Unit 7 - Paleoptera, Plecoptera, origin of wings

Open Entomology Project

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Introduction

In the insect phylogeny and fossil record we observe several adaptive radiations—*i.e.*, events where the emergence of some key innovation (or opportunity) facilitates the rapid diversification of new forms. The emergence of wings is arguably the most important of these key innovations, yet the origin of the structures and the selective forces that acted on early versions of wings remain enigmatic. We will discuss hypotheses of the origin of wings, including the strength of their evidence, before moving on to **Paleoptera** (or Palaeoptera) and the neopteran order **Plecoptera**.

Materials

- specimens (provided)
- fine forceps, probes (provided)
- sorting tray, watch glasses, gloves, safety glasses, glycerol, ethanol (provided)
- pencil/paper for sketches

Safety

We will be working with sharp tools. Wear your personal protective gear at all times. Specimens are to be returned to their vials after lab, and glycerol and ethanol will be collected for proper disposal or reuse.

Methods

Working with a partner, organize your space, specimens, tools, and microscope. Use your probe and forceps to manipulate the specimen. In this lab, however, we will not be dissecting specimens (unless otherwise noted). You can start anywhere in the handout.

Insecta: Pterygota

We're now looking at insects that have *wings*, which are usually present as two pairs: fore wings, which articulate with the mesothorax, and hind wings, which articulate with the metathorax.

Question 7-1: Why is the thoracic integument so heavily sclerotized, relative to other body parts and those structures in non-pterygote hexapods? What are the consequences of this phenotype?

Question 7-2: Why aren't there wings on the prothorax?

Pterygota: Palaeoptera

In the next two orders, the wing base inhibits wing folding (*i.e.*, wings held out or vertically over the thorax when at rest). The latest evidence indicates that these two orders comprise a monophyletic group, called Palaeoptera.

1 Ephemeroptera (mayflies)

1.1 Naiads

Mayflies are aquatic as immatures, and these stages are usually referred to as naiads or larvae (Not to be confused with the immature stages of holometabolous insects; more on that later.) Mayflies also spend the vast majority of their lives as naiads, and we can observe numerous adaptations for feeding and locomotion. We have naiads of the following three families, which should give you a sense of the phenotypic variation in Ephemeroptera: **Baetidae**, **Hetageniidae**, and **Ephemeridae**. After observing the immature stages see if you can answer the following questions:

Question 7-3: The bodies and head shapes of these mayflies yield clues about their life histories. Can you predict where each family is typically found and how eat it eats and moves through the water?

Question 7-4: Can you find evidence of developing wings or even evidence that suggests the origin of wings? Describe your observations.

Figure 1: Ephemeridae larva. Photo (CC BY-NC 2.0) by Roger Sanderson `https://flic.kr/p/fEVW7i`

(a) Heptageniidae larva. Photo (CC BY-NC 2.0) by Bob Henricks `https://flic.kr/p/9ExxWu`

(b) Baetidae habitus. Photo (CC BY-NC 2.0) by Bob Henricks `https://flic.kr/p/bqgXsZ`

1.2 Adults

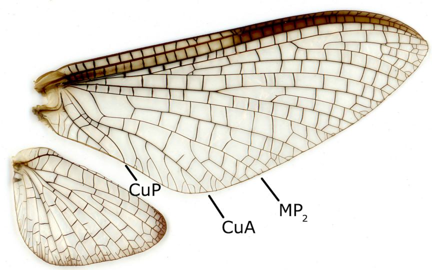
Wing venation and appendage phenotype offer important characters for family-level diagnosis of adults. See if you can understand the following set of characters, which could be used to recognize adults of three common families in Pennsylvania: **Ephemeridae**, **Heptageniidae**, and **Baetidae**. Note that these are not the only families you can collect easily in Pennsylvania!

- Male compound eye morphology: 0 = round, unmodified (Ephemeridae, Heptageniidae), 1 = turbinate (Fig. 5b) (Baetidae)
- Cubital intercalaries (between CuA and CuP) in fore wing: 0 = present as 2 parallel pairs (Heptageniidae), 1 = not present as 2 parallel pairs (Baetidae, Ephemeridae)
- Angle of MP_2 of fore wing: 0 = sharply angled towards Cu proximally (Ephemeridae), 1 = not sharply angled towards Cu proximally (Baetidae, Heptageniidae)
- Hind wing relative size: 0 = Very small, in some species almost absent (Baetidae), 1 = large, visible, with many veins (Ephemeridae, Heptageniidae)
- Hind leg tarsus subdivision number: 0 = 5 tarsomeres (Heptageniidae), 1 = 4 tarsomeres (Baetidae, some Ephemeridae), 2 = 3 tarsomeres (some Ephemeridae)
- Apical appendage number (*i.e.*, the thread-like appendages that are not genitalia): 0 = 3 (some Ephemeridae), 1 = 2 (*i.e.*, the median filamentous appendage is absent) (Baetidae, Heptageniidae, some Ephemeridae)

Test yourself

If you were given a naiad specimen (of the three families you looked at in lab) could you identify it by sight? What about the adult form?

Figure 3: Heptageniidae. Photo (CC BY-SA 2.5) by Richard Bartz `https://goo.gl/lIU2qx`



(a) Wing venation. Photo (CC BY 2.0) by Andy Deans `https://flic.kr/p/nDpya5`

(b) Habitus. Photo (CC BY-NC 2.0) by Anita Gould `https://flic.kr/p/f9eHPo`

Figure 4: Ephemeridae

(a) Female habitus. Photo (CC BY 2.0) by Andrey Zharkikh `https://flic.kr/p/AnyRSm`

(b) Male habitus, not conspecific with 5a. Photo (CC BY 2.0) by A N Suresh Kumar `https://flic.kr/p/F3WMQQ`

Figure 5: Baetidae

2 Odonata (dragonflies, damselflies)

Like their putative sister lineage, Ephemeroptera, immature Odonata are almost exclusively aquatic. All species are predaceous in all stages, with adaptations that facilitate prey tracking, stalking, and capture.

Question 7-5: Can you list at least three adaptations you see across Odonata families that you hypothesize are adaptations for predation?

Another conspicuous synapomorphy for Odonata is the evolution of a secondary copulatory organ ventrally on the first abdominal segment of males. Females are grabbed and held behind the head by the male, using his apical abdominal appendages. Be sure to look for adaptations associated with this unusual copulatory habit.

Question 7-6: Sketch an adaptations on the female head that you suspect is an adaptation to this kind of copulation. How do you think the secondary male genitalia evolved? What did the early, intermediate form look like?

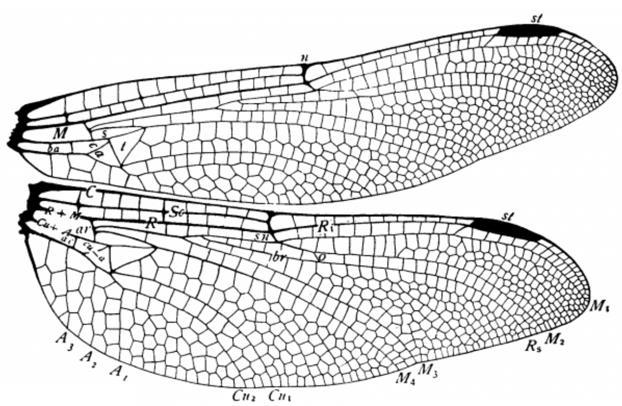
Odonata is the first group where each wing has a distinct pterostigma (pigmented spot on anterior edge of wing). The pterostigma is not only highly pigmented but also more sclerotized and more massive than other wing areas.

Question 7-7: What might be the function of the pterostigma in pterygote insects?

2.1 Gomphidae (clubtails)

Diagnostic characters: Compound eyes separated dorsally, triangular wing cells ("triangles") in fore wing and hind wing similar in shape and location, apical abdominal segments often expanded laterally.

Natural history: Larvae are usually found in lotic systems, where they bury themselves in the substrate and wait for prey. Look for adults on flat perches, *e.g.*, on the ground or on leaves. Approximately 900 spp. have been described worldwide.



(a) Wing venation (Comstock, 1918, Fig. 229)

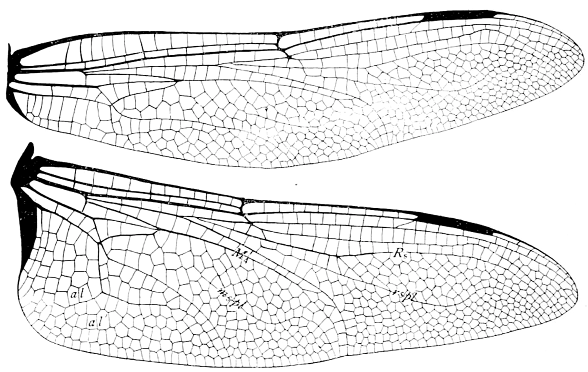
(b) Head and thorax. Photo (CC BY-NC-SA 2.0) by Matthew Oâ€™Donnell `https://flic.kr/p/dukePj`

Figure 6: Gomphidae

2.2 Aeshnidae (darners, hawkers)

Diagnostic characters: Compound eyes adjacent dorsally, triangular wing areas ("triangles") in fore wing and hind wing similar in shape and location, ovipositor well developed.

Natural history: Larvae are often thought of as being part of the "climber" guild of aquatic insects, as they are usually found in aquatic vegetation. Do they appear to be adapted for climbing and hunting in vegetation (see Fig. 12)? Adults are typically large and are very strong fliers. One can find these dragonflies in/near almost any aquatic habitat. Approximately 440 spp. have been described worldwide.



(a) Wing venation (Comstock, 1918, Fig. 236)

(b) Habitus. Photo (CC BY-NC 2.0) by Adedotun Ajibade `https://flic.kr/p/fn8NtW`

Figure 7: Aeshnidae

2.3 Libellulidae (common skimmers)

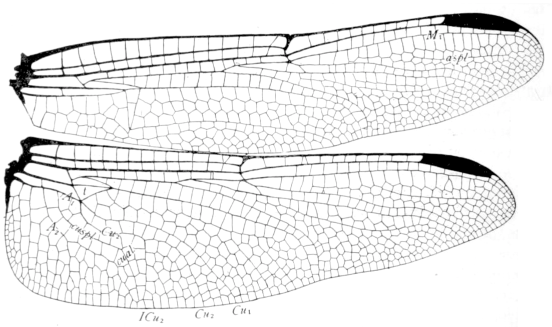
Diagnostic characters: Compound eyes meeting dorsally, triangles in fore wing and hind wing different in shape, hind wing with boot-shaped area, ovipositor absent.

Natural history: Larvae are usually thought of as "sprawlers", which generally sit relatively still on the bottom, in the sediment, waiting for prey. Can you see major morphological differences between these larvae and other odonates? Adults are diverse in size, color, and habitat. More than 1,000 spp. have been described worldwide.

2.4 Calopterygidae (jewelwings, broad-winged damselflies)

Diagnostic characters: Wings tapered at base, numerous antenodal crossveins present (proximal to nodus).

Natural history: Like other damselflies, larvae are usually thought of as climbers. Larvae and adults are usually found along streams (*i.e.*, lotic systems). Approximately 150 spp. have been described

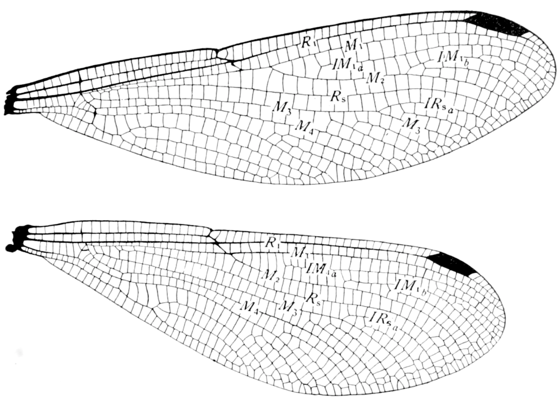


(a) Wing venation (Comstock, 1918, Fig. 240)

(b) Head. Photo (CC BY-NC-SA 2.0) by e_monk `https://flic.kr/p/8ua4sD`

Figure 8: Libellulidae

worldwide.



(a) Wing venation (Comstock, 1918, Fig. 235)

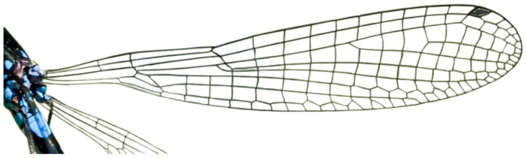
(b) Habitus. Photo (CC BY-NC-SA 2.0) by Mark Gurney `https://flic.kr/p/Cey6u8`

Figure 9: Calopterygidae

2.5 Coenagrionidae (bluets, narrow-winged damselflies)

Diagnostic characters: wings stalked at base, few antenodal crossveins present, M_3 arises near nodus, quadrangle wing cell actually triangular.

Natural history: Given the high level of diversity (>1,100 spp.), one can find these odonates in almost any aquatic habitat. Like other damselflies, larvae are usually thought of as climbers. Females oviposit in or near vegetation.



(a) Fore wing. Photo (CC BY-SA 3.0) by L. B. Tettenborn `https://goo.gl/WLujq8`

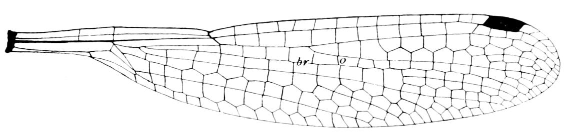
(b) Habitus. Photo (CC BY-NC-SA 2.0) by Patrick Coin `https://flic.kr/p/2t47VF`

Figure 10: Coenagrionidae

2.6 Lestidae (spreadwings)

Diagnostic characters: wings stalked at base, few antenodal crossveins present, M_3 arises near arculus, quadrangle wing cell actually quadrangular.

Natural history: Naiads are found in a variety of aquatic environments and have a distinctive, elongate habitus and a spoon-like labium. Unlike other damselflies, adult lestids usually rest on vegetation with their wings at least partially spread. Approximately 150 spp. have been described worldwide.



(a) Wing venation (Comstock, 1918, Fig. 232)

(b) Habitus. Photo (CC BY-NC 2.0) by Mathesont `https://flic.kr/p/d3aZu3`

Figure 11: Lestidae

2.7 Naiads

Take a moment to observe Odonata naiads of these families under your microscope. Could you determine each family by sight?

Question 7-8: Can you find two larval adaptations for predation?

Question 7-9: What morphological differences to you see between a dragonfly naiad and a damselfly naiad? Make a sketch.

Figure 12: Aeshnidae. Photo (CC BY-NC 2.5) by Brad Carlson `https://flic.kr/p/bLjCAp`

Pterygota: Neoptera

The remaining insect orders are classified in Neoptera, a lineage whose members can pull their wings over their abdomens when they're at rest. This movement is accomplished by flexing a pleural muscle that inserts on the 3rd axillary sclerite. The wing then folds along flexion lines that are not present in Palaeoptera, allowing the wing to be pulled back posteriorly.

> **Question 7-10:** In this unit we've touched on two evolutionary events that are considered to be *`key innovations`*: the origin of wings and the the origin of neoptery. Why do you think these two adaptations led to explosive diversification?

3 Plecoptera (stoneflies)

Like the previous two orders, Plecoptera are aquatic during their immature stages and semi-aquatic/terrestrial as adults. More than 100 million years of evolution probably separates Plecoptera from Odonata and Ephemeroptera (Misof *et al.*, 2014), however, so stoneflies are not closely related (relatively speaking) to dragonflies and mayflies. It is useful to treat them here, however, as they have similar habits to mayflies, are important for monitoring water quality (like Ephemeroptera), and have inspired much speculation on the origin of wings.

Naiads

Stonefly naiads are almost exclusively found in lotic environments—*e.g.*, clear, clean, highly oxygenated streams—and they are generally very sensitive to water quality. The immature stages develop as predators of other aquatic invertebrates or as shredders of vegetative material. They can be recognized from other aquatic non-holometabolous insects by (a) the presence of two tarsal claws on each leg and (b) two cerci on the apex of the abdomen.

Select specimens of at least three families and look for phenotypic differences in these diagnostic traits:

- presence/absence of gill tufts on the thorax and/or abdomen

– width and shape of nota in dorsal view

Adults

Stoneflies are generally not good dispersers and so are found near the features from which their naiads emerged. The diagnostic features can be subtle, so it's important to spend some time understanding the relevant morphology:

- Glossa length relative to paraglossa length (*cf.*[1] Perlidae or Perlodidae *vs.* Leuctridae or Capniidae)
- Presence/location of gill remnants (*cf.* Perlidae *vs.* Perlodidae. Hint: look near the coxae)
- Wing phenotype at rest (*cf.* Perlidae or Perlodidae *vs.* Leuctridae)
- Wing venation (Figure 13)
- Relative length of the cerci (*cf.* Perlidae or Perlodidae *vs.* Leuctridae)

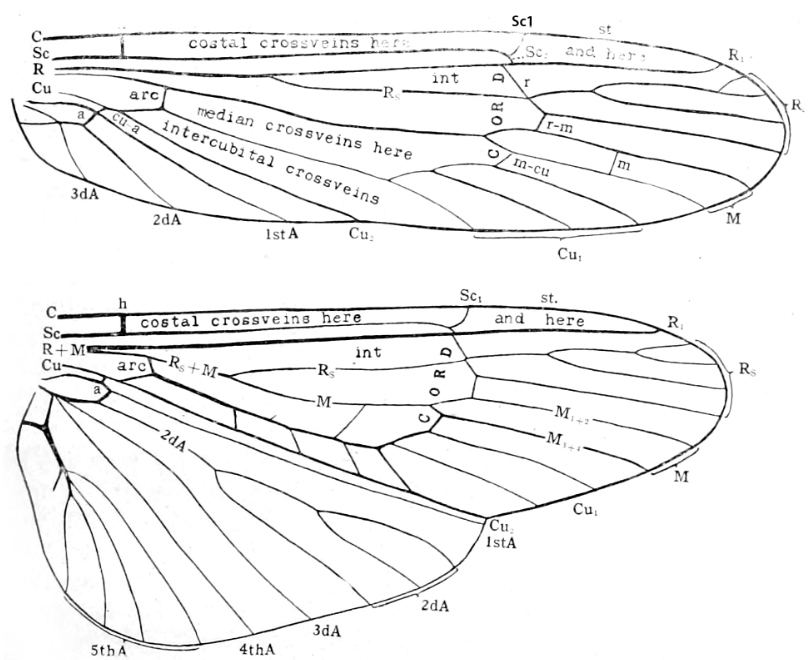


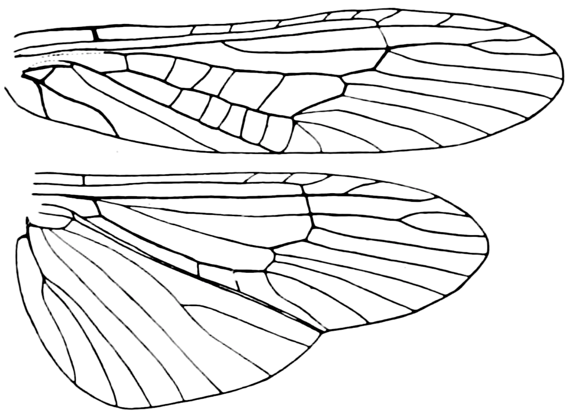
Figure 13: Plecoptera wing venation (modified from Needham and Claassen, 1925, Fig. 1)

3.1 Perlidae (common stoneflies)

Diagnostic characters: Glossae much shorter than paraglossae, cercus longer than pronotum width, branched gill remnants present behind leg bases, , fore wing not rolled around body.

[1] From the Latin verb *conferre*, to bring together, used here to invite the reader to compare the listed taxa.

Natural history: More than 80 species are known, the vast majority of which can be found in eastern North America. Naiads are predators of other invertebrates, primarily in lotic habitats.



(a) Wings (modified from Needham and Claassen, 1925, Plate 11, Fig. 3)

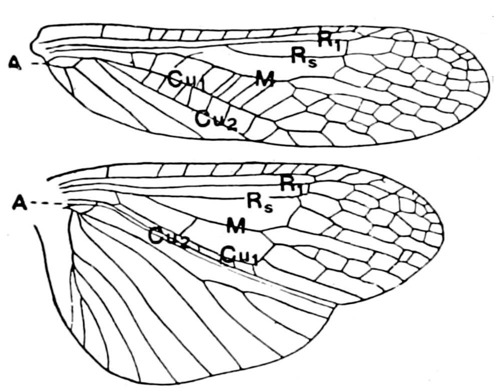
(b) Perlidae. Photo (CC BY-SA 2.0) by Jerry Schoen `https://flic.kr/p/o3rdmk`

Figure 14: Perlidae

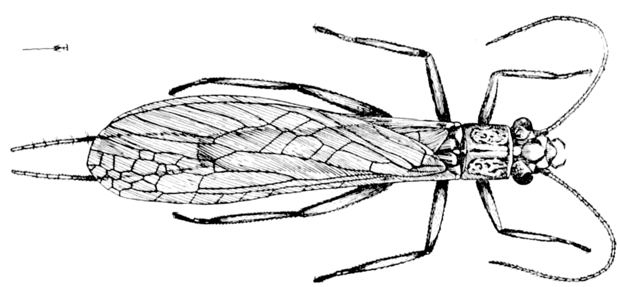
3.2 Perlodidae

Diagnostic characters: Glossae much shorter than paraglossae, cercus longer than pronotum width, branched gill remnants absent, cubito-anal crossvein arising distal to anal cell, 4 or more Cu crossveins on fore wing, 2A forked, fore wing not rolled around body.

Natural history: More than 100 species are known. Naiads are somewhat flattened dorso-ventrally and are predators of other invertebrates, usually in lotic environments.



(a) Wings (modified from Needham and Claassen, 1925, Plate 9, Fig. 1)



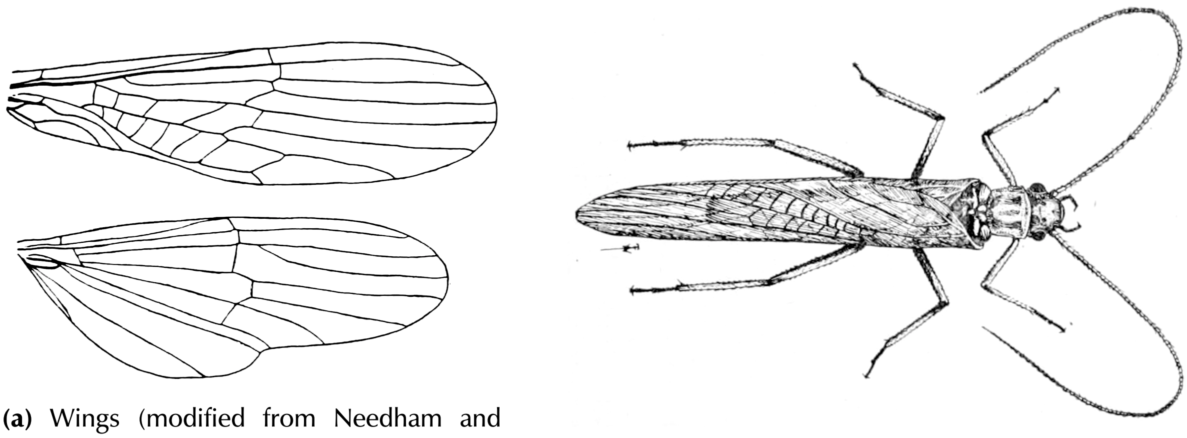
(b) Wings (modified from Needham and Claassen, 1925, Fig. 12)

Figure 15: Perlodidae

3.3 Leuctridae (rolled-wing stoneflies)

Diagnostic characters: Glossae same length as paraglossae, cercus very short composed of one segment, branched gill remnants absent, cubito-anal crossvein arising distal to or from anal cell, 4 or more Cu crossveins on fore wing; 2A forked, fore wings rolled around body.

Natural history: Relatively small as adults (~1 cm long). Naiads feed on plants. More than 350 species are known worldwide, distributed primarily across the Holarctic.



(a) Wings (modified from Needham and Claassen, 1925, Plate 32, Fig. 1)

(b) Wings (modified from Needham and Claassen, 1925, Fig. 26)

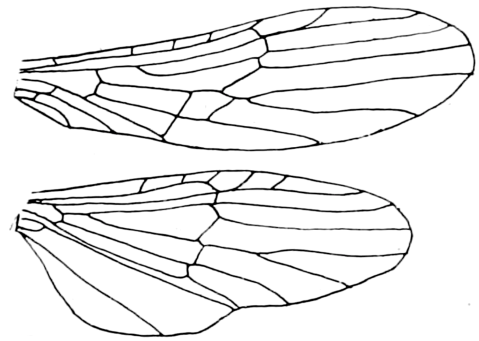
Figure 16: Perlodidae

3.4 Capniidae (winter stoneflies)

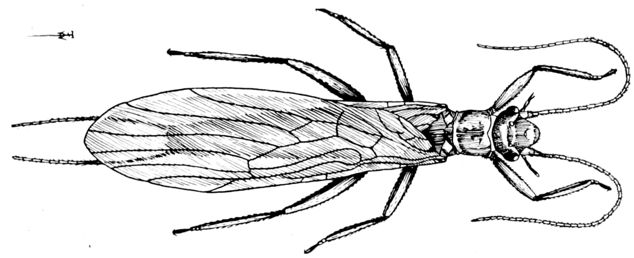
Diagnostic characters: Glossae same length as paraglossae, cercus with at least 4 segments, gill remnants absent, cubito-anal crossvein arising distal to or from anal cell, 1–2 or more Cu crossveins on fore wing, 2A not forked.

Natural history: Similar in size, habitus, and diversity to Leuctridae. Adults are active in winter. Naiads are lotic, primarily in hyporheic zone.

Question 7-11: How did wings evolve? Did they develop *de novo* or from existing structures? Why? Based on what you have learned in this course, what is the most plausible explanation for the origin of wings?



(a) Wings (modified from Needham and Claassen, 1925, Plate 47, Fig. 2)



(b) Habitus (modified from Needham and Claassen, 1925, Fig. 28)

Figure 17: Capniidae

Test yourself

After listening to the class discussion, which hypothesis do you think most accurately explains the origin of wings in insects and why?

We talked about several adaptations one can see in paleopterans—for feeding, flying, mating, living in aquatic habitats, *etc*. Which three are the most significant or interesting to you and why?

Epilogue

This handout is part of an open curriculum. Original files are available free for anyone to download, copy, modify, and improve at the Open Entomology GitHub repository (Open Entomology Project, 2016), which also provides a mechanism for reporting problems and other feedback:
`https://github.com/OpenEntomology/InsectBiodiversityEvolution/issues`

Acknowledgments

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References

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