22: larval habitus. 16 *Nixe inconspicua*, 17 *Nixe rusticalis*, ventral view of abdomen, 18 *Notacanthurus* sp, 19 *Paegnioides* sp, 20 *Parafronurus youi*, 21 *Raptoheptagenia cruentata*, 22 *Raptoheptagenia cruentata*, ventral habitus.

doi: 10.3752/cjai.2008.07

Figs. 23-29: larval habitus. 23 *Rhithrogena robusta*, 24 *Rhithrogena robusta*, ventral habitus, 25 *Spinadis simplex*, lateral habitus, 26 *Stenacron interpunctatum*, 27 *Stenonema femoratum*, ventral view of abdomen, 28 *Thalerosphyrus determinatus*, 29 *Ironodes nitidus*.

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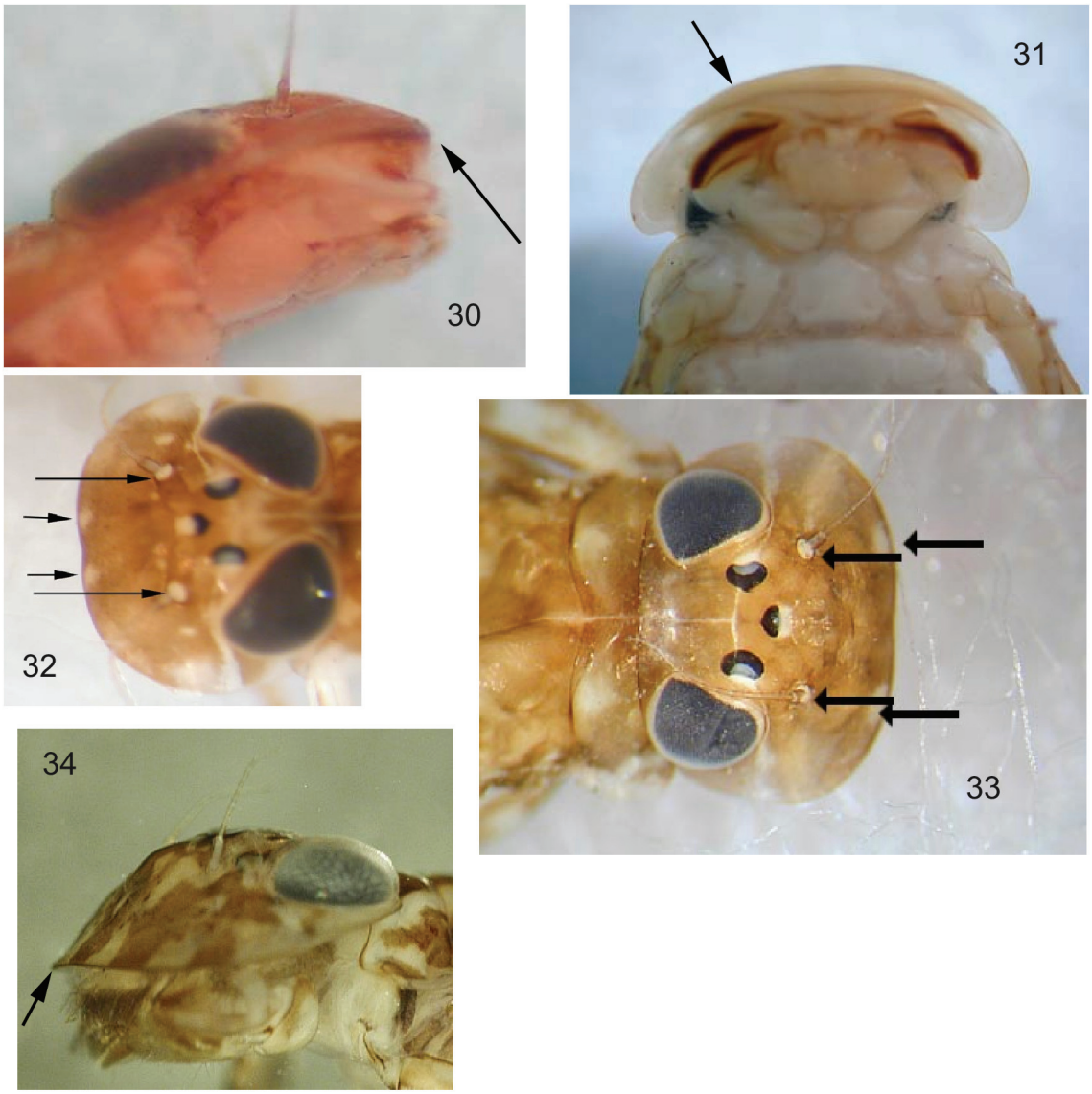

Figs. 30-34: larval head capsule. 30. *Afronurus* sp, lateral view showing slightly thickened, rounded anterior margin, 31 *Atopopus tarsalis*, ventral view showing distinctly thickened anterior margin, 32 *Nixe rusticalis*, arrows indicate arrangement of anteromedial pair of pale markings relative to bases of antennae, 33 *Ecdyonurus simplicioides*, 34 *Compsoneuria* sp, lateral view showing unthickened, sharply delimited anterior margin.

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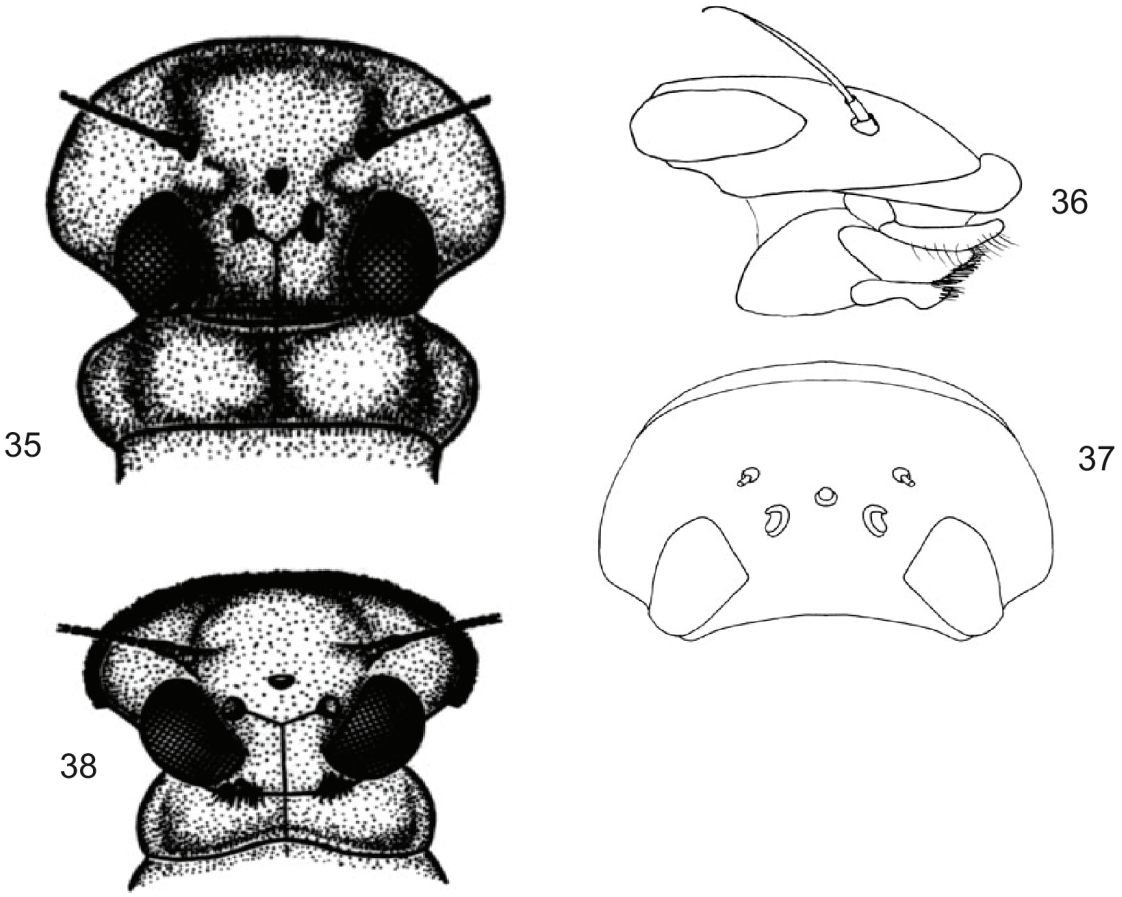
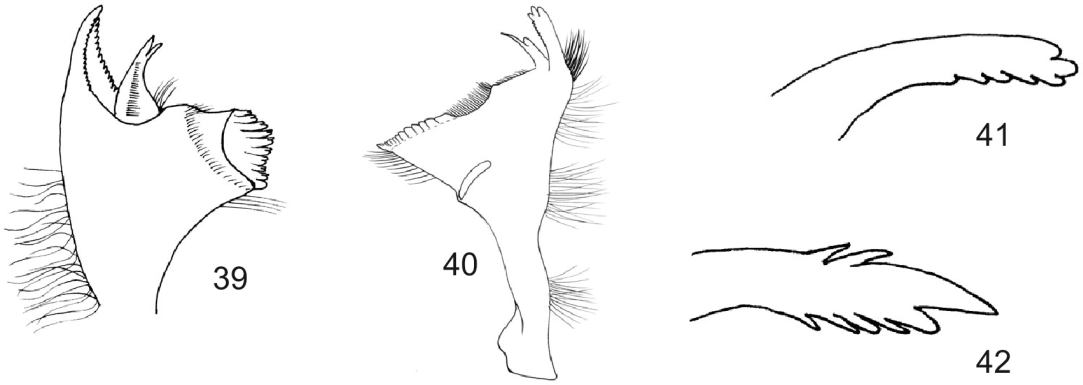


Figs 35-38: larval head capsule. 35 *Bleptus fasciatus*, 36 *Thalerosphyrus* sp, lateral view, 37 *Thalerosphyrus* sp, 38 *Epeorus grandis*.



Figs. 39-42: larval mandibles. 39. *Dacnogenia coerulans*, aplanate mandible, 40 *Trichogenia hubleyi*, planate mandible, 41 *Heptagenia elegantula*, apex of outer incisor of planate mandible, 42 *Asionurus primus*, apex of outer incisor of planate mandible.

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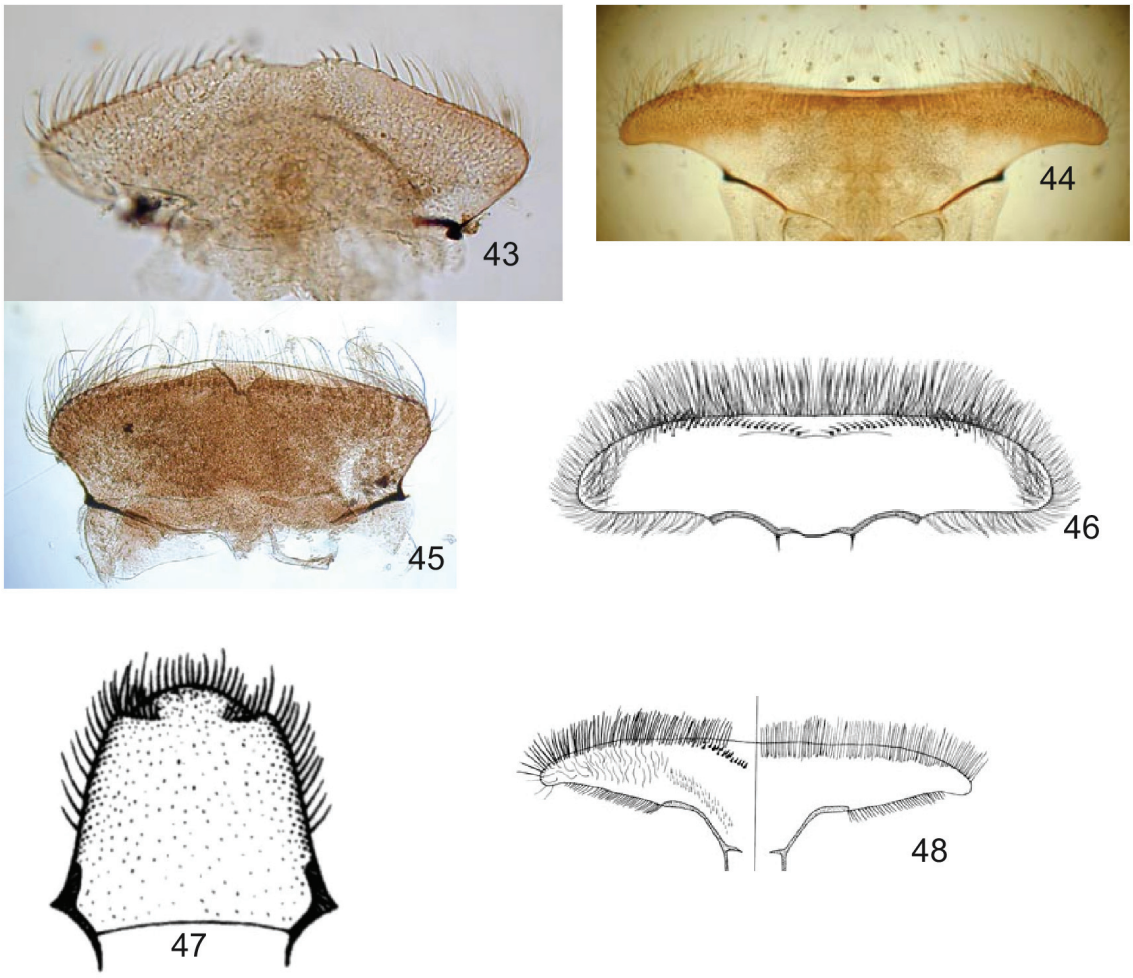

Figs. 43-48: larval labrum. 43 *Nixe* sp, 44 *Ecdyonurus bellus*, 45 *Ecdyonurus simplicioides*, 46 *Heptagenia* sp, 47, *Cinygma integrum*, 48, *Trichogenia hubleyi*, left side showing ventral view, right side showing dorsal view.

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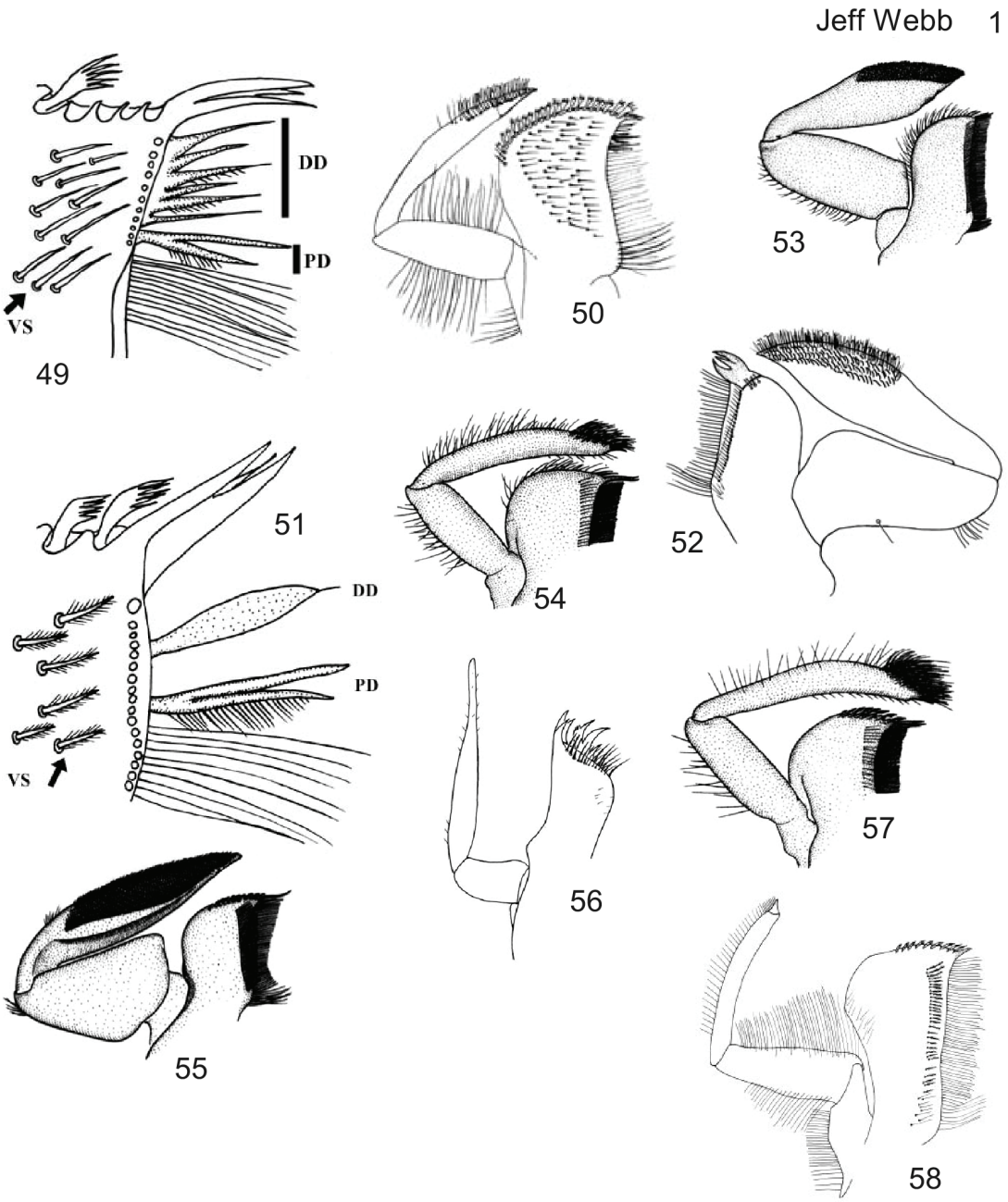

Figs. 49-58: larval maxilla, ventral view. 49 *Compsoneuria* sp, apex, 50 *Darthus vadorus*, 51 *Ecdyonurus torrentis*, apex, 52 *Epeorus namatus*, 53 *Ironodes nitidus*, 54 *Maccafferium* sp, 55 *Rhithrogena* sp, 56 *Spinadis simplex*, 57 *Stenacron interpunctatum*, 58 *Trichogenia hubleyi*. DD = distal dentiseta, PD = proximal dentiseta, VS = ventral seta.

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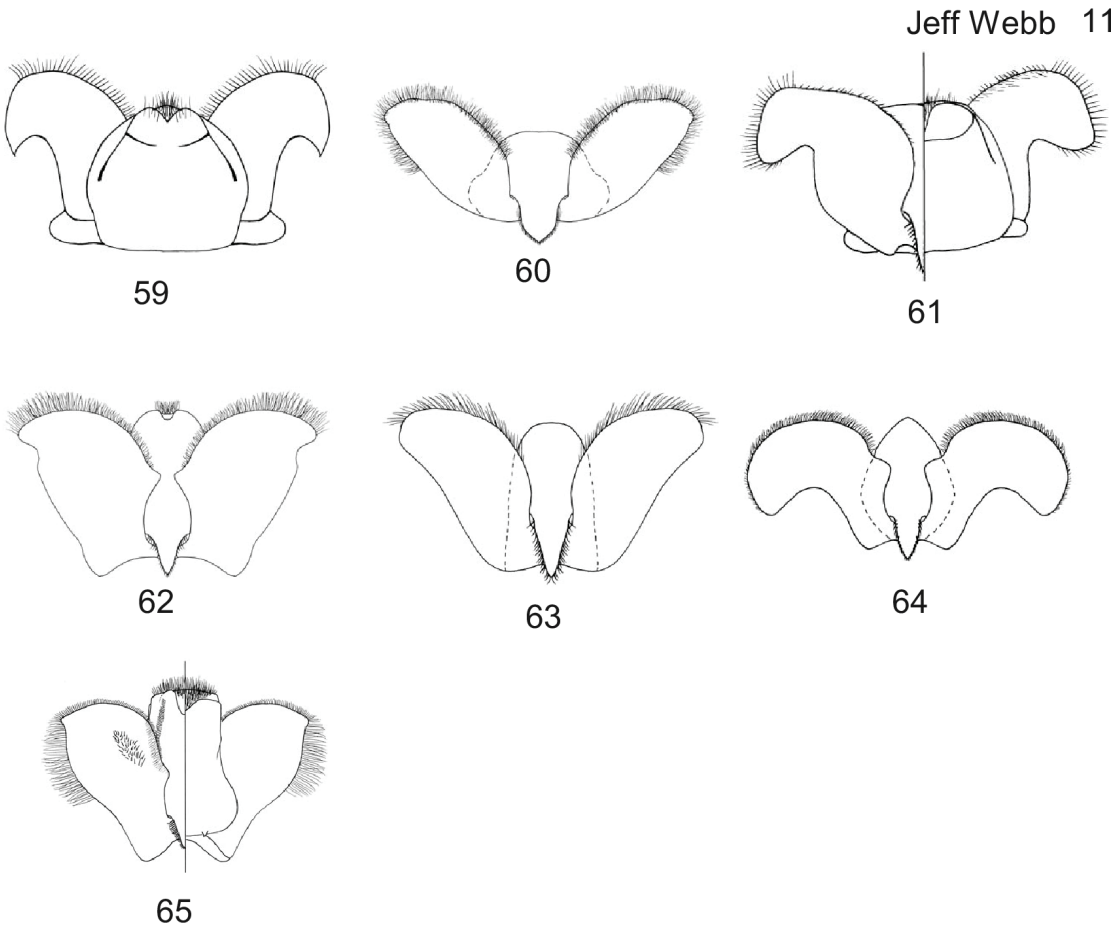

Figs. 59-65: larval hypopharynx. 59 *Asionurus primus*, ventral view, 60 *Dacnogenia coerulans*, dorsal view, 61 *Darthus vadorus*, dorsal view on left, ventral view on right, 62 *Heptagenia flavescens*, dorsal view, 63 *Kageronia orbiticola*, dorsal view, 64 *Stenacron interpunctatum*, dorsal view, 65 *Trichogenia hubleyi*, dorsal view on left, ventral view on right.

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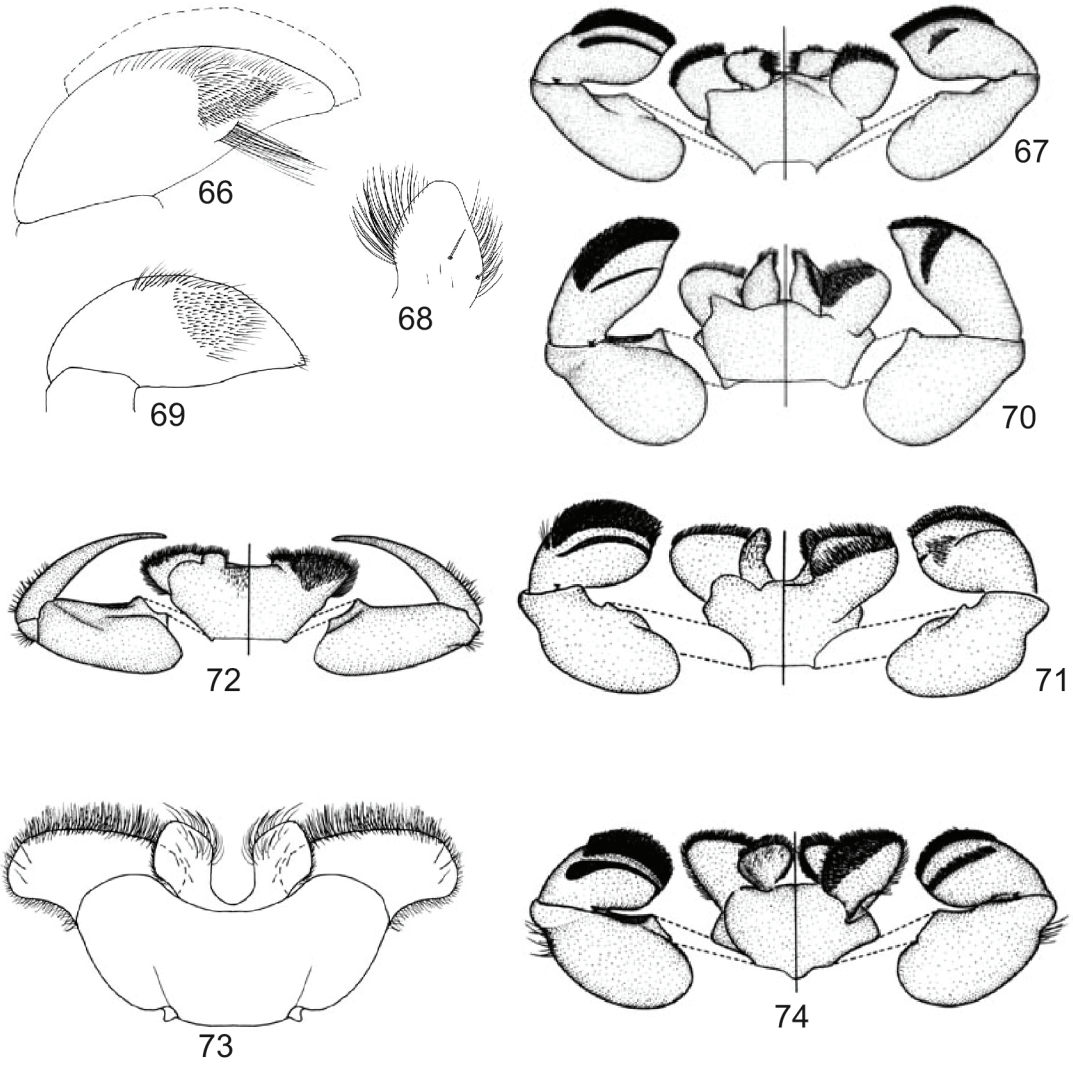

Figs. 66-74: larval labium. 66 *Afronurus* sp, terminal segment of palp, 67 *Bleptus fasciatus*, 68 *Compsoneuria* sp, glossa, 69 *Darthus vadorus*, terminal segment of palp, 70 *Epeorus albertae*, 71 *Heptagenia* sp, 72 *Raptoheptagenia cruentata*, 73 *Thalerosphyrus determinatus* (palps removed), ventral view, 74 *Cinygma intergrum*. For figures 67, 70-72, 74: ventral view shown on left side, dorsal view shown on right.

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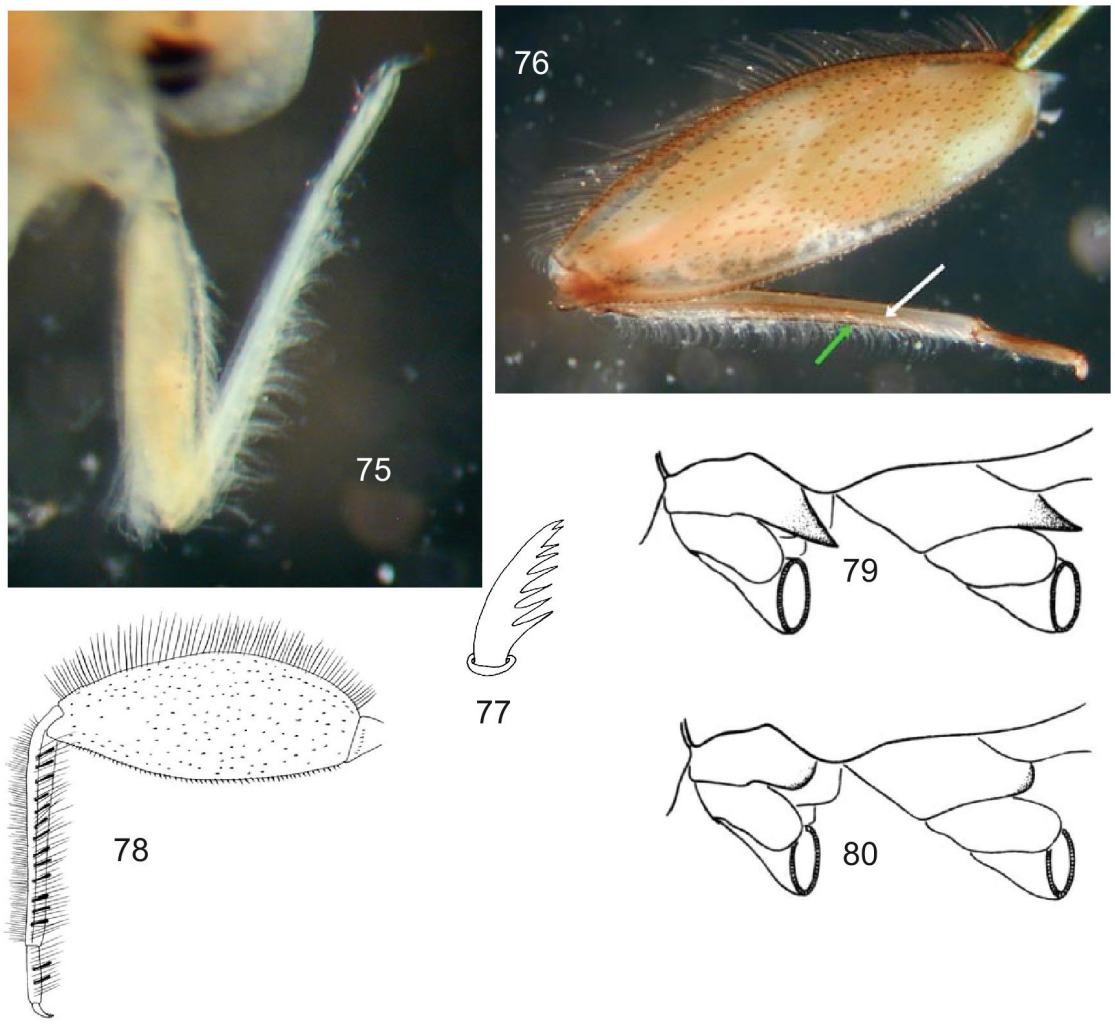

Figs. 75-80: thoracic structures. 75 *Anepeorus rusticus*, foreleg 76 *Afronurus* sp, hindleg, white arrow indicate row of setae on lateral ridge of tibiae, green arrow indicates row of setae on posterior ridge, 77 *Asionurus primus*, pectinate setae from hindtarsus, 78 *Darthus vadorus*, hindleg, 79-80 lateral view of thorax, supracoxal sclerites shades, 79 *Thalerosphyrus* sp, 80 *Afronurus* sp.

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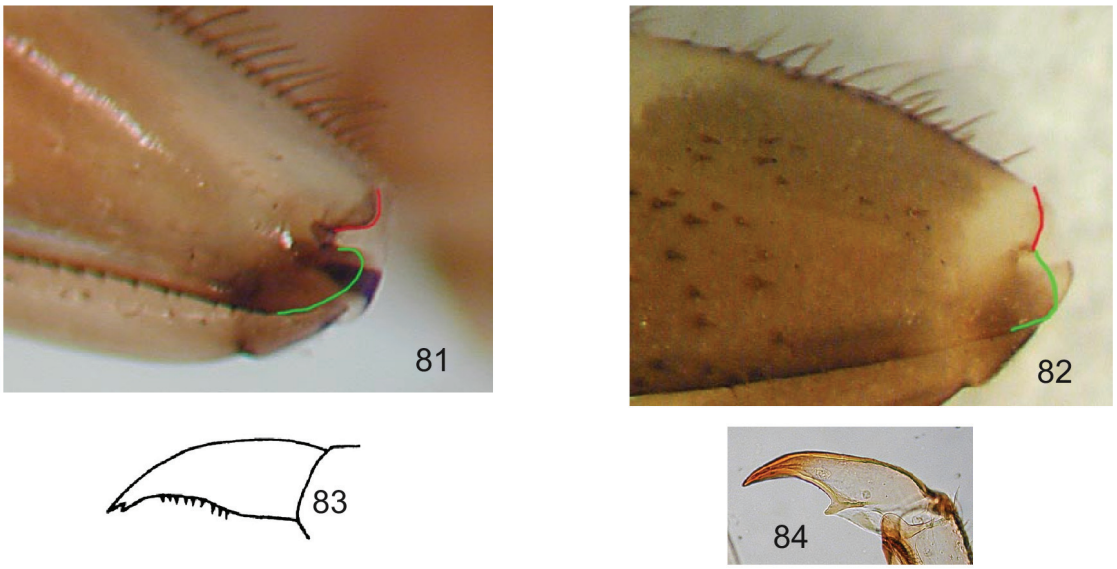
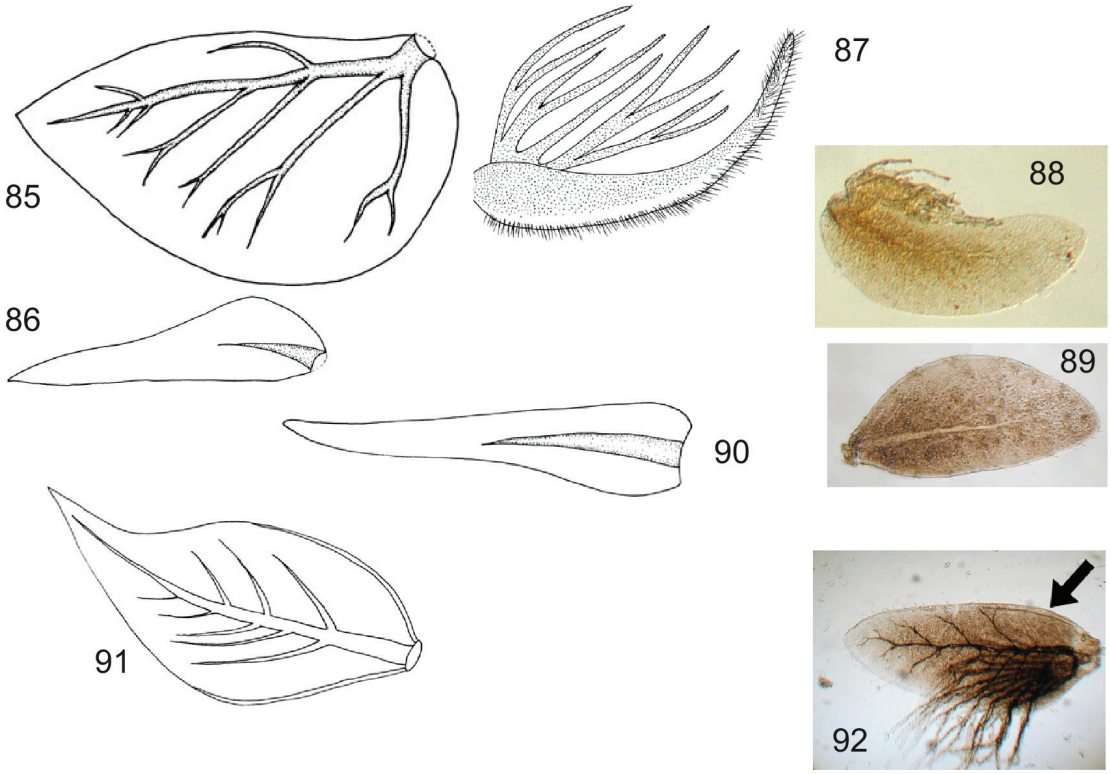
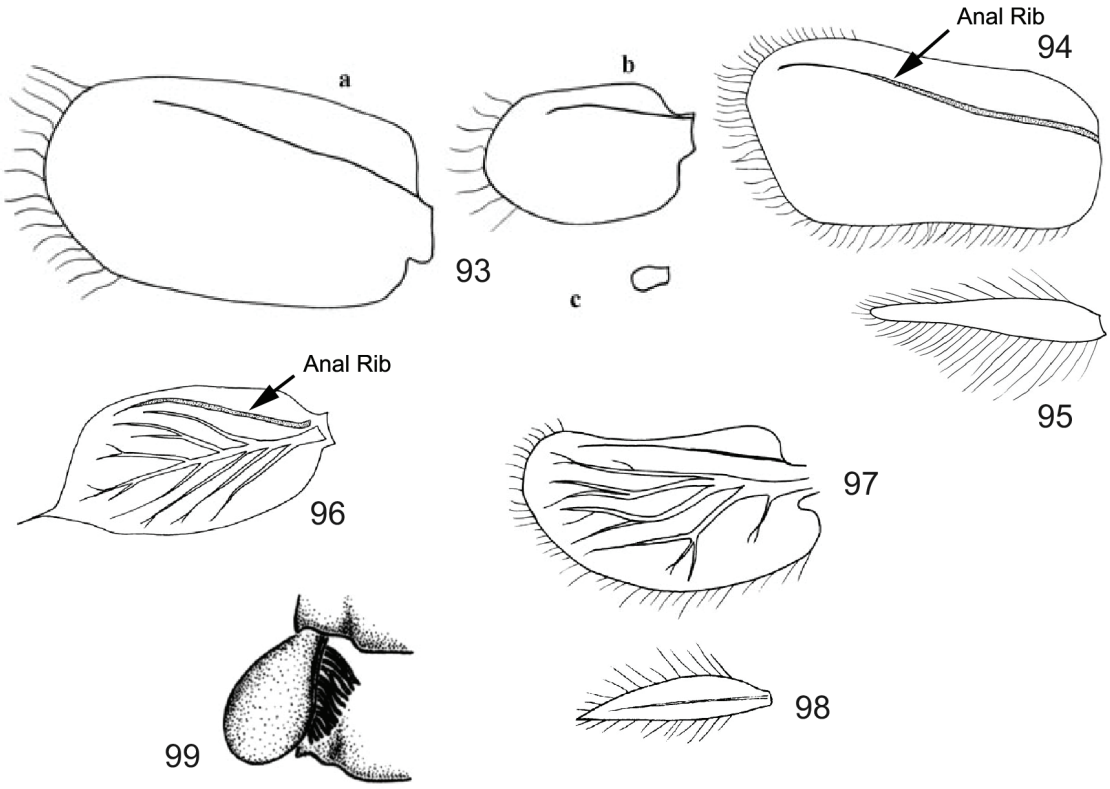


Figs. 81-84: thoracic structures. 81-82 apex of forefemur, red indicates dorsal projection, green indicates ventral projection, 81 *Cinygmula* sp, 82 *Stenacron interpunctatum*, 83-84 tarsal claw, 83 *Kageronia orbiticola*, 84 *Heptagenia adaequata*.



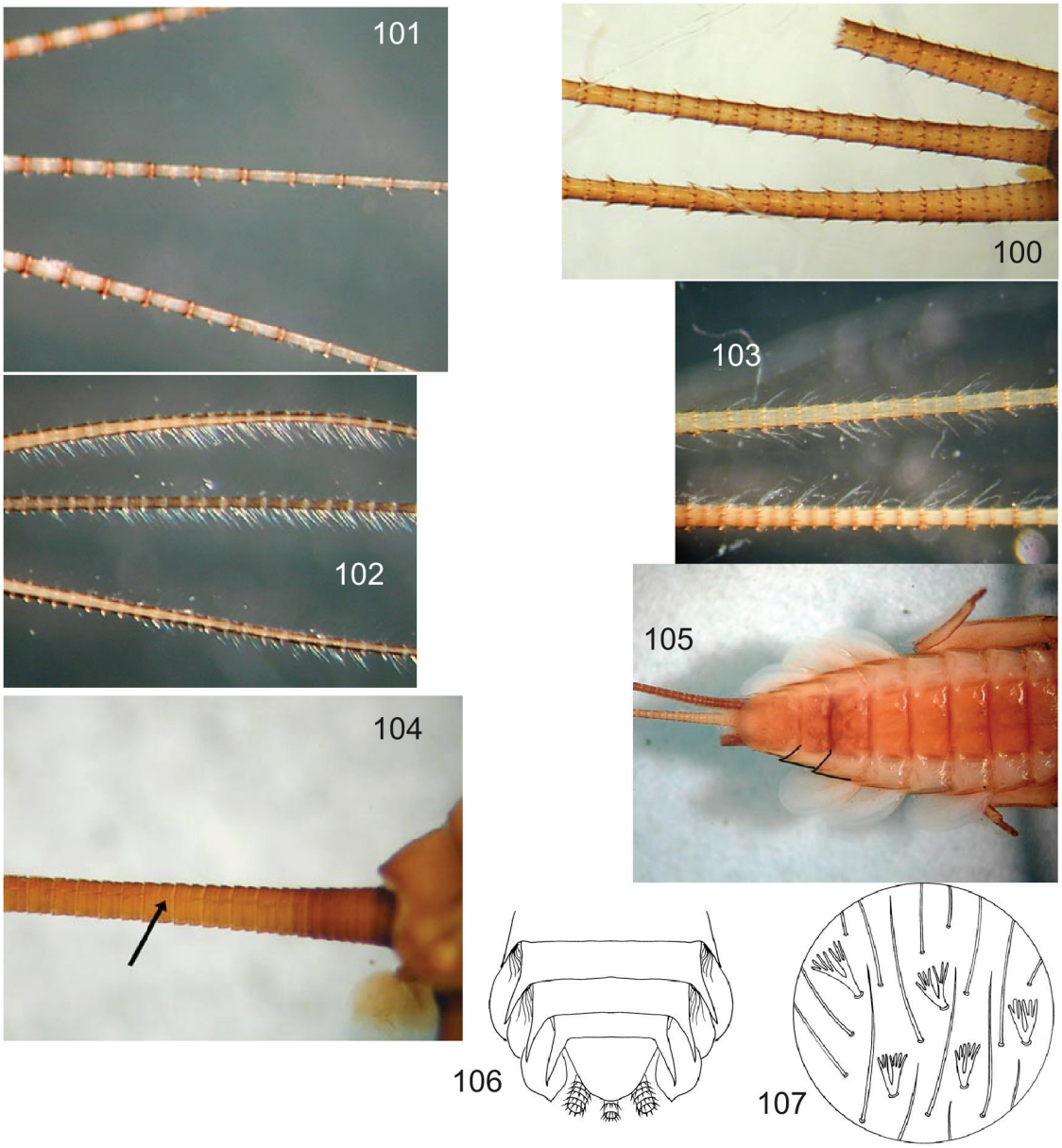
Figs. 85-92: larval gills. 85-86 *Asionurus primus*, 85 lamella of gill 1, 86 gill 7, 87 *Darthus vadorus*, gill 4, 88-89 *Ecdyonurus simplicioides*, 88 gill 1, 89 gill 7, 90 *Dacnogenia coerulans*, lamella of gill 4, 91 *Kageronia kihada*, lamella of gill 4, 92 *Heptagenia pulla*, gill 4, arrow indicates anal rib.

doi: 10.3752/cjai.2008.07



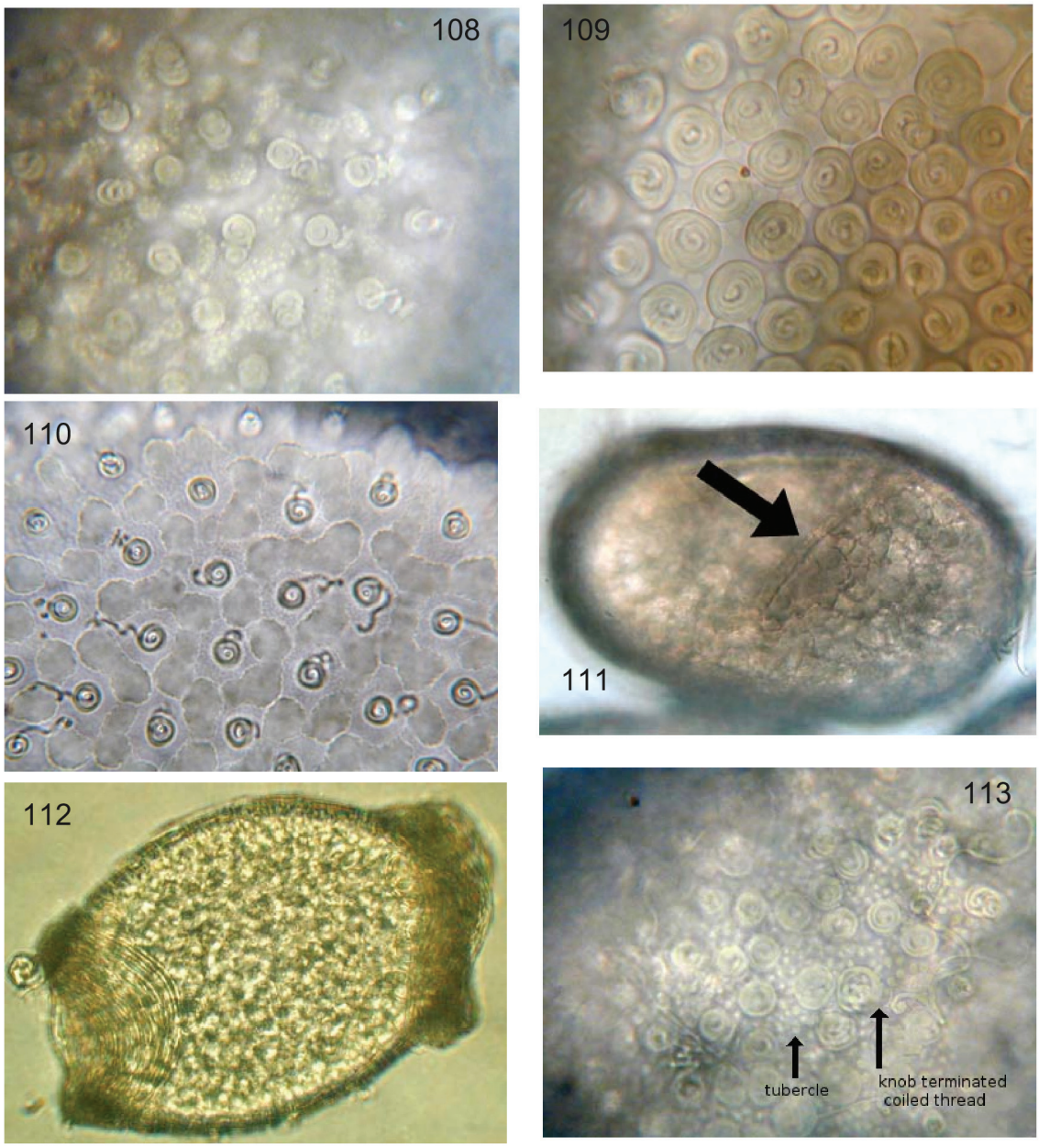
Figs. 93-99: larval gills. 93 *Macdunnoa brunnea*, lamellae of gills 4(a), 6(b), 7(c), 94-95 *Maccaffertium* sp, 94 lamella of gill 5, 95 lamella of gill 7, 96 *Stenacron interpunctatum*, lamella of gill 4, 97-98 *Stenonema femoratum*, 97 lamella of gill 4, 98 lamella of gill 7, 99 *Ironodes nitidus*, gill 1.

doi: 10.3752/cjai.2008.07



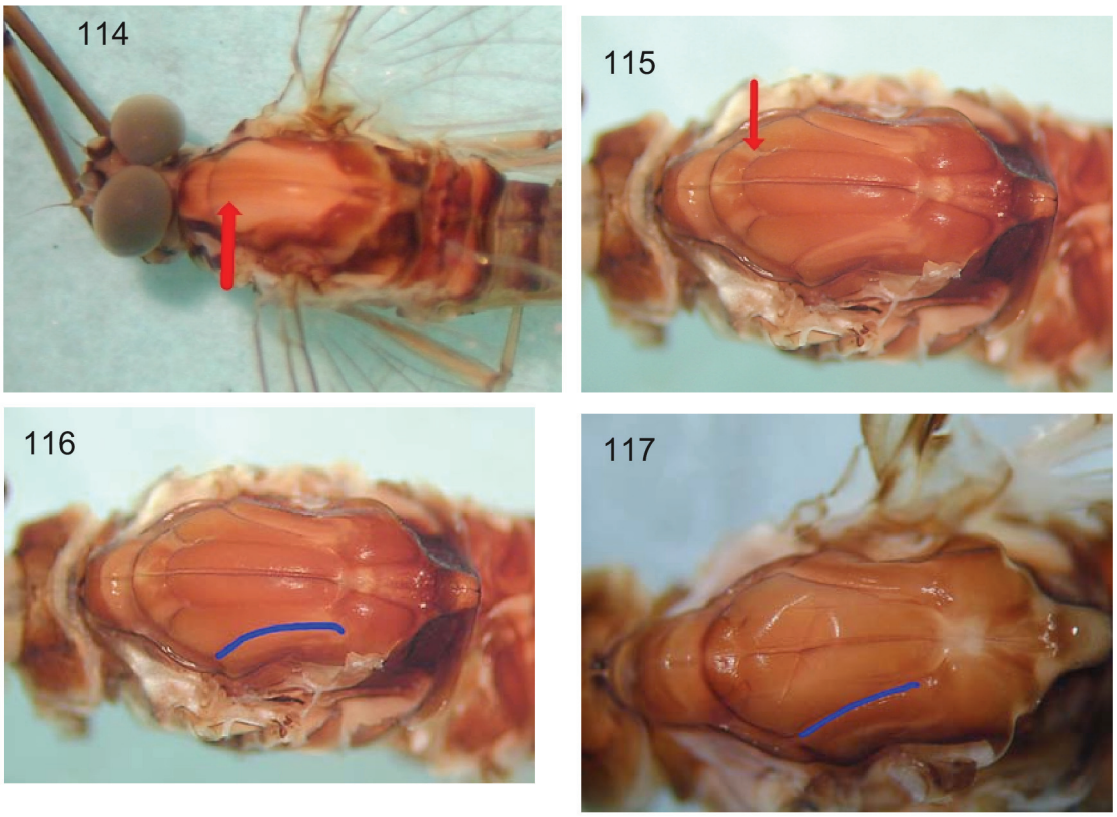
Figs. 100-107: abdominal structures. Figs. 100-104: caudal filaments, 100 *Afronurus scotti*, 101 *Leucrocuta hebe*, 102 *Nixe rusticalis*, 103 *Parafronurus youi*, 104 *Epeorus* sp, arrow indicates dorsal row of fine setae. 105 *Atopopus tarsalis*, posterolatal spines outlined in black, 106 *Thalerosphyrus* sp, ventral view of segments 5-10, 107 *Trichogenia ulmeri*, fine and branched robust setae of abdominal terga.

doi: 10.3752/cjai.2008.07



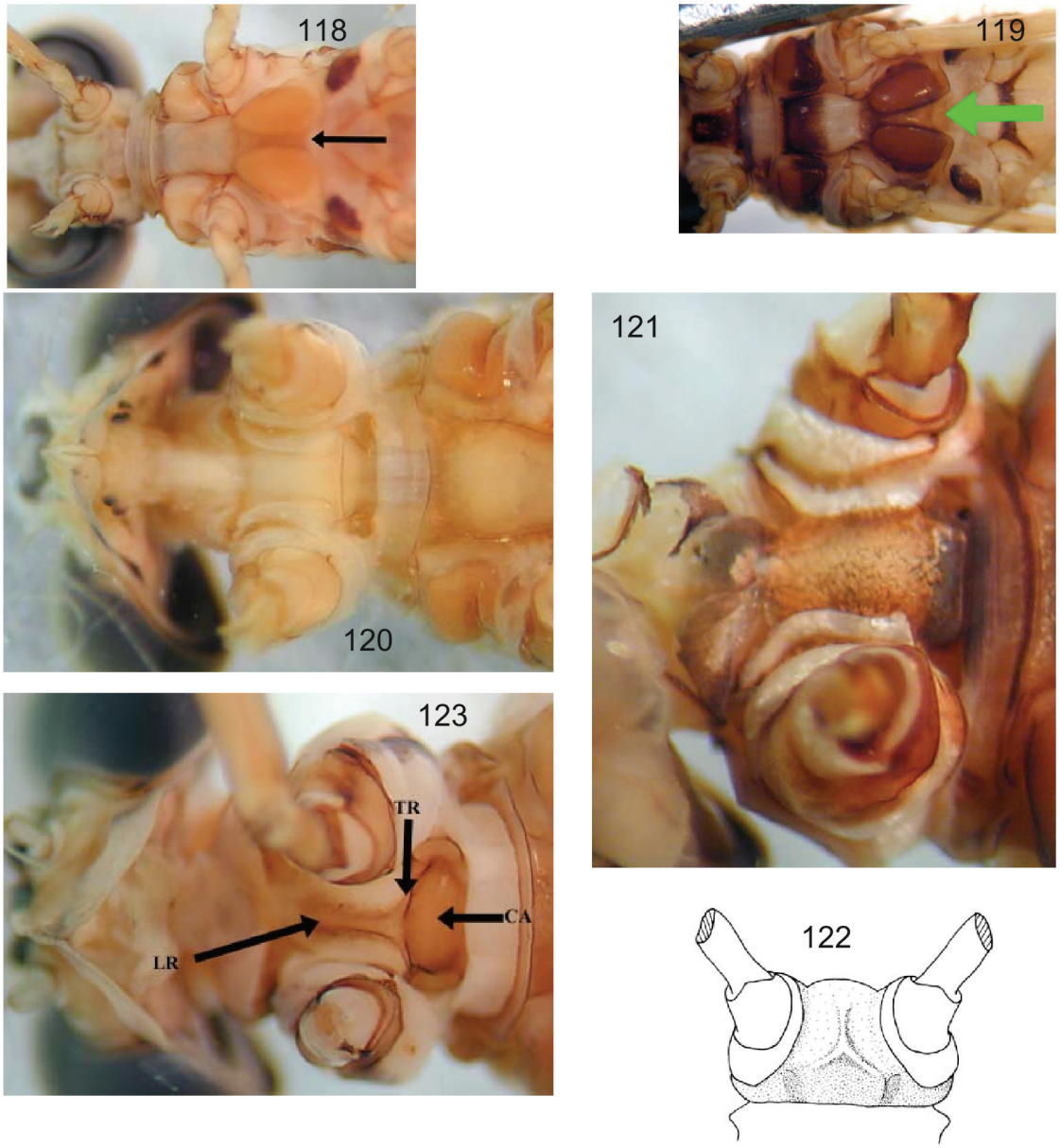
Figs. 108-113: eggs. 108 *Ecdyonurus simplicioides*, chorion, 109 *Ecdyonurus criddlei*, chorion, 110 *Nixe* sp, chorion, 111 *Stenonema femoratum*, arrow indicates spermguide, 112 *Stenacron interpunctatum*, 113, *Heptagenia elegantula*, chorion.

doi: 10.3752/cjai.2008.07



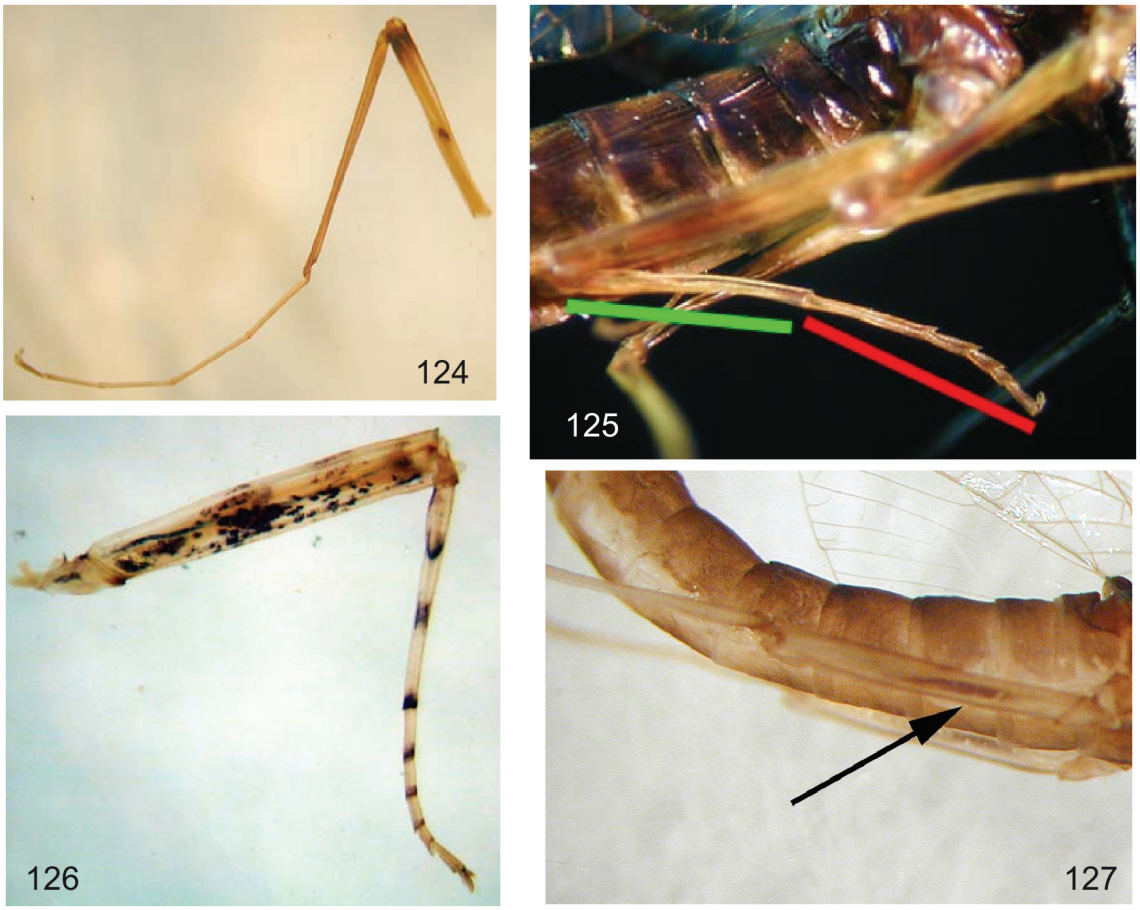
Figs. 114-117: adult thorax, dorsal view. 114 *Epeorus grandis*, arrow indicates lack of transverse suture, 115 *Rhithrogena robusta*, arrow indicates transverse suture, 116-117 blue line indicates lateroparapsidal sutures, 116 *Rhithrogena robusta*, 117 *Maccaffertium vicarium.*

doi: 10.3752/cjai.2008.07



Figs. 118-123: 118-119 mesosternum, arrow indicates medial depression of furcasternum, 118 *Compsoneuria njalensis*, 119 *Epeorus aculeatus,* 120-123 prosternum, 120 *Bleptus fasciatus*, 121 *Rhithrogena robusta*, 122, *Heptagenia flavescens*, 123 *Maccaffertium vicarium*. LR = longitudinal ridge, TR = transverse ridge, CA = concave area.

doi: 10.3752/cjai.2008.07



Figs. 124-127: adult legs. 124 *Epeorus aculeatus*, male foreleg, 125 *Atopopus edmundsi*, male hindleg, green indicates tibia, red indicates tarsus, 126 *Compsoneuria thienemanni* male, hindleg, 127 *Rhithrogena futilis*, male hindleg, arrow indicates dark streak on femur.

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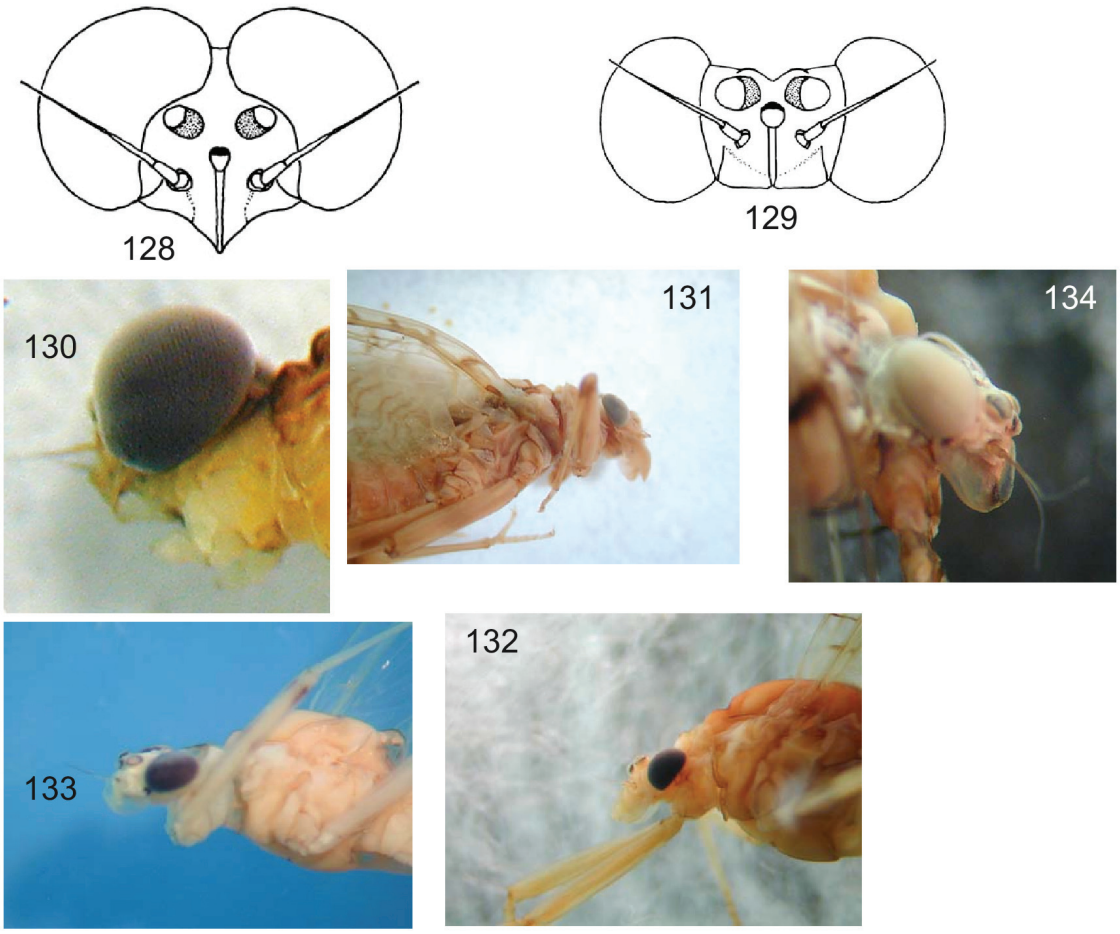

Figs. 128-134: adult head capsule. 128 *Anepeorus rusticus*, male 129 *Spinadis simplex*, male, 130 *Nixe lucidipennis*, male, 131 *Notacanthurus* sp, female subimago, 132 *Raptoheptagenia cruentata*, female, 133 *Heptagenia flavescens*, female, 134 *Maccaffertium vicarium*, female,

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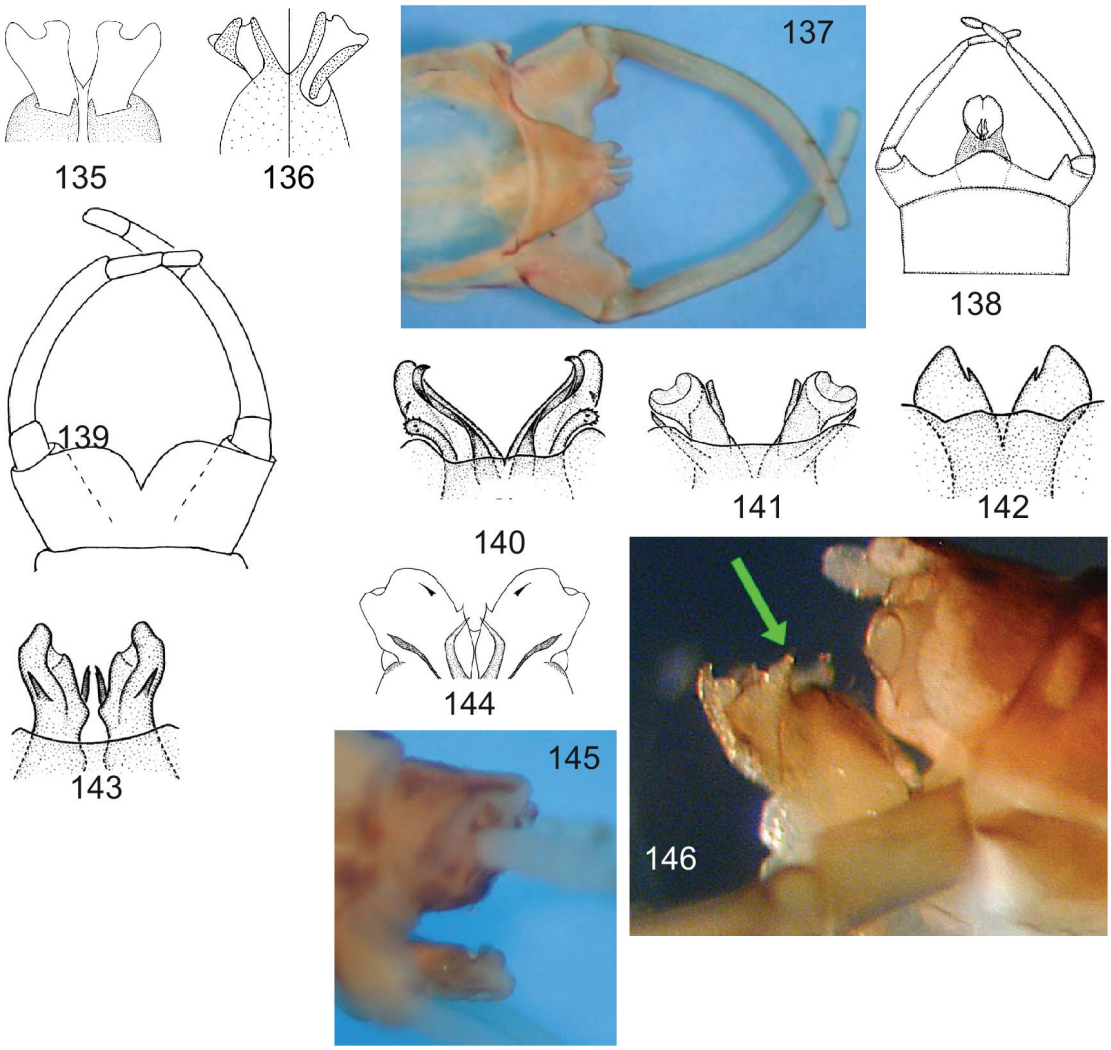

Figs. 135-146: male genitalia. 135 *Afronurus obliquistriatus*, ventral, 136 *Afronurus* sp, 137 *Afronurus peringueyi*, dorsal, 138 *Asionurus petersi*, modified from Braasch (2006), 139 *Bleptus fasciatus*, forceps, 140-143 *Cinygmula* spp, 140 *C. kootenaei*, 141 *C. par*, 142 *C. tarda*, 143 *C. uniformis*, 144 *Compsoneuria thienemanni*, ventral, 145 *Compsoneuria njalensis*, lateral, 146 *Ecdyogymnurus inversus*, lateral, dorsolateral projection indicated.

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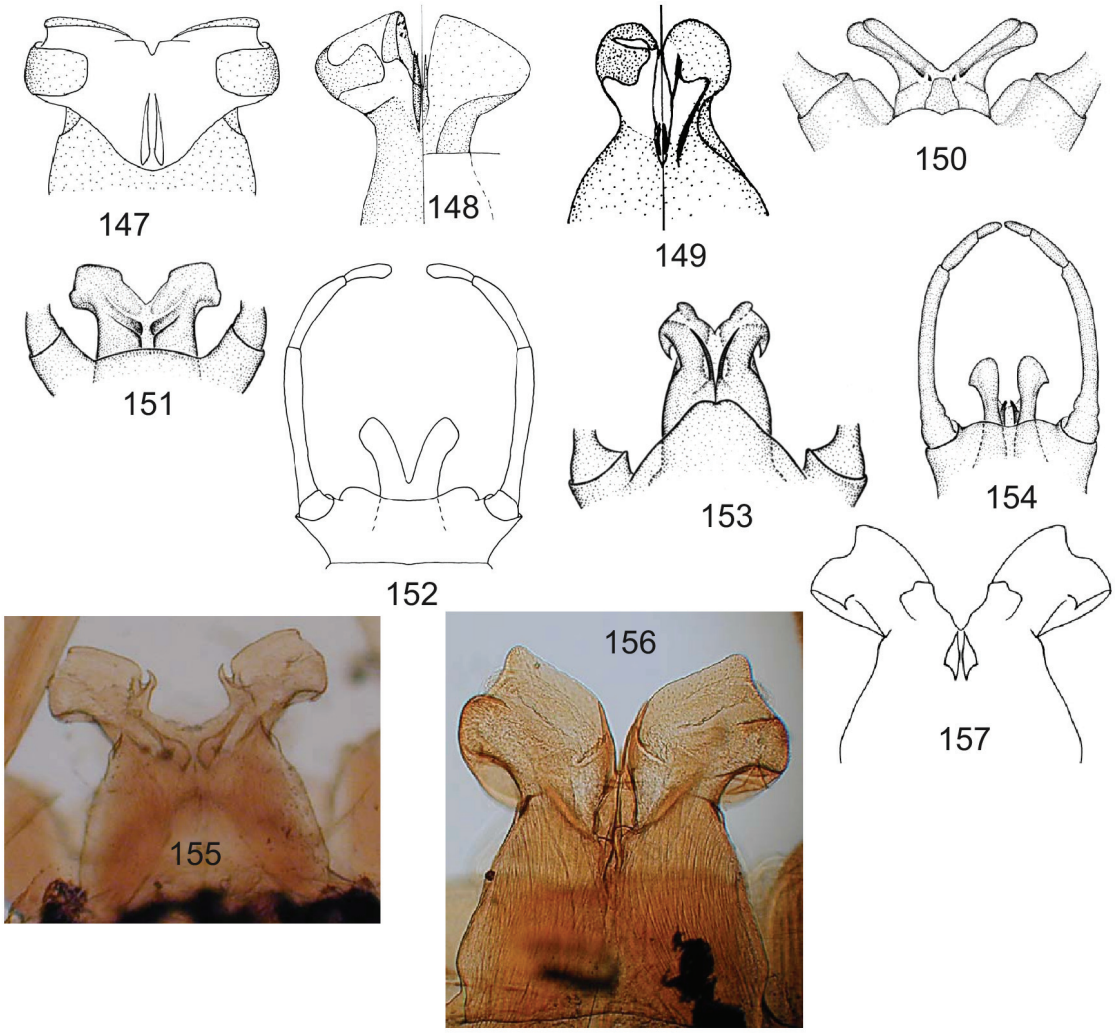
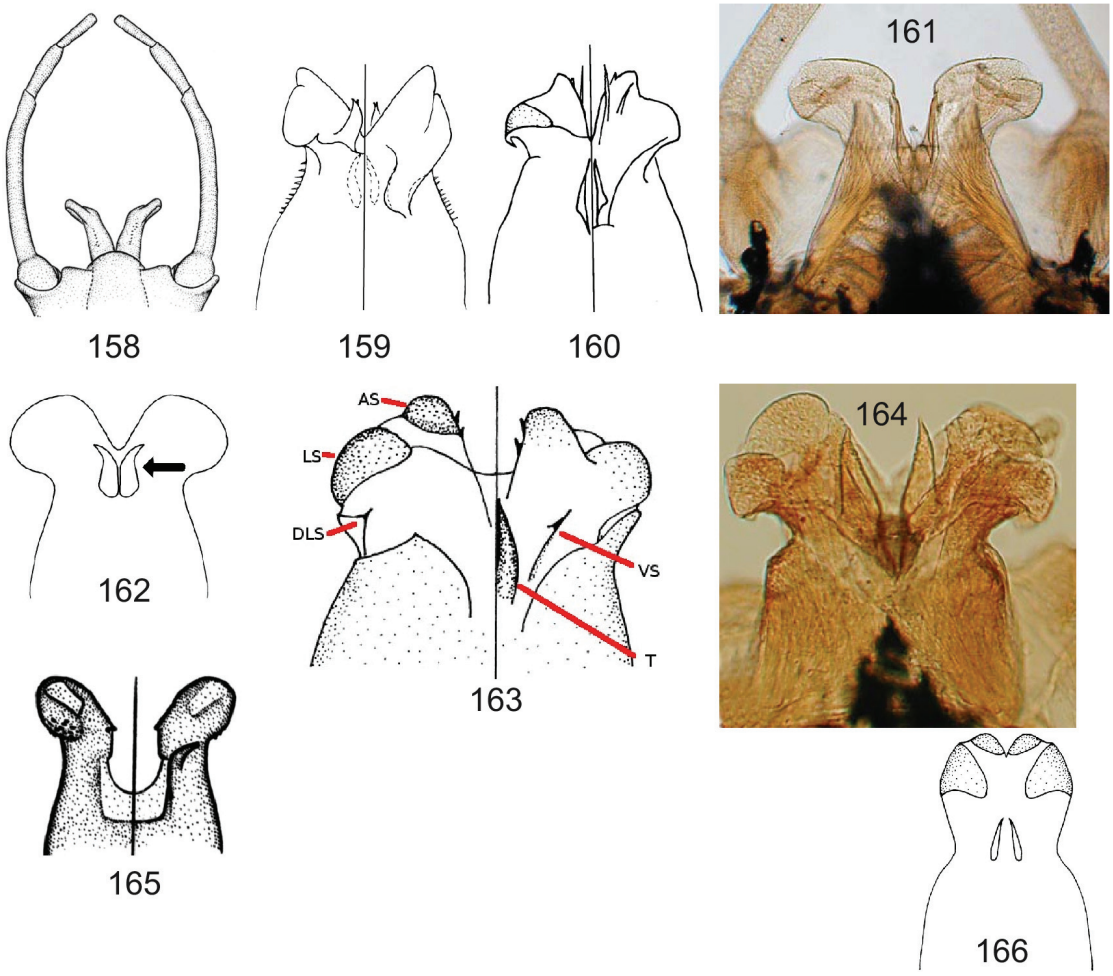


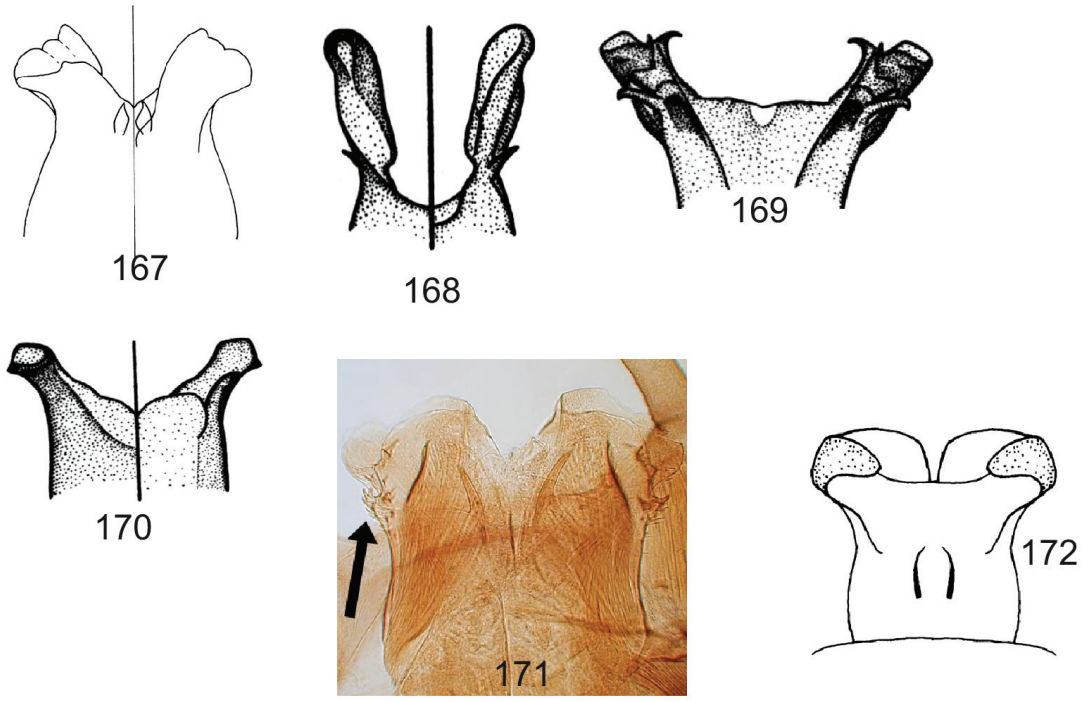
Figs. 147-157: male penes. 147 *Ecdyonurus criddlei*, dorsal, 148 *Ecdyonurus dispar*, left side shows dorsal view, right side ventral, 149 *Electrogena* sp, left side shows dorsal view, right side ventral, 150-154 *Epeorus* spp, 150 *E. aculeatus*, dorsal, 151*E. assimilis*, 152 *E. grandis*, 153 *E. longimanus*, 154 *E. margarita*, 155-157 *Heptagenia* spp, dorsal 155 *H. elegantula*, 156 *H. pulla*, 157 *H. flavescens.*

doi: 10.3752/cjai.2008.07



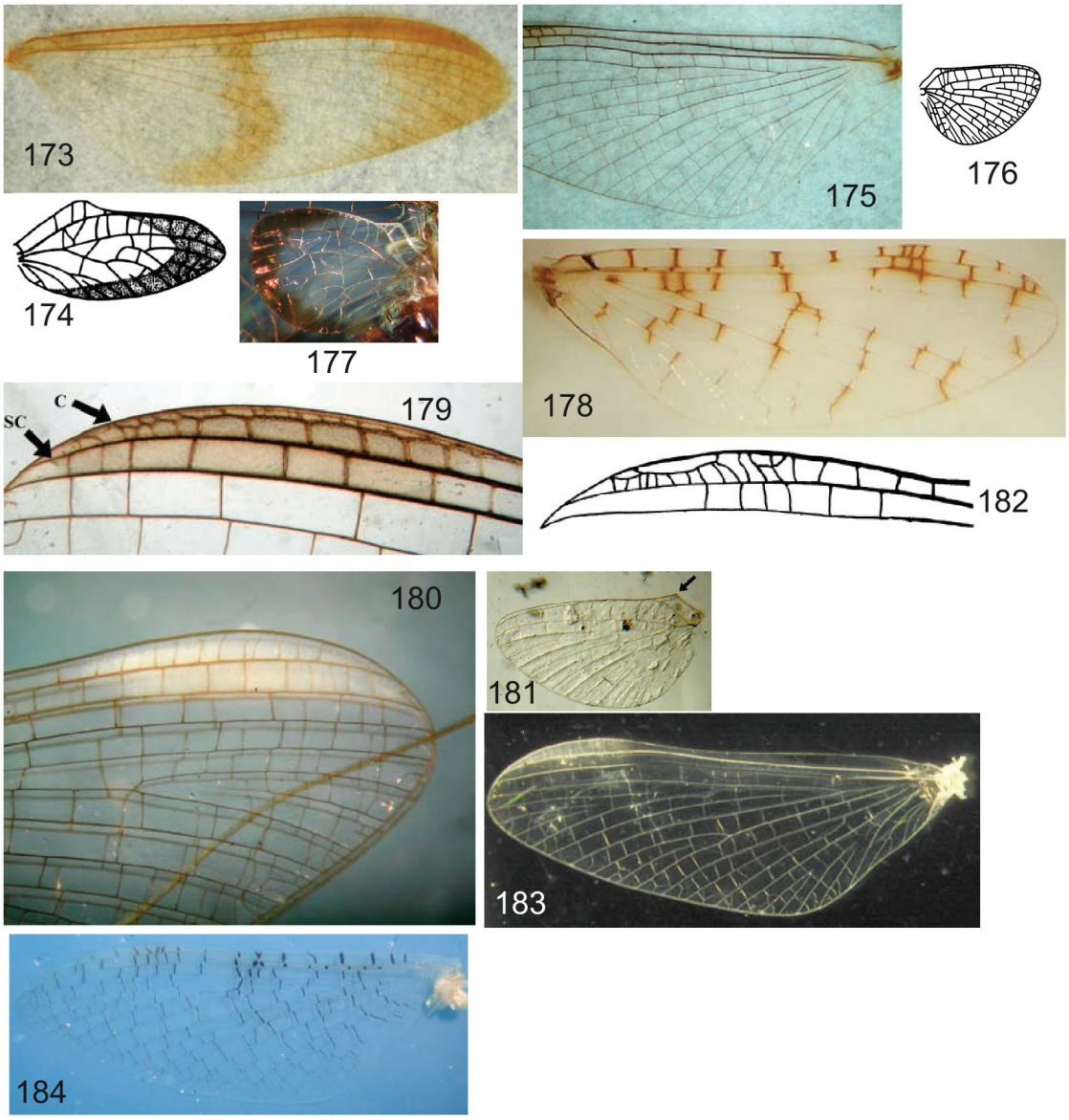
Figs. 158-166: male penes. 158 *Ironodes nitidus*, 159 *Kageronia kihada*, left side shows dorsal, right side shows ventral, 160 *Leucrocuta hebe* left side shows dorsal, right side shows ventral.161 *Maccaffertium terminatum*, dorsal, 162 *Macdunnoa brunnea*, dorsal, 163 *Nixe* sp, left side shows dorsal, right side shows ventral, AS=apical sclerite LS=lateral sclerite DLS=dorsolateral spine VS=ventral spine T=titillator, 164 *Nixe rusticalis*, dorsal, 165 *Paegnioides cupulatus*, left side shows dorsal, right side shows ventral, 166 *Parafronurus youi*, dorsal.

doi: 10.3752/cjai.2008.07



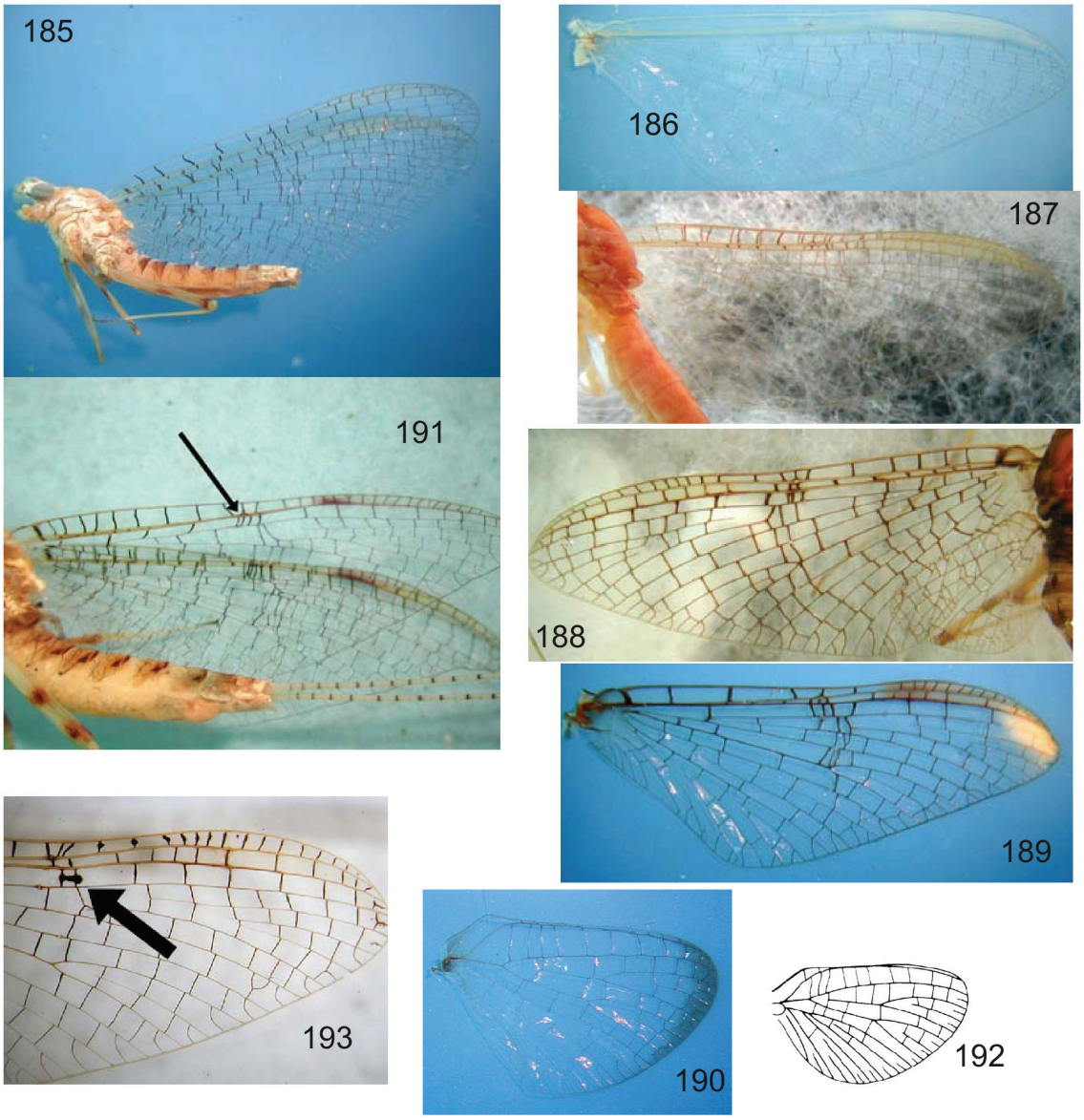
Figs. 167-172: male genitalia. 167 *Raptoheptagenia cruentata*, left side shows dorsal, right side shows ventral, 168-170 *Rhithrogena* spp, 168 *R. hageni*, left side shows dorsal, right side shows ventral, 169 *R. robusta* ventral, 170 *R. semicolorata* , left side shows dorsal, right side shows ventral, 171 *Stenacron interpunctatum*, dorsal, 172 *Thalerosphyrus determinatus*, dorsal.

doi: 10.3752/cjai.2008.07



Figs 173-184: adult wings. Figs. 173,175,178-180, 182-186: forewings; Figs. 174,176,177,181: hindwings.173-174 *Bleptus fasciatus*, 175-176 *Epeorus grandis*, 177 *Atopopus edmundsi*, 178 *Compsoneuria thienemanni*, 179 *Cinygma integrum* stigmatic region, 180 *Cinygmula subaequalis*, 181 *Cinygmula mimus*, 182 *Rhithrogena sp* stigmatic region, 183 *Ecdyonurus simplicioides*, 184 *Leucrocuta hebe*.

doi: 10.3752/cjai.2008.07



Figs. 185-193: wings. 185 *Heptagenia adaequata* female, 186 *Heptagenia flavescens,* forewing, 187 *Raptoheptagenia cruentata,* 188 *Maccaffertium vicarium*, forewing, 189-190 *Maccaffertium pudicum*, 189 forewing, 190 hindwing, 191 *Stenonema femoratum*, forewing, arrow indicates crowded crossveins, 192 *Spinadis simplex*, hindwing, 193 *Stenacron interpunctatum*, forewing, arrow indicates spot below bulla.

doi: 10.3752/cjai.2008.07

Figs. 194-199: adult habitus. 194 *Epeorus grandis*, male, 195 *Stenonema femoratum*, female, 196 *Bleptus fasciatus*, male, 197 *Ironodes californicus*, male, 198 *Heptagenia adaequata*, female, 199 *Heptagenia culacantha*, female subimago.

doi: 10.3752/cjai.2008.07

Figs. 200-204: adult habitus. 200 *Heptagenia flavescens*, female, 201 *Heptagenia marginalis*, female, 202 *Heptagenia pulla*, female, 203 *Raptoheptagenia cruentata*, female, 204 *Maccaffertium* spp (modified from Bednarik and McCafferty, 1979).

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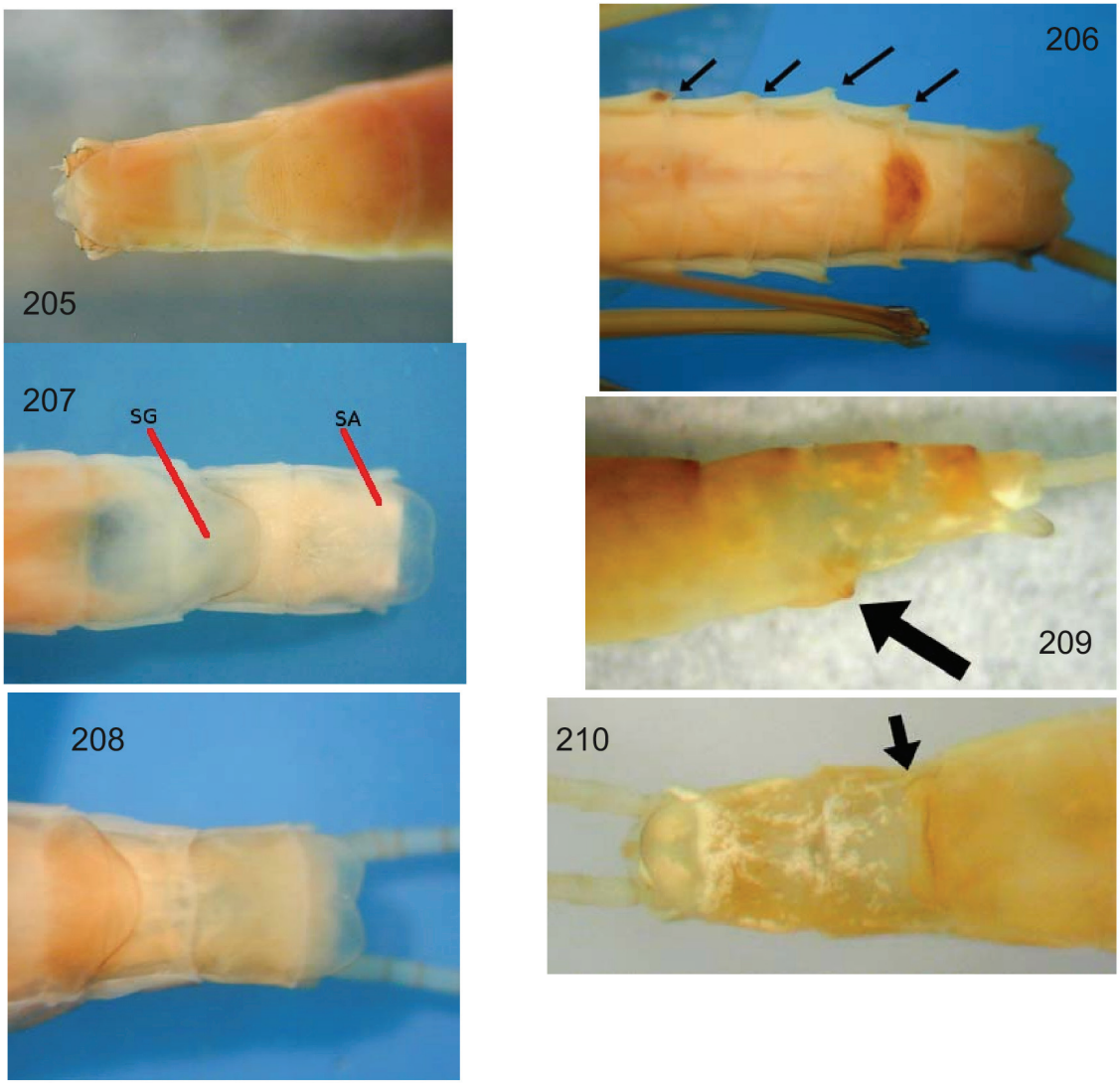

Figs. 205-210: terminal segments of female. 205 *Raptoheptagenia cruentata*, 206 *Heptagenia culacantha*, female subimago, arrows indicate posterolateral spines, 207 *Heptagenia flavescens* SG=subgenital plate SA=subanal plate, 208 *Heptagenia pulla*, 209-210 *Nixe lucidipennis*, arrow indicates marginal lip on subgenital plate, 209 lateral, 210 ventral.

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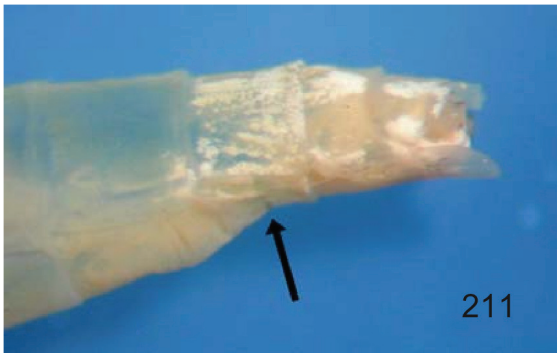
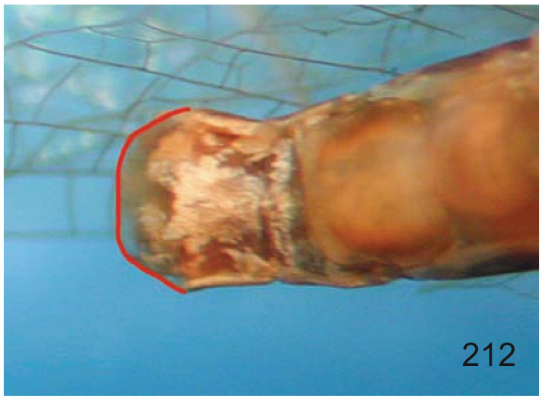
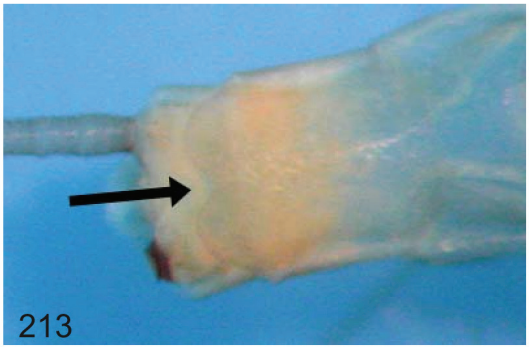




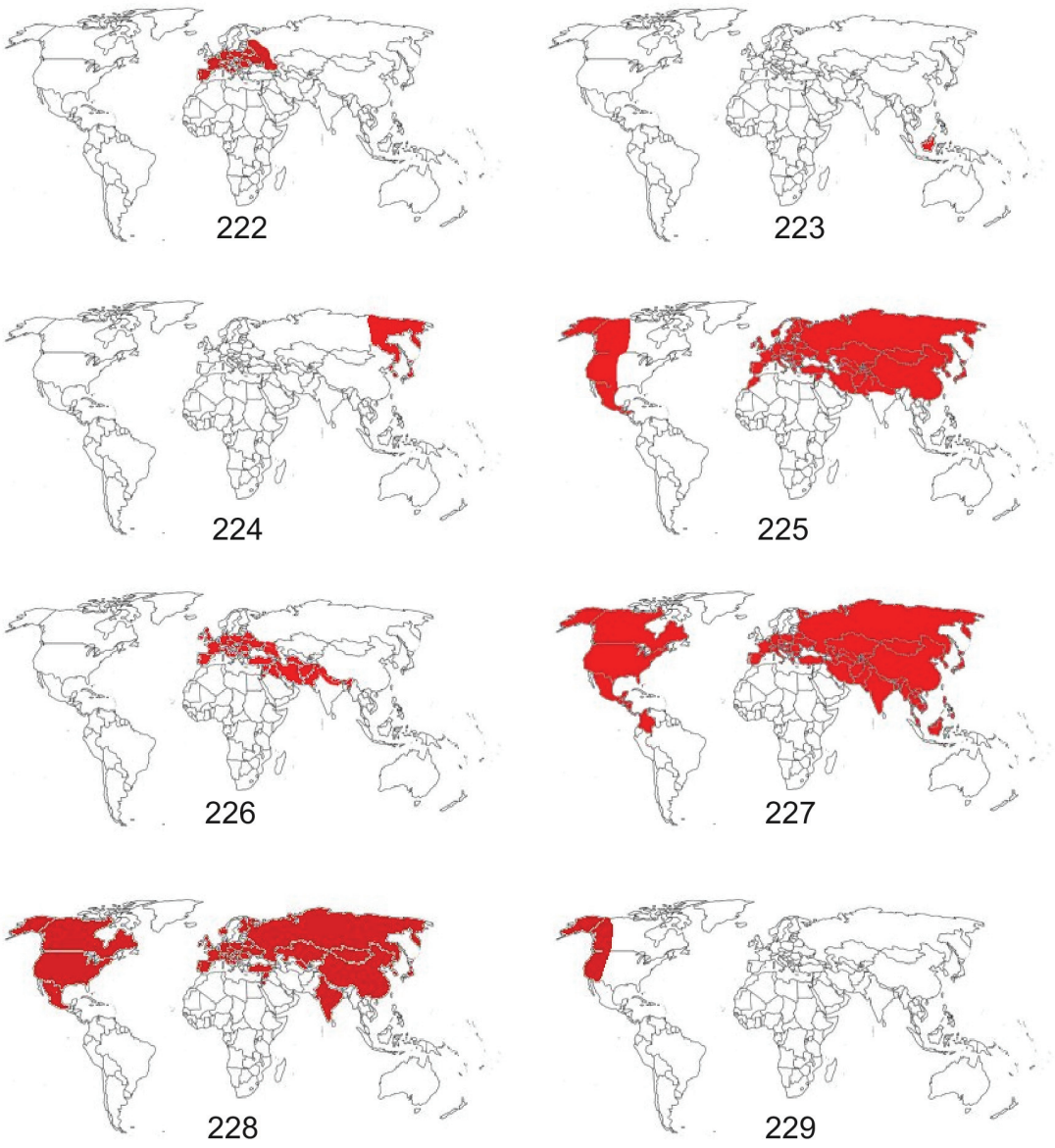


Figs. 211-213: female subanal plate. 211 *Ecdyonurus simplicioides*, arrow indicates lack of marginal lip on subgenital plate, 212 *Rhithrogena robusta*, subanal plate outlined in red, 213 *Cinygmula* sp, arrow indicates cleft in subanal plate.

doi: 10.3752/cjai.2008.07

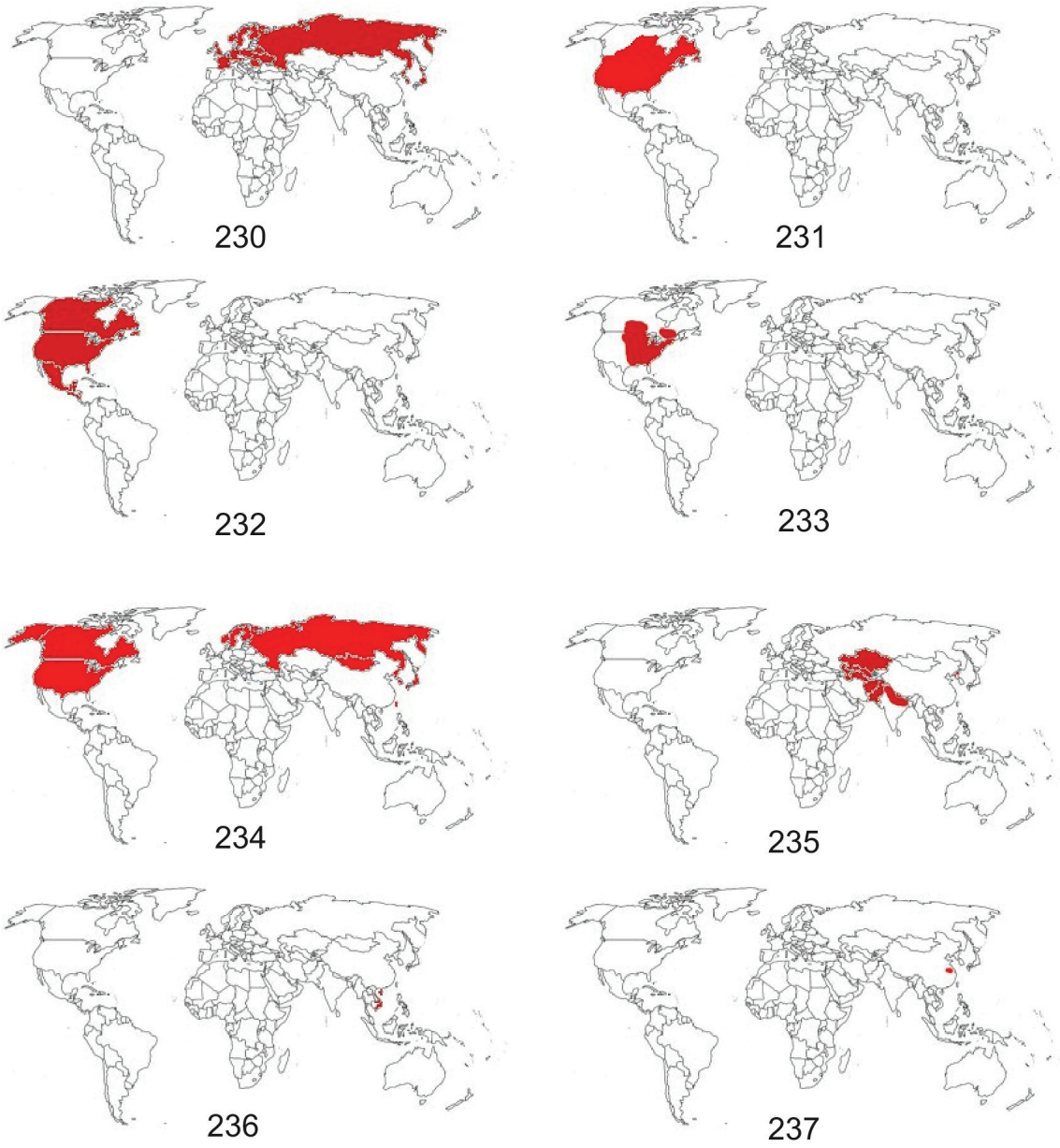
Figs. 214-221: General distribution. 214 *Afronurus*, 215 *Aneopeorus*, 216 *Asionurus*, 217 *Atopopus*, 218 *Bleptus*, 219 *Cinygma*, 220 *Cinygmula*, 221 *Compsoneuria*.

doi: 10.3752/cjai.2008.07



Figs. 222-229: General distribution. 222 *Dacnogenia*, 223 *Darthus*, 224 *Ecdyogymnurus*, 225 *Ecdyonurus*, 226 *Electrogena*, 227 *Epeorus*, 228 *Heptagenia*, 229 *Ironodes*.

doi: 10.3752/cjai.2008.07



Figs. 230-237: General distribution. 230 *Kageronia*, 231 *Leucrocuta*, 232 *Maccaffertium*, 233 *Macdunnoa*, 234 *Nixe*, 235 *Notacanthurus*, 236 *Paegnioides*, 237 *Parafronurus*.

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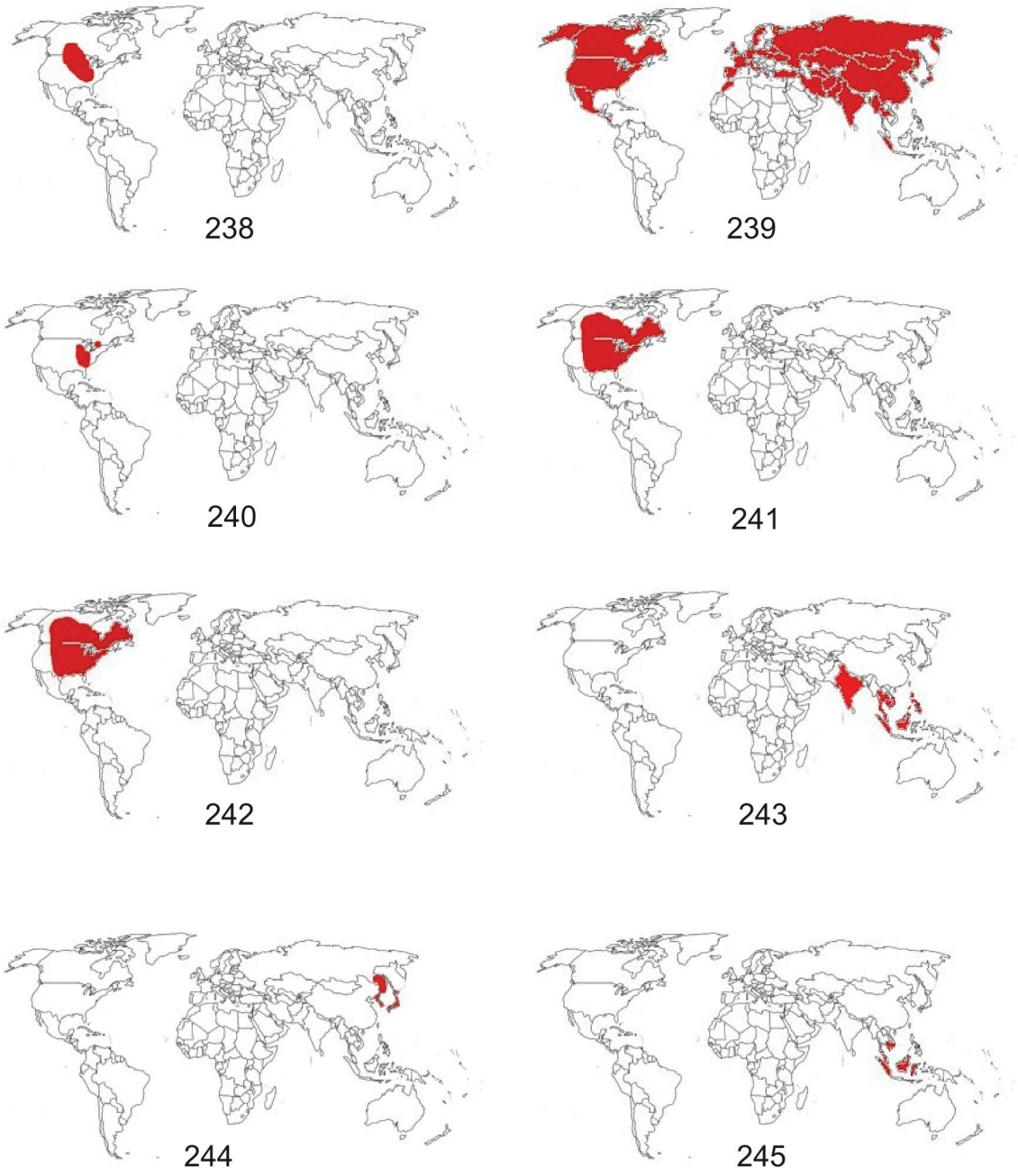

Figs. 238-245: General distribution. 238 *Raptoheptagenia*, 239 *Rhithrogena*, 240 *Spinadis*, 241 *Stenacron*, 242 *Stenonema*, 243 *Thalerosphyrus*, 244 *Thamnodontus*, 245 *Trichogenia*.

doi: 10.3752/cjai.2008.07

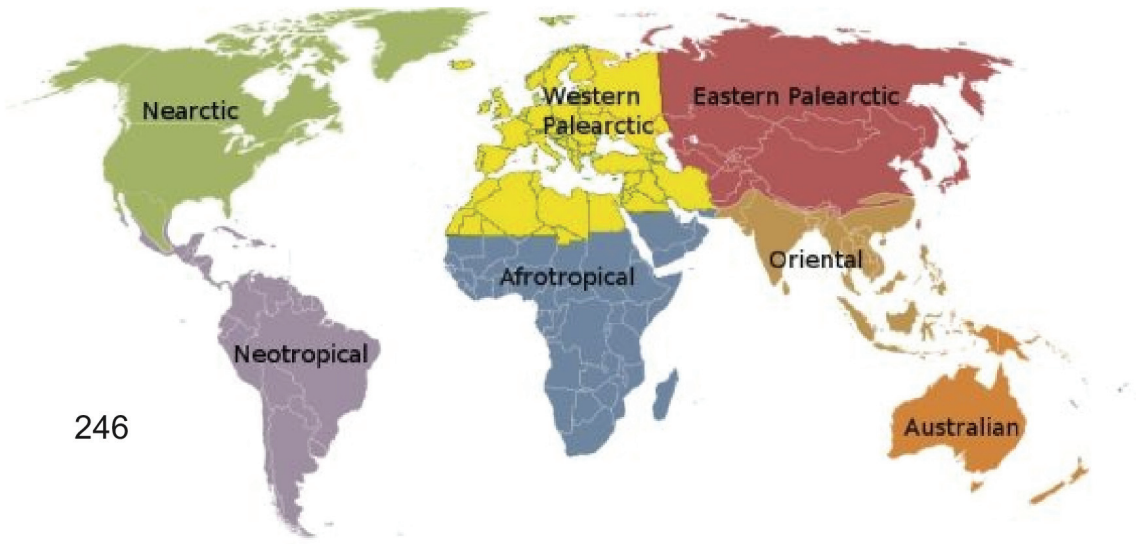

Fig. 246: Biogeographic realms.

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