Tabanid Flies C to T

Chrysops to *Tabanus*

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The Tabanid Flies (Class Insecta: Order Diptera: Family Tabanidae)

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The Flies – (Order Diptera: Family Tabanidae)

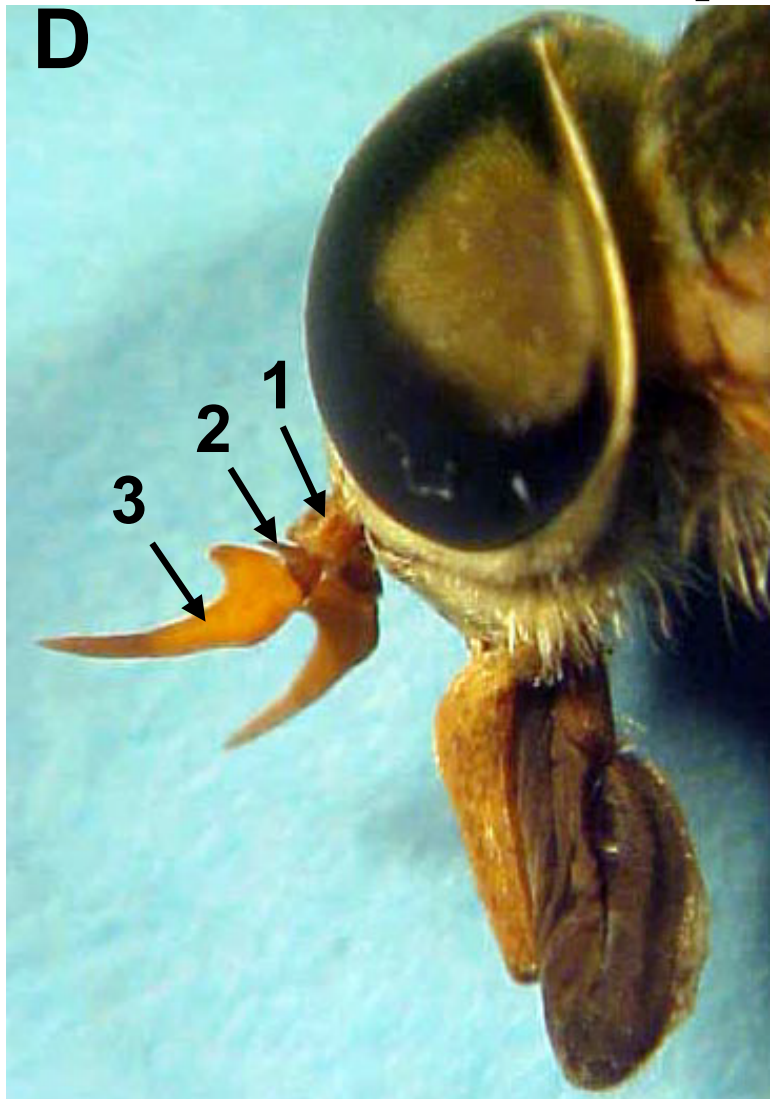
A. Study Goals

The principle aim of this e-Book is to assist the beginning reader in gaining a better understanding of basic morphology of deer flies and horse flies rather than offering discussions on pathogens or epidemiology of pathogens vectored by these dipterans. There are many genera and species with wide geographic distributions, but it is not the intent of this e-Book to discuss taxonomic issues that are best left to the experienced tabanid specialist. Readers are referred to the following reference work for a thorough treatment of these insects, the pathogens they vector, and for an extensive coverage of the literature.

Mullen, G. R. and L. A. Durden (eds.). 2009. Medical and Veterinary Entomology, 2nd Ed., Academic Press, 637 pp.

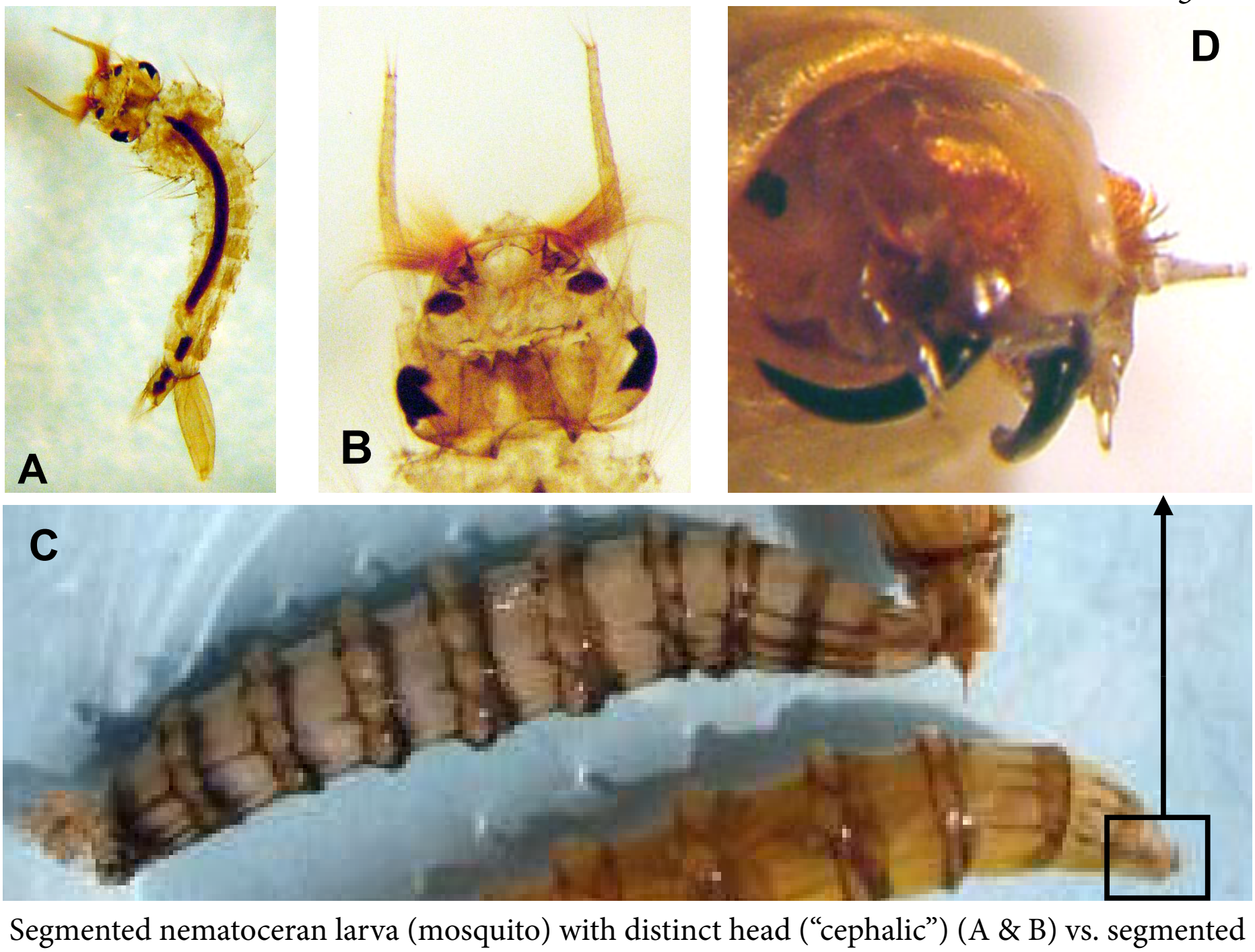
B. The Diptera – General Comments

The Order Diptera (meaning "two-winged) is a large assemblage of insects (Class Insecta) with many species of medical and veterinary importance. This Order may be divided into two suborders: the Nematocera, and the Brachycera. Members of the Nematocera (i.e., "nematocerans") are small, "light-bodied", flies possessing filamentous (long, thin) antennae having many segments (more than six), with each segment equivalent in size, whereas members of the Brachycera are "stout-bodied" flies that possess antennae with two, short, basal segments, and a long third segment. Some brachycerans bear a prominent structure called the arista on the antenna, but this structure is not present in tabanids. Additionally, larvae of nematocerans have a distinct head (i.e., "cephalic"); those of brachycerans exhibit a reduced, indistinct, head (sometimes referred to as "acephalic"). We will confine our discussion in this e-Book to selected members of the Brachycera, specifically the "tabanids", or members of the family Tabanidae. The principal focus of this e-Book is to learn some identifying characteristics of tabanid flies, rather than providing discussion on geographic distributions, or pathogens associated with these flies.



Light-bodied nematoceran (*Aedes* sp.) with many-segmented filamentous antennae (A & B) vs. robust-bodied brachyceran (*Tabanus* sp.) with 3-segmented antennae (C & D).

Brachyceran with arista (arrow) on antenna.

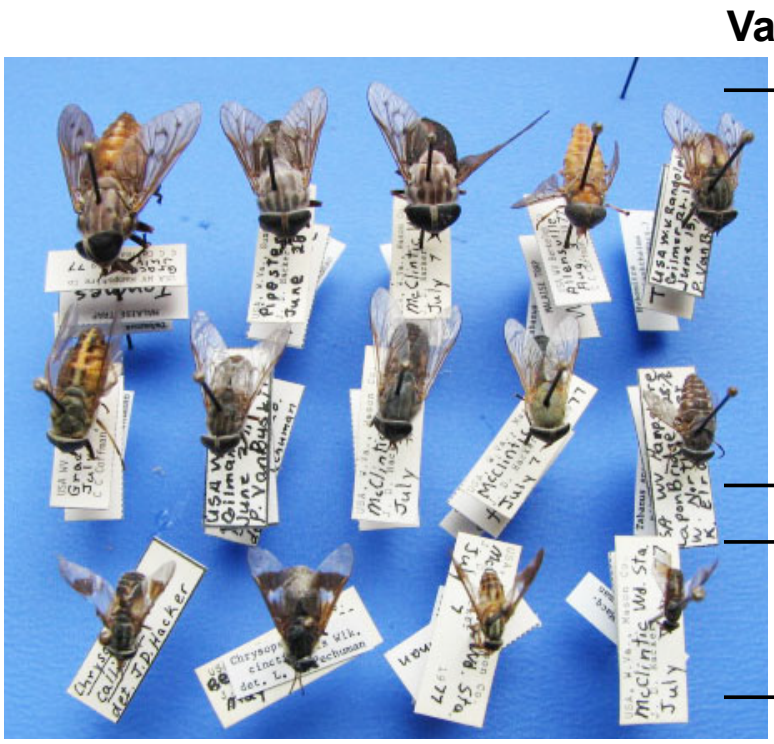


Segmented nematoceran larva (mosquito) with distinct head (“cephalic”) (A & B) vs. segmented brachyceran larva (horse fly) with indistinct head (“acephalic) (C & D).

C. The Tabanidae

Members of the Tabanidae are large flies with diurnal biting habits. These flies are the “horse flies” and “deer flies” that we are familiar with because of their persistent, painful, biting activity. Indeed, common names, such as “bulldog”, or “gadfly”, reflect the aggressiveness of these flies in seeking blood meals. These flies often pose a serious nuisance to livestock, and they are mechanical vectors of pathogens that cause surra, anaplasmosis, and equine infectious anemia. The activity of even a moderate number of flies feeding on livestock can result in significant losses in production.

Tabanid flies tend to be seasonal, with different species emerging for short periods (sometimes just a few weeks) throughout the year; hence the common names of “March fly”, or “May fly” that are sometimes used.



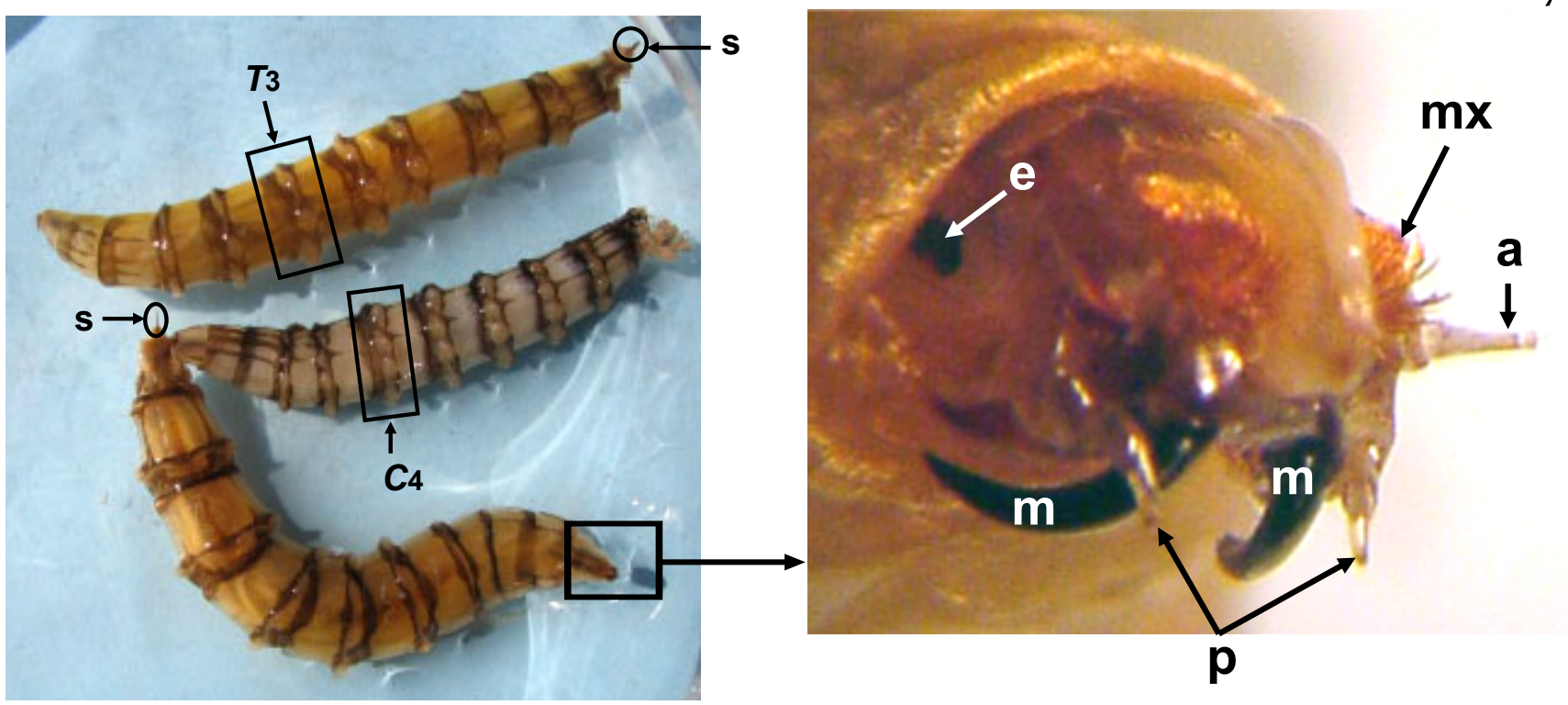
Relative sizes of "tabanids."

D. Life cycle

Female tabanids lay eggs on leaves, rocks, or debris overhanging water. Eggs of *Chrysops* are often deposited in a single layer; those of *Tabanus* stratified into three to four layers. Hatching is temperature dependent, taking place in four (or more) days.

The larva emerges from the egg and molts soon after emergence. The second instar (i.e., 2nd stage larva) does not feed, but moves over the substrate closely associated with water. In 3 to 6 days the 2nd instar molts to the 3rd instar which burrows into the substrate where it will remain for several months. The number of molts is variable, from 7 to 11 instars, even in the same species.

Larval instars are soft bodied, and cylindrical, with a reduced head that can be retracted into the thorax. The thorax and abdomen of larvae merge imperceptibly. There are three thoracic segments, and eight abdominal segments. Spiracles (openings to the breathing system) open at the end of a siphon, located dorsally on the 8th (terminal) abdominal segment. Larval movement is aided by ventro-lateral pseudopodia, with three pairs of these structures in *Chrysops* and four pairs in *Tabanus*. Larvae of *Tabanus* are carnivorous, sometimes cannibalistic, whereas *Chrysops* larvae feed on plant debris. The head is indistinct when compared with that of a nematoceran larvae, but close examination reveals a pair of simple eye(s), maxillae, antennae, palps, and well developed mandibles. *Chrysops* larvae generally occur in the wettest situations (they are said to be hydrobionts), whereas *Tabanus* larvae are hemi-hydrobionts (occurring in soil near water).



Examples of tabanid larvae: C4 indicating the four pseudopodia characteristic of *Chrysops* larvae, and the T3 indicating three pseudopodia of *Tabanus*. Legend: a, antenna; e, simple eye; m, mandible; mx, maxilla; p, palp; s, siphon.

Last stage larvae migrate to the edge of aquatic habitats and burrow into the muddy substrate, eventually forming a pupa that exists for one to three weeks. Pupae have a distinct head, thorax, and abdomen, but they are limited in movement. Breathing takes place through a pair of thoracic spiracles and seven pairs of abdominal spiracles that occur on small projections extending laterally. Adults emerge from the pupa, moving up through the thin layer of overlying substrate. Emergent males form swarms and females fly through the swarms where they are seized by males. After insemination, females seek blood meals which, in most species, are required for egg development. In a few species the females are said to be autogenous; that is they are capable of laying eggs without a prior blood meal. Males do not take blood meals.

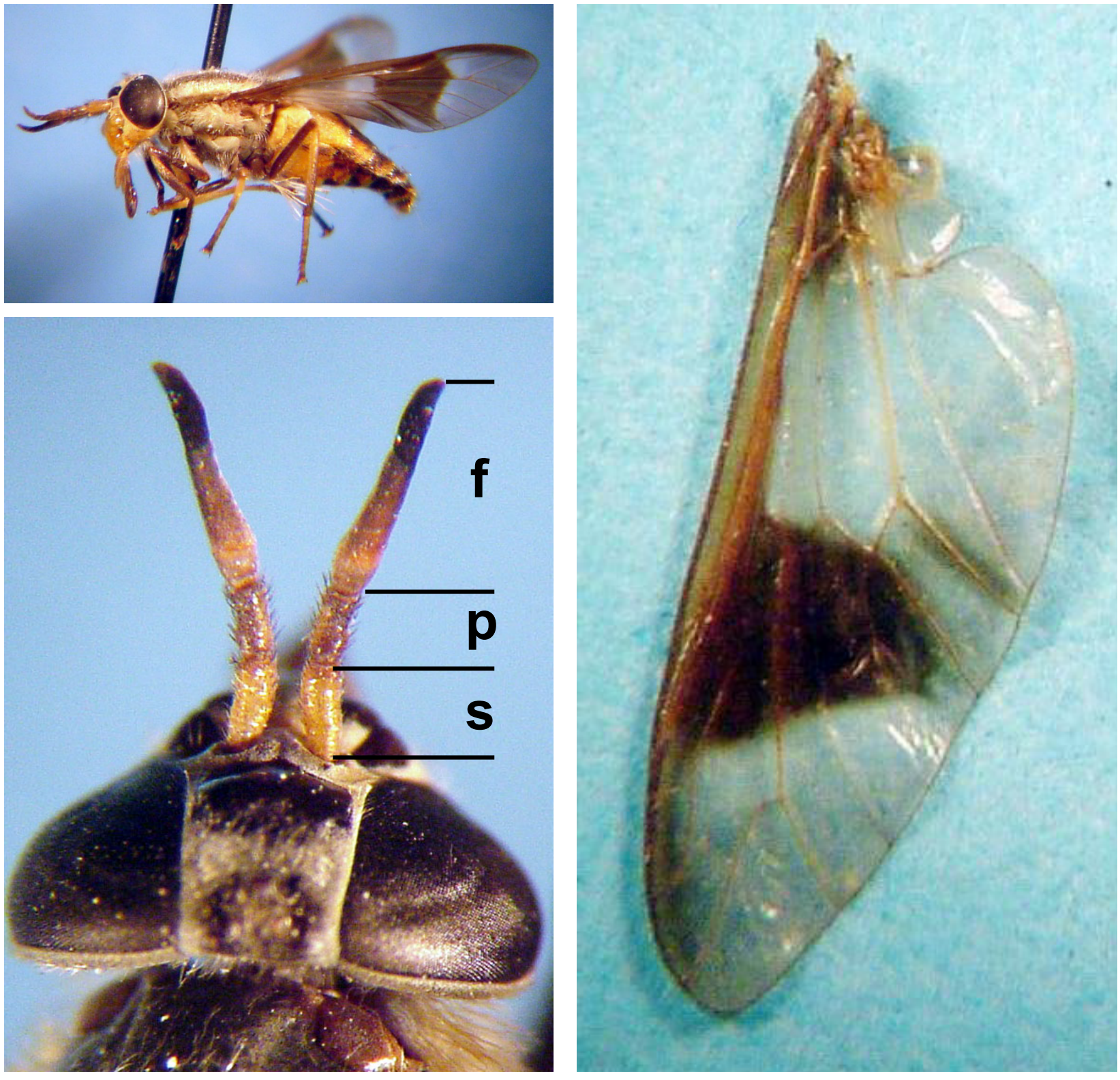
E. Taxonomy

There are approximately 4,300 species and subspecies of tabanids known worldwide, of which 335 species are known in the Nearctic Region. The temperate fauna is relatively well known, but the tropical fauna has received less attention.

We will consider two subfamilies of the Tabanidae: (1) the Chrysopsinae; and (2) the Tabaninae. (Note in zoological nomenclature the family name ends with "-idae"; the subfamily with "-inae"). For our purposes we will concentrate on *Chrysops* (deer flies), the dominant genus in the former subfamily, and *Tabanus* and *Hybomitra* (horse flies), dominant North American genera of the latter subfamily.

E-1. *Chrysops*

Deer flies are the smaller tabanids, adults ranging from 6 to 10 mm in length. Two characteristic features of deer flies are their "pictured wings", which have a dark anterior border and a dark "splotch" in the middle of the wing, and their very long antennae and mouthparts, relative to body size .



"Pictured" wings and elongate antennae of *Chrysops* sp. Legend: f, flagellum; p, pedicile; s, scape.

There are three segments making up the antennae of these flies; the proximal scape, the pedicle, and the flagellum (terminal segment of the antenna). The flagellum is further divided into small flagellomeres, or pseudosegments. The flagellum of deer flies is considerably longer than that of horse flies.

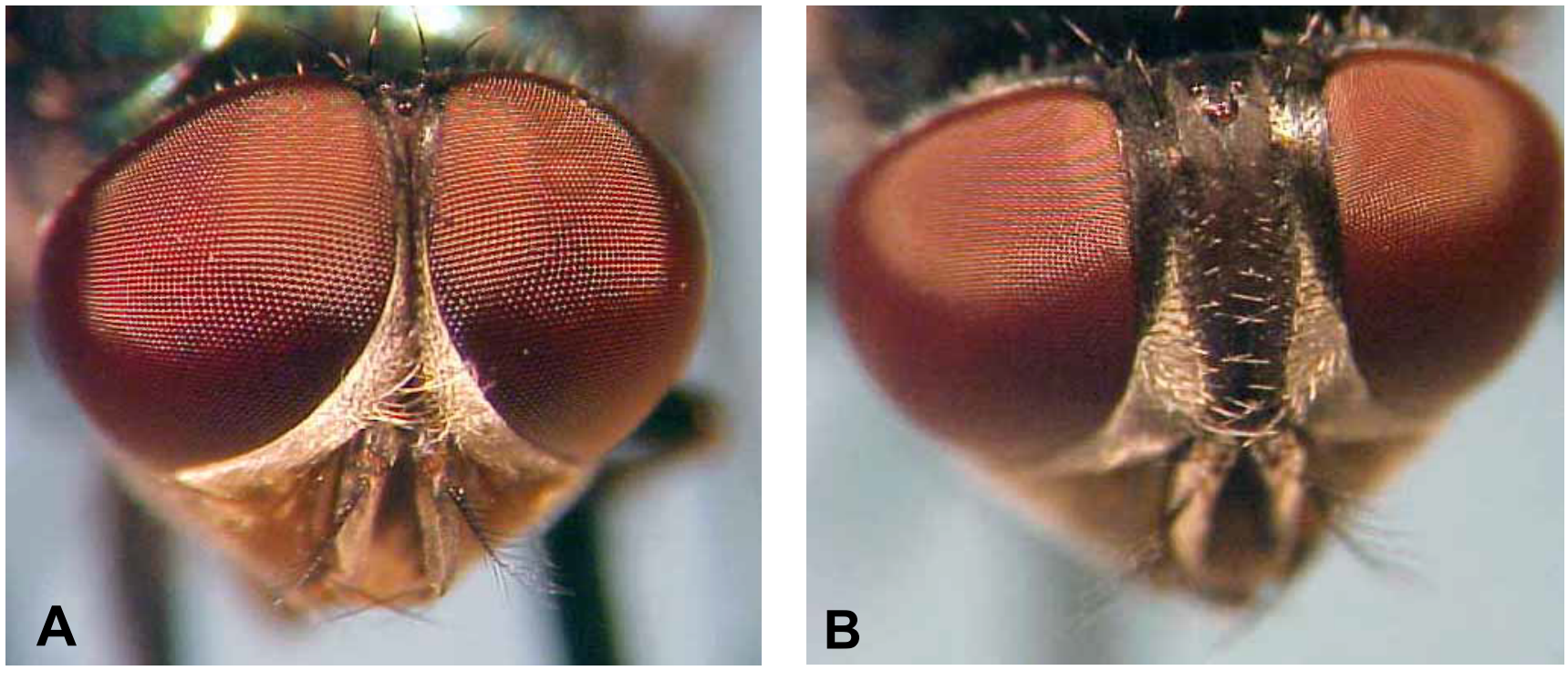
Only females take blood meals (i.e., they are hematophagus); males feed on plant juices. As a consequence of these differences in feeding strategies by gender, the tip of

the labrum is different. In females, for example, there is a distinct “rasping” structure at the tip of the labrum, whereas males do not possess this feature.

Tabanus americanus *Tabanus atratus*

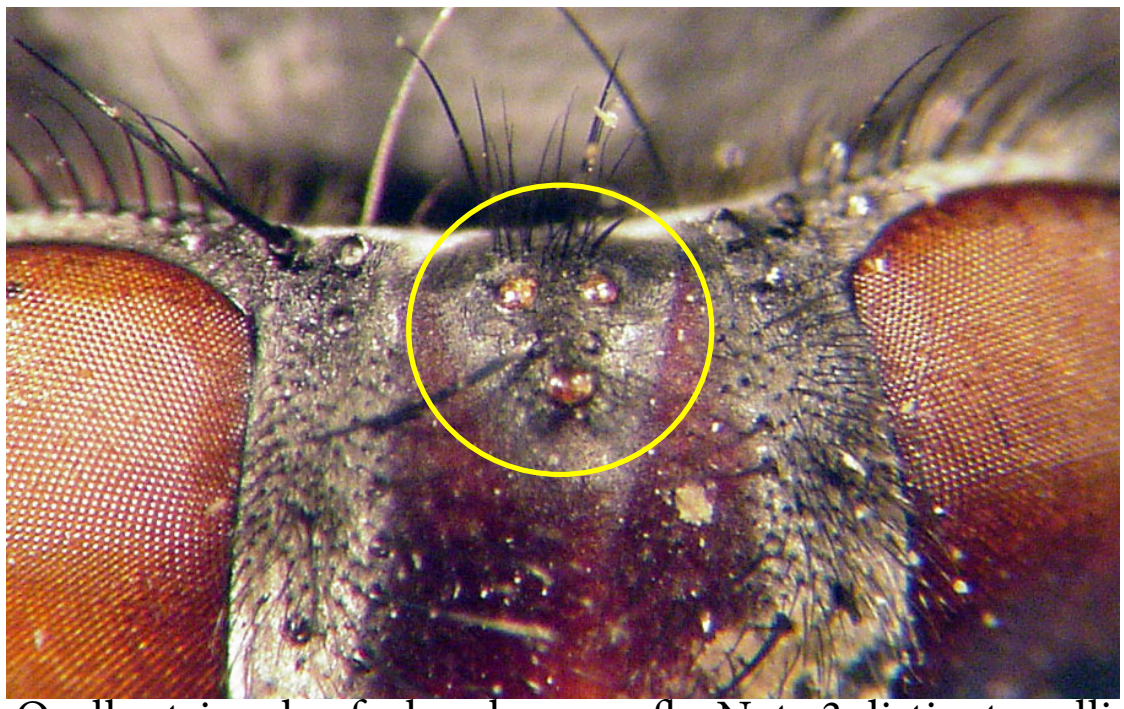
Tip of labrum in male (A, *Tabanus americanus*) vs. female (B, *Tabanus atratus*) horseflies. Note: only females take blood meals. Scale bars = 50 *u*m.

There is a distinct sexual dimorphism (i.e., morphological feature used to distinguish between males and females) in deer flies. The eyes of males are very large, occupying most of the head, nearly touching when seen in an en face view. This condition is known as holoptic. The eyes of females, on the other hand, are distinctly separated by the frons, a condition known as dichoptic.



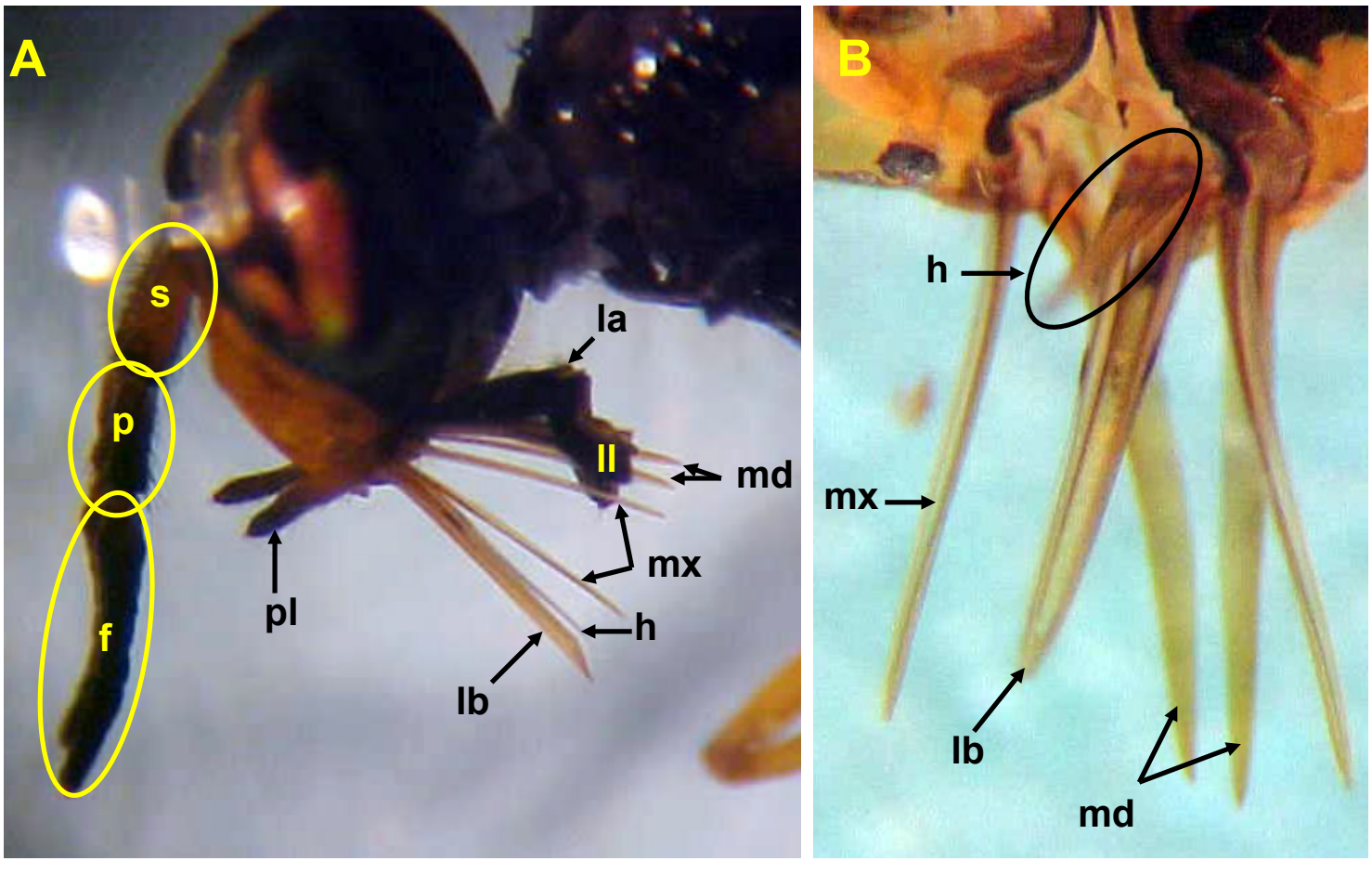
Sexual dimorphism in a brachyceran fly: A, holoptic condition (male); B, dichoptic condition (female). Note ocelli, or simple eyes in ocellar triangle.

In addition, there are three well developed simple eyes (i.e., ocelli, sing. ocellus) at the vertex (top) of the head positioned to form the ocellar triangle. Ocelli do not form images, but rather are light sensing organs.



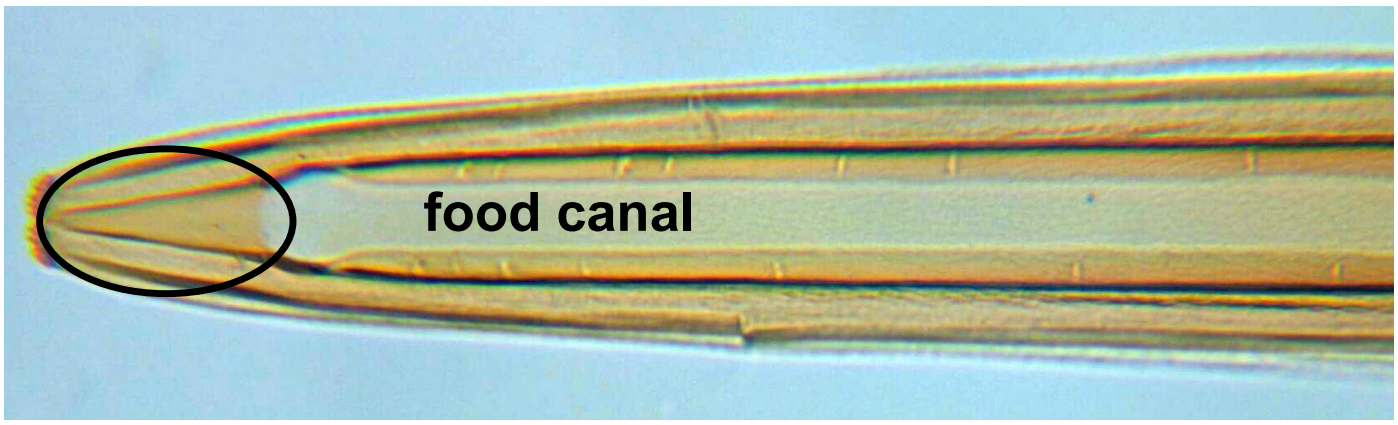
Ocellar triangle of a brachyceran fly. Note 3 distinct ocelli (highlighted by oval) positioned on vertex of head between compound eyes.

The mouthparts of deer flies are of the piercing-sucking type. Six blade-like mouthparts penetrate the skin to facilitate feeding: 1 labrum; 1 hypopharynx; 2 mandibles; and 2 maxillary laciniae. When the fly is at rest (i.e., not feeding) these six piercing stylets are ensheathed in a labial groove of the labium (which does not enter the host's skin during feeding). The labium terminates in small structures called the labella.

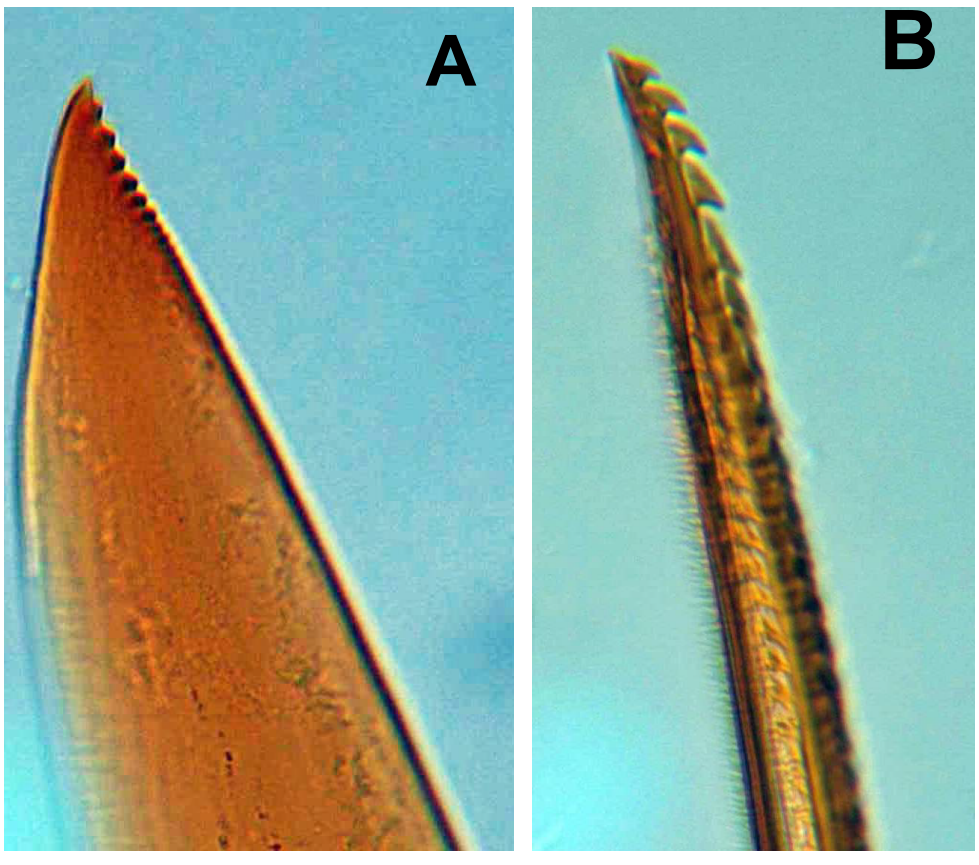


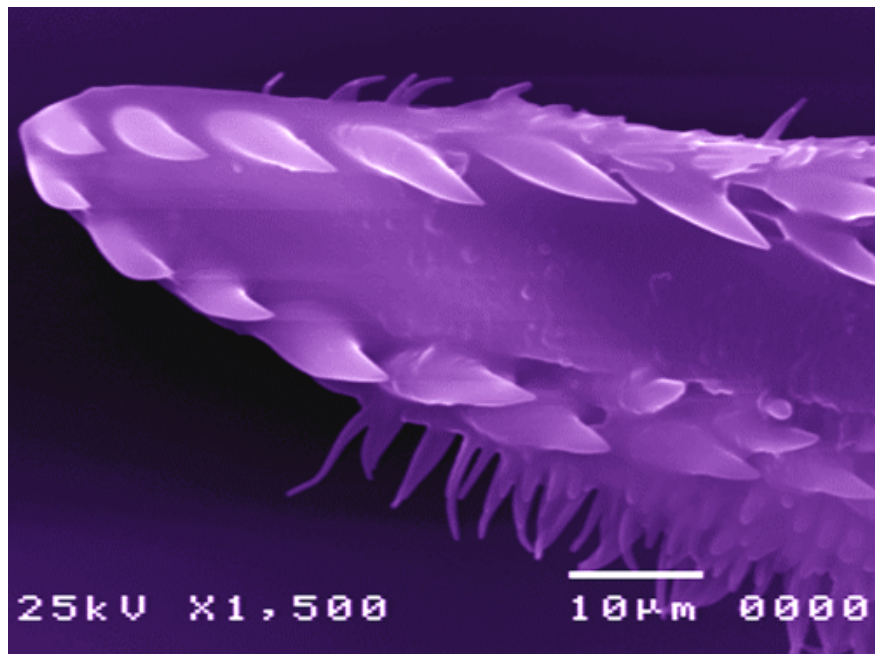
Chrysops sp.: A, lateral view of head; B, mouthparts. Legend: antenna (f, flabellum; p, pedicle; s, scape); h, hypopharynx; la, labium; lb, labrum (with food canal); ll, labellum; md, mandibles; mx, maxillae; pl, palp.

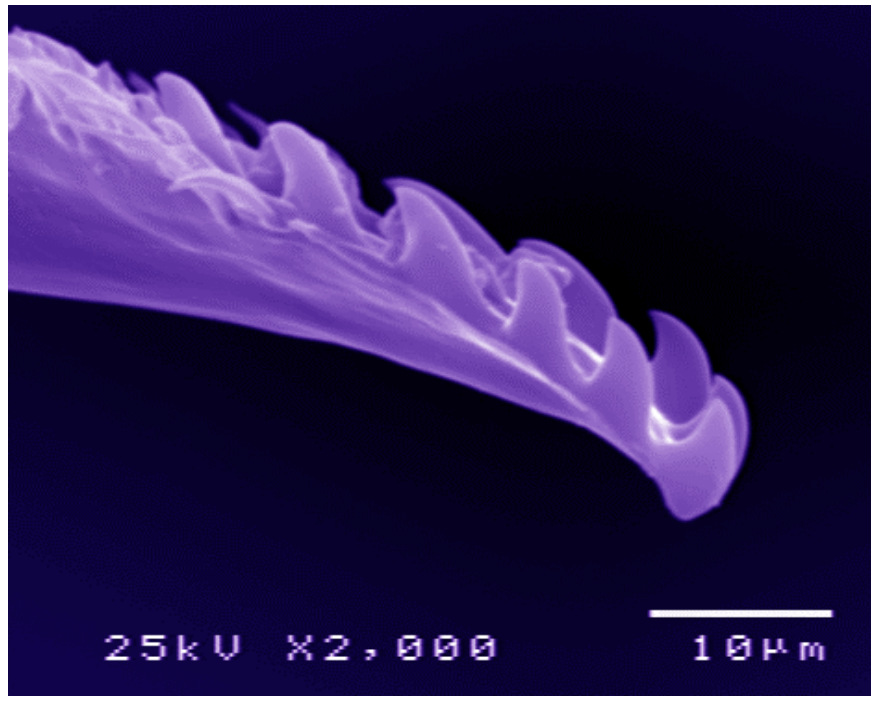
The mandibles and maxillae are employed to lacerate capillaries to form a pool of blood which is drawn up through a food canal that is housed in the labrum. Note that a short, funnel-shaped, vestibule immediately precedes the food canal. Mandibles possess small serrations on their inner margins, whereas laciniae have prominent backward pointing teeth. Mandibles, with small serrations on the medial edge, move laterally in a scissor-like cutting motion, while the maxillae with recurved teeth move "in and out." The combined action of these four structures is very effective in lacerating capillaries to create a small pool of blood. The hypopharynx carries a small tube, the salivary canal. Saliva entering the wound, inhibits the clotting action of platelets, enabling the free flow of blood. There are likely other anti-clotting factors associated with saliva, as well.



Anterior portion of *Chrysops callidus* labrum showing vestibule (oval).

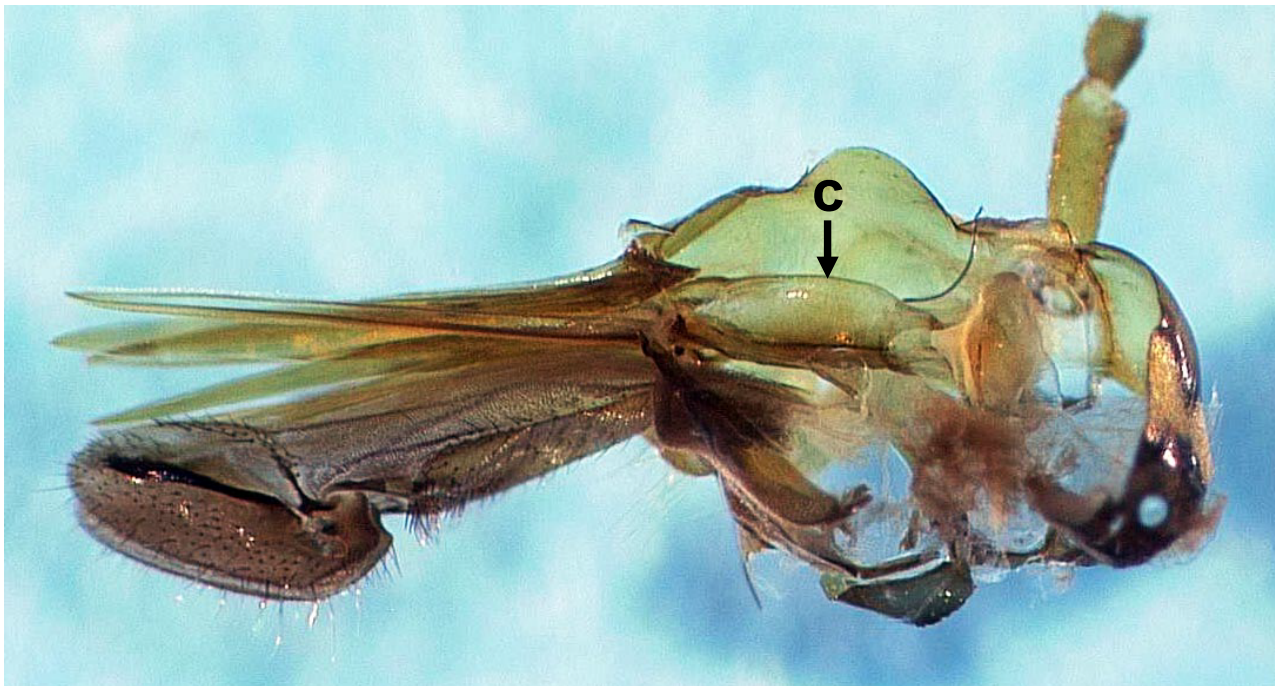


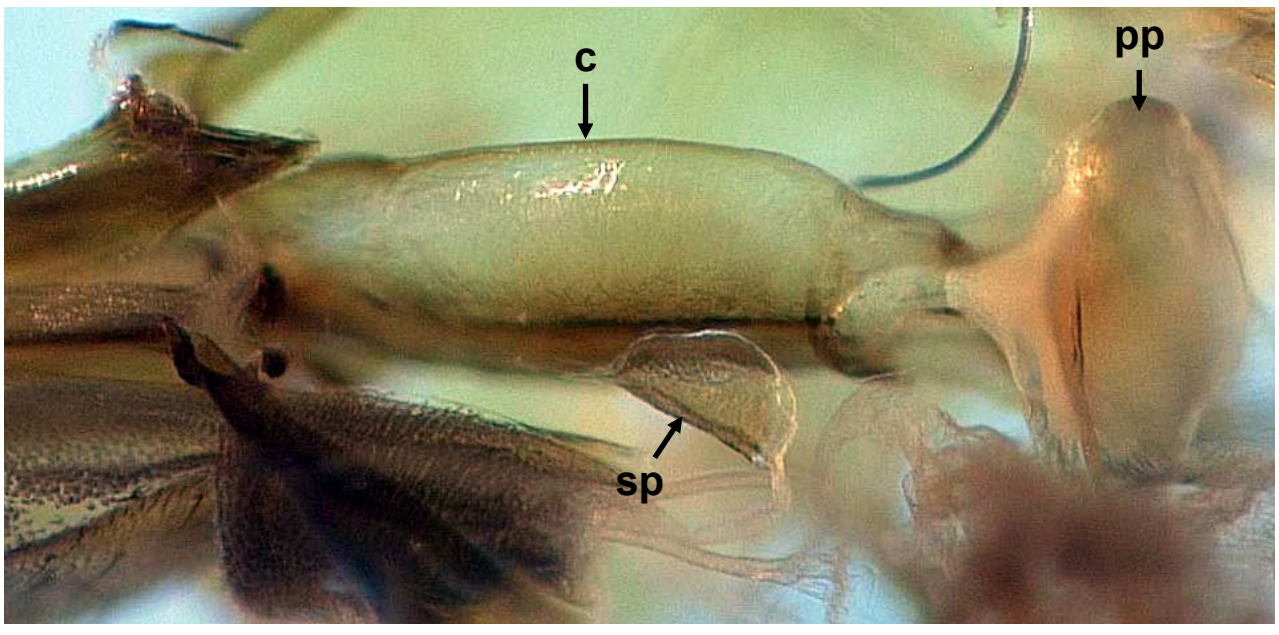




"Specialized" cutting mouthparts of tabanid flies: A, mandible (note small serrations on inner margin); B, maxillary lacinia (note backward-pointing teeth). Photos to right are ventral (top) and lateral (bottom) SEM views of the lacinia.

Three other accessory feeding structures can be seen in carefully dissected deer fly specimens: (1) the cibarium (a pumping structure), (2) the salivary pump lying immediately below the cibarium, and (3) the pharyngeal pump, immediately posterior to the cibarium. The esophagus leaves the pharyngeal pump, carrying blood to the gut.

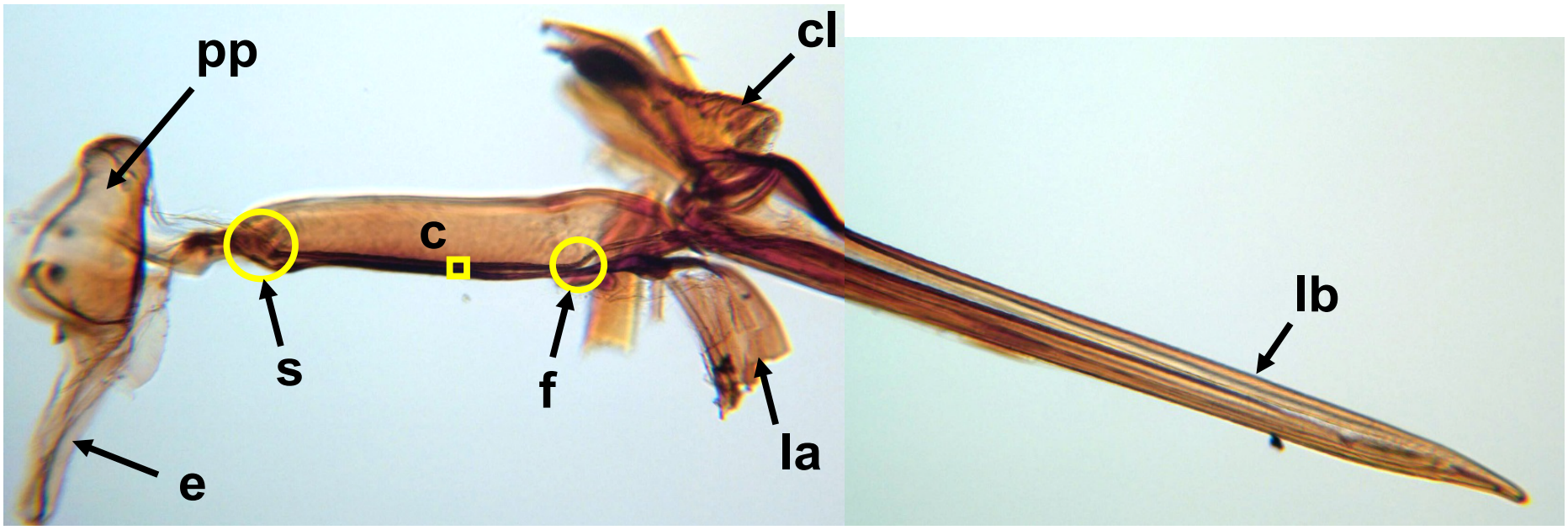


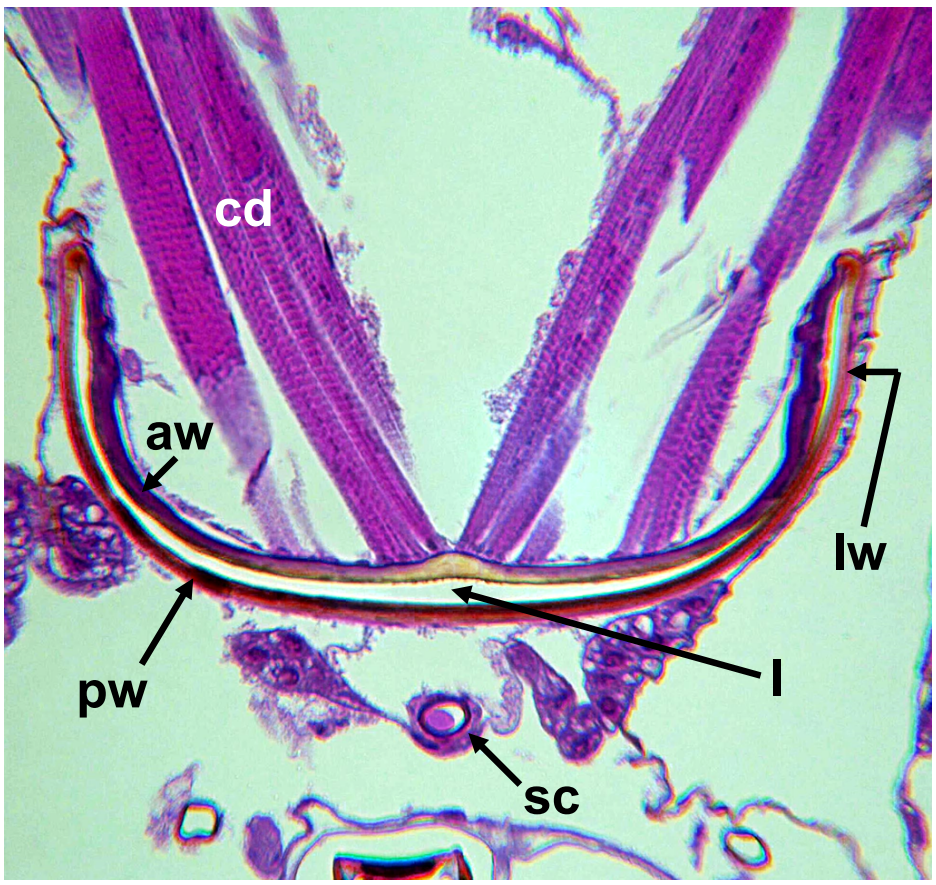


Sagittal view, head and mouthparts of *Chrysops vittatus* (top); cibarium enlarged (bottom).

Legend: c, cibarium; pp, pharyngeal pump; sp, salivary pump.

These structures (i.e., the feeding complex) can also be viewed in whole mount and in cross-sectional aspects which show a "functional mouth" (where blood enters the cibarium) and stomodaeum (the "true mouth" where blood exits the cibarium). The tubular cibarium has three walls; rigid lateral and posterior walls, and a highly elastic anterior wall. When cibarial dilator muscles, attached to the anterior cibarial wall, are relaxed, the anterior wall lies close to the posterior wall and thus the lumen of the cibarium is small. When dilator muscles contract, the anterior wall is drawn upward, increasing the lumen and drawing blood into the feeding complex. This "pumping action" may occur at a rate of several times per second when the fly is actively feeding.





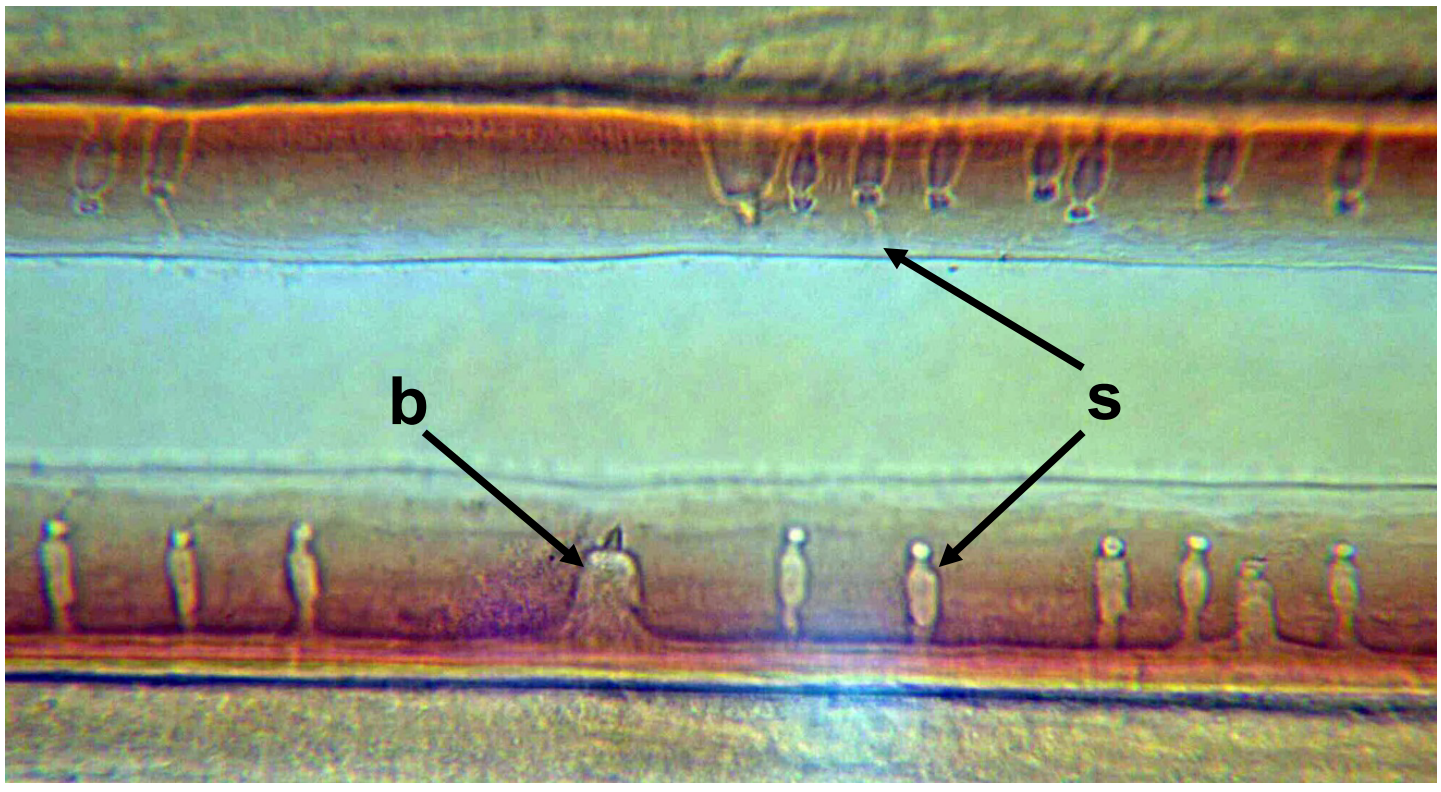
Lateral view of *Chrysops exitans* feeding complex (top) dissected from the head. Legend: c, cibarium; cl, clypeus; e, esophagus; f, functional mouth; la, labium (base of); lb, labrum; pp, pharyngeal pump; s, stomodaeum. Cibarium length ≈ 550 *u*m. Lumen of cibarium (yellow box) ≈ 30 *u*m high.

Insert (below) is x-sect. view mid-region of cibarium. Legend: aw, anterior wall; lw, lateral wall; pw, posterior wall of cibarium; cd, cibarial dilator muscles; l, lumen of cibarium; sc, salivary canal.

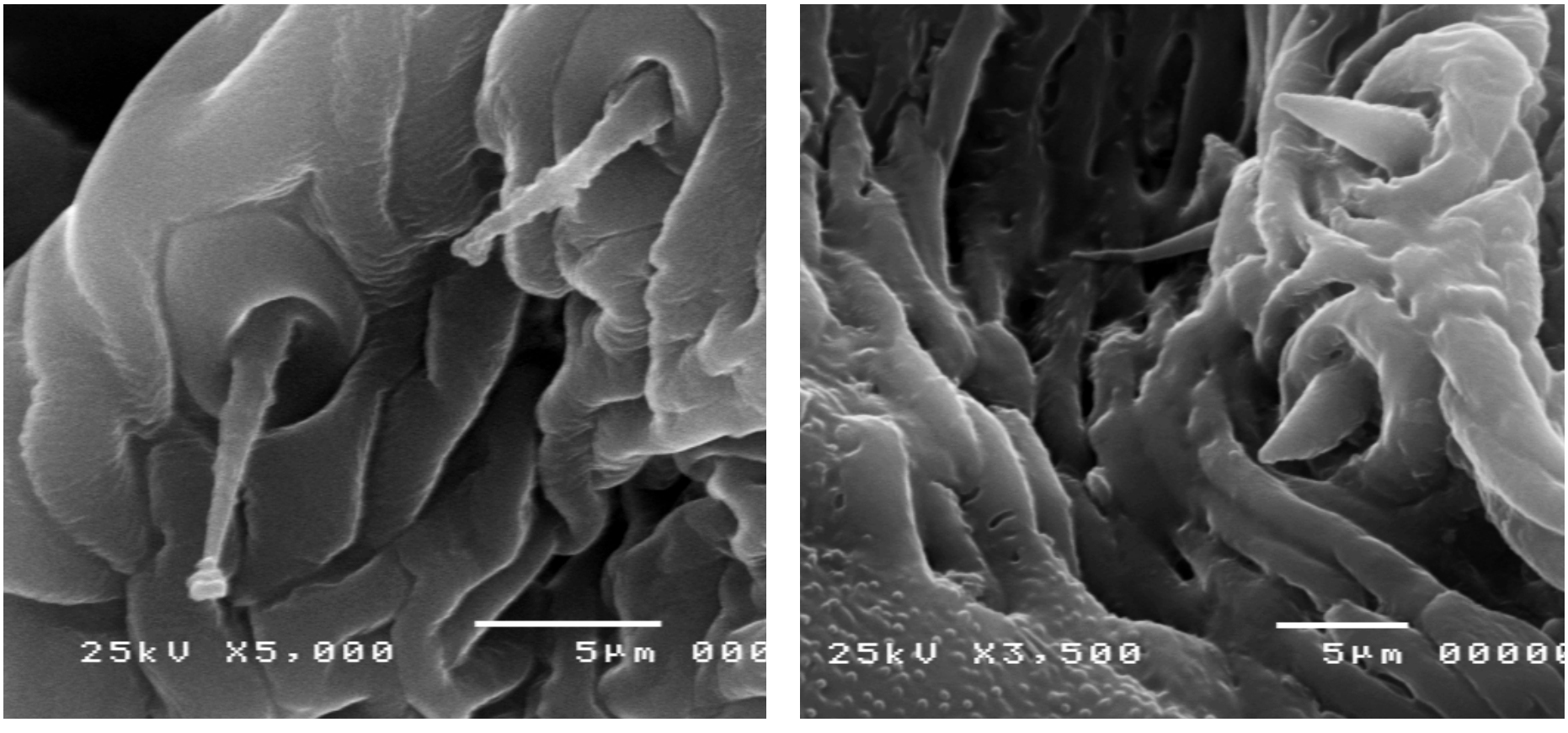
Sensory sensilla (beyond the scope of this book) lie in the food canal, and the epipharynx (a region immediately in front of the cibarial opening). These sensilla monitor blood flow, and detect certain chemical constituents (e.g., adenine nucleotides) in the blood. Sensilla in the epipharynx are positioned in three "patches"; two lateral patches consisting only of setiform (mechanoreceptor) design, and a median "patch" consisting of six basiconic sensilla and a variable number of setiforms.

E-1a. Supplemental Materials (PowerPoint Presentations)

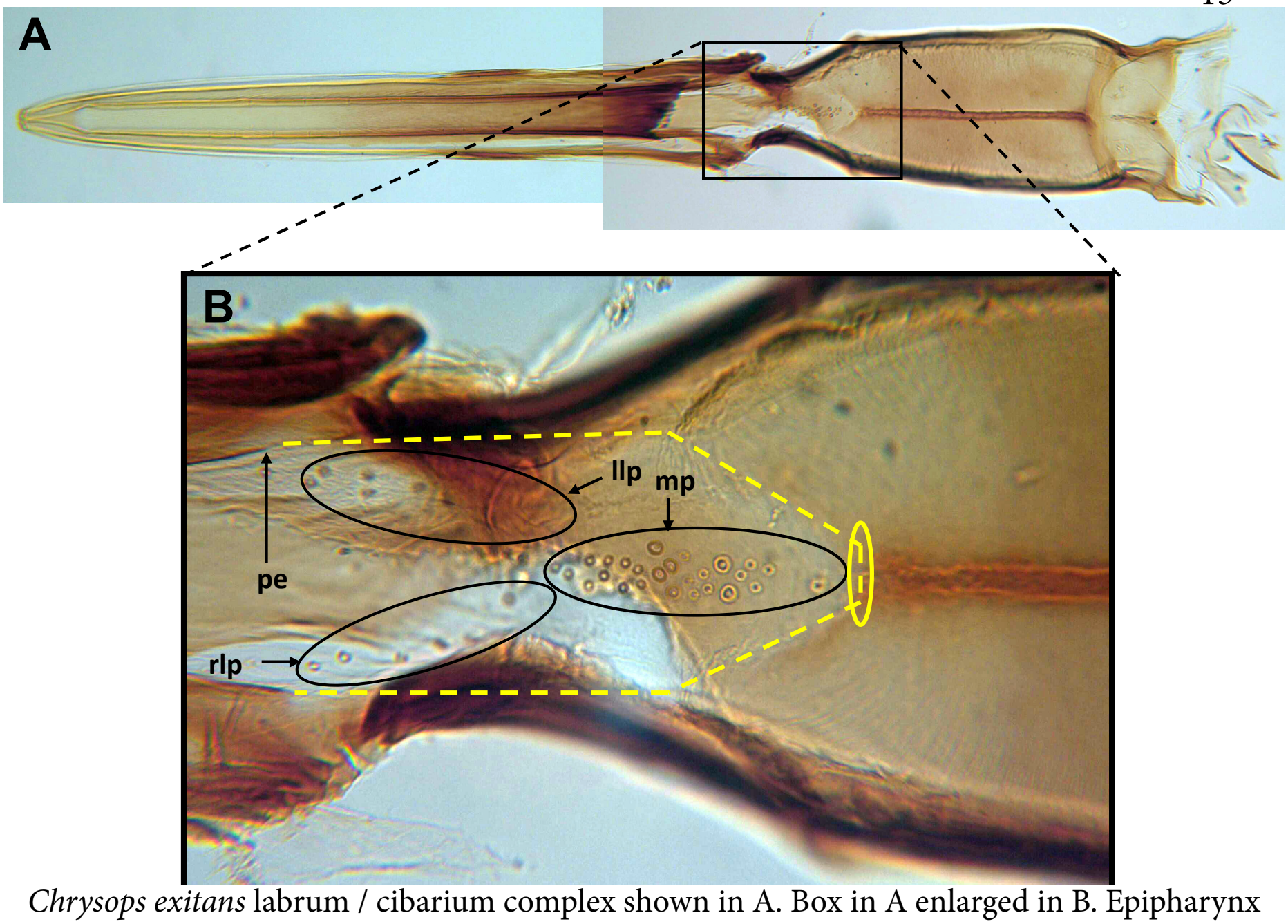
Chrysops exitans
Chrysops moechus
C. *exitans* dissections



Sensory sensilla in food canal of *Tabanus abdominalis*. Note: There are two types of these sensory structures, a single pair of bullet-shaped sensilla called basiconic sensilla, and a variable number of sensilla with minute hair-like, projections, called setiform sensilla. Basicones are often chemosensory, whereas setiforms are mechanoreceptors. Diameter, or width, of the basiconic sensilla ≈ 14 *u*m. Arrangement of sensilla is similar in *Chrysops* sp., except that there are fewer setiforms in the *Chrysops* sp. food canal.



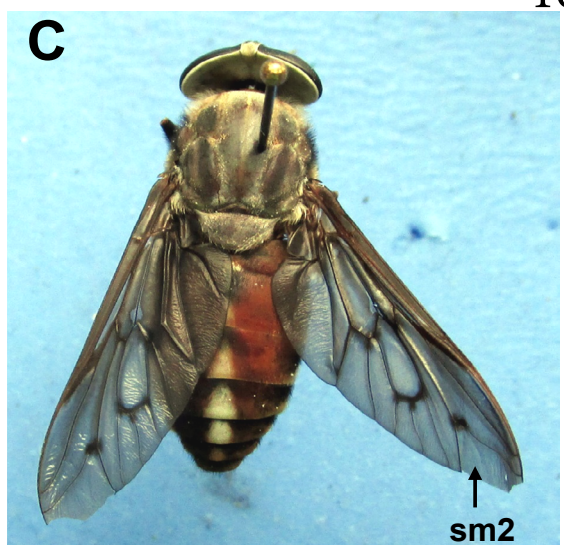
SEM views of elongate setiform sensilla (left) and "bullet-shaped" basiconic sensilla near the opening into the cibarium of *Chrysops* sp.

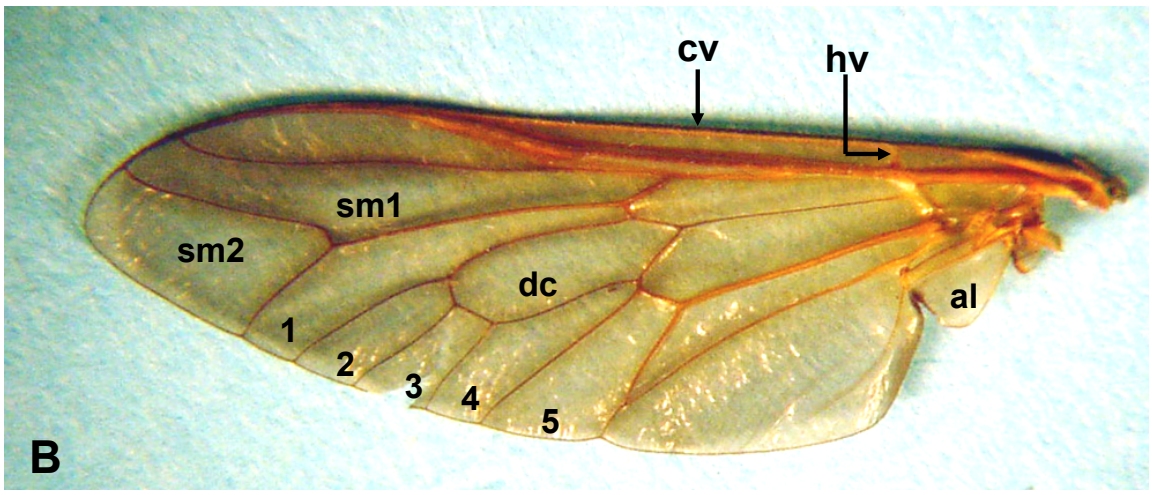


Chrysops exitans labrum / cibarium complex shown in A. Box in A enlarged in B. Epipharynx positioned between food canal and cibarial opening ("functional mouth", yellow oval), outlined by dashed yellow lines in B. Legend: pe, proximal extremity of food canal; llp, left lateral patch; rlp, right lateral patch; mp, medial patch of sensilla.

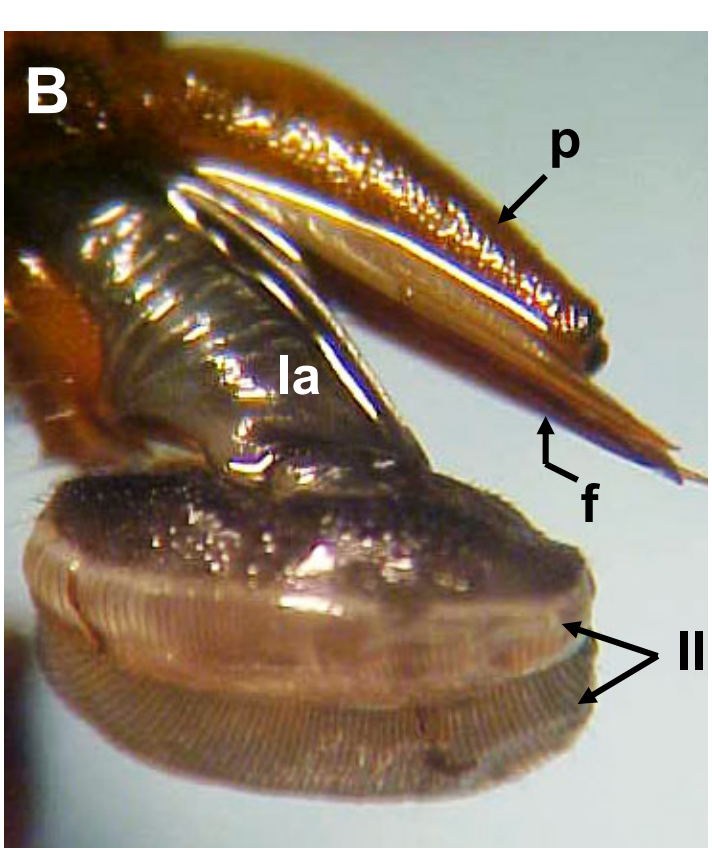
E-2. *Hybomitra & Tabanus*

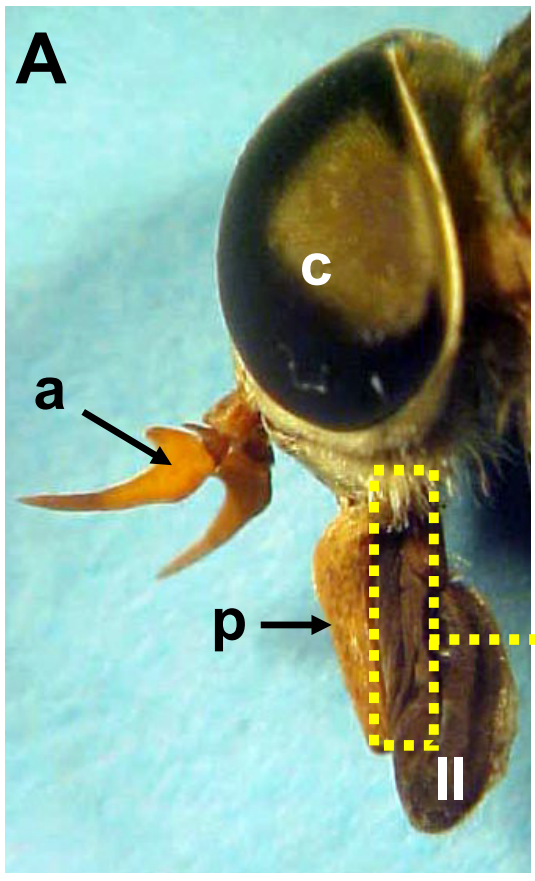
Horse flies are the larger tabanids (i.e., somewhat larger than deer flies), adults ranging from 10 to 26 mm in length. Four characteristic features of horse flies, other than their large bodies, are: (1) "clear, sometimes spotted, wings"; (2) prominent forwardly directed antennae; (3) the absence of ocelli and the ocellar triangle (present in deer flies); and (4) robust piercing-sucking mouthparts. The six blade-like mouthparts that penetrate the skin to facilitate feeding are the same as those found in deer flies: (i.e., 1 labrum; 1 hypopharynx; 2 mandibles; and 2 maxillary laciniae), except that the mouthparts in these larger tabanids are more robust. Also, when the fly is at rest (i.e., not feeding) these six piercing stylets, sometimes collectively referred to as the fascicle, are ensheathed in a labial groove of the labium (which does not enter the host's skin during feeding). The labium of horse flies terminates in robust structures called the labella. The vestibule is similar to that seen in deer flies, and always has a pair of distally positioned basiconic sensilla followed by a pair of setiform sensilla.

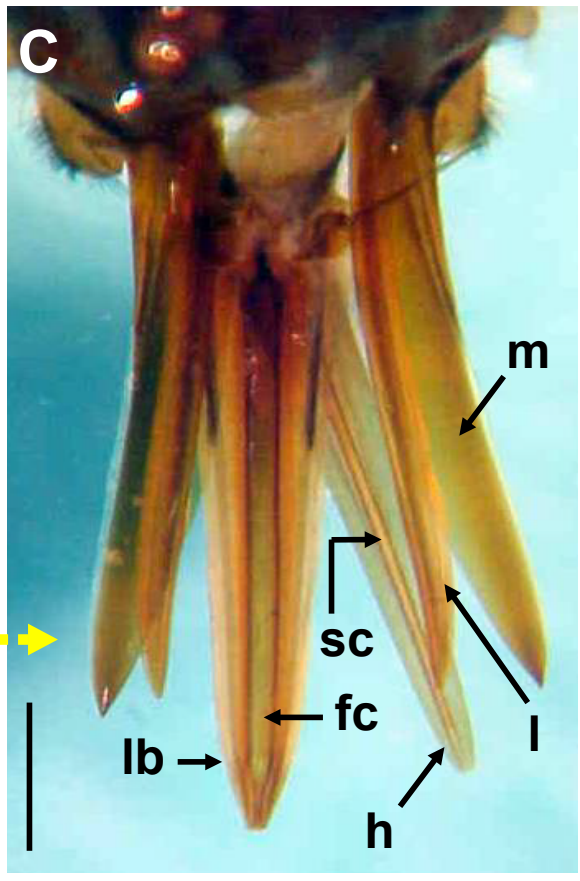




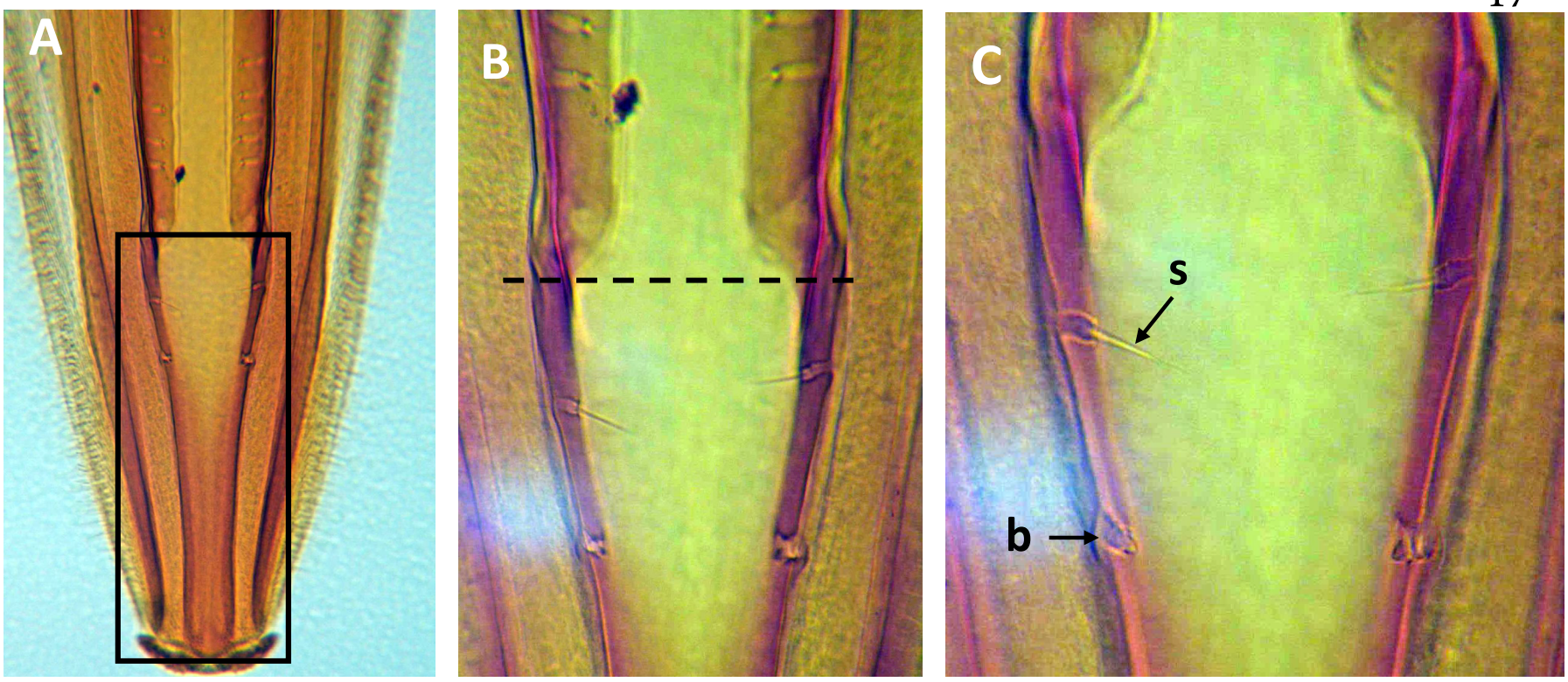
"Pictured" wing of a deer fly, *Chrysops* sp. (A) vs. wing of horse fly, *Tabanus fulvulus* (B), or *Tabanus abdominalis* (C). Legend: al, alula; cv, costal vein; dc, discal cell; hv, humeral vein; sm1 & sm2, submarginal cells; 1-5, posterior cells.





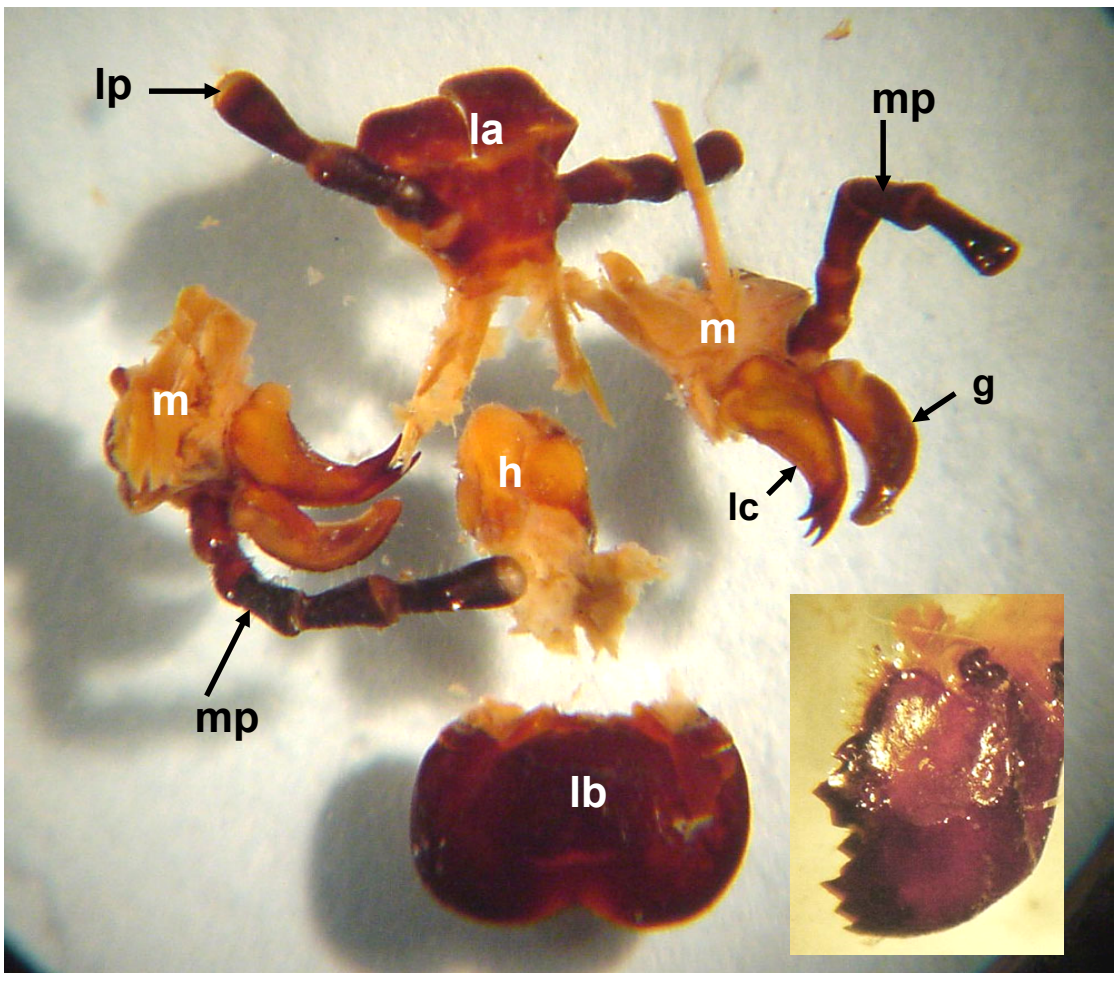


Tabanus atratus head and "specialized" mouthparts. A, lateral view; B, oblique view; C, mouthparts with surrounding labium removed (lying in labial groove indicated by dotted box in A). Legend: a, antenna; c, compound eye; f, fascicle (bundle of mouthparts); fc, food canal; h, hypopharynx; la, labium; lb, labrum; l, maxillary lacinia; ll, labella; m, mandible; p, palp; sc, salivary canal. Scale bar in C = 1.0 mm.



Tabanus atratus vestibule (box in A), with two different depths of field (B & C) showing basiconic (b) and setiform (s) sensilla in the vestibule. Dashed line indicates the vestibule/ food canal junction.

Mouthparts of horse flies (and deer flies) are sometimes considered "specialized"; that is they have become adapted for blood feeding (or feeding on plant juices in males), and thus differ from the "generalized" design of mouthparts in other insects, such as the grasshopper.

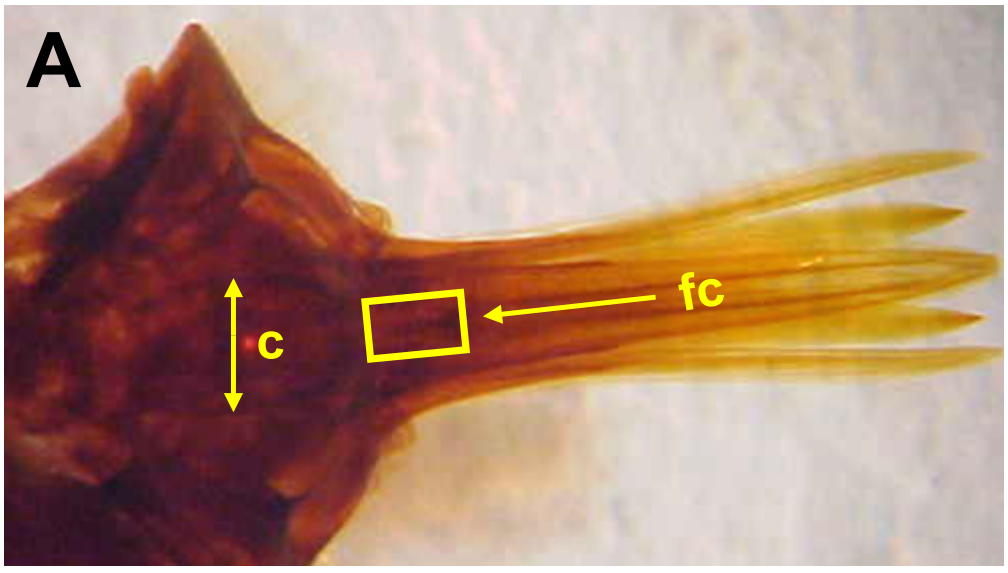


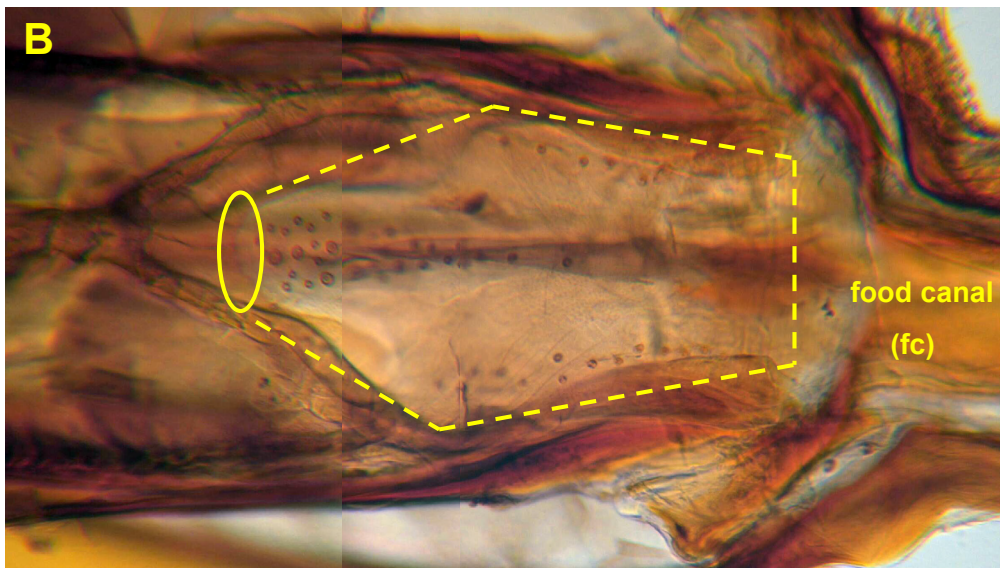
Mouthparts of a "generalized" insect (the grasshopper). Legend: g, galea; h, hypopharynx; la, labium; lb, labrum; lc, lacinia; lp, labial palp; m, maxilla; mp, maxillary palp. Note: left mandible (insert) with inner margin serrated for grasping and crushing food, lies immediately behind labrum.

Note that in the general insect the mandibles are used for crushing food, whereas in the horse flies these structures are used for cutting host tissues. Additionally, the labrum of horse flies houses the food canal, which is not the case for the generalized insect. Conversely, in the generalized insect there is a "pre-oral" cavity bounded anteriorly by the labrum (i.e., the "upper lip"), posteriorly by the labium (i.e., the "lower lip"), and laterally by the two mandibles. The hypopharynx of the generalized insect surrounds the salivary canal which empties saliva into the pre-oral cavity. Note that maxillary palps and labial palps, which aid in food manipulation in the generalized insect, are missing from horseflies, as are the galea. The epipharyngeal region of horse flies is structured as in deer flies.

E-2a. Supplemental Materials (PowerPoint Presentations)

Hybomitra labrum cibarium
Tabanus abdominalis
Tabanus atratus
T. atratus basiconic sensilla
Tabanid head
Tabanus 31





Box in A approximate location of epipharyngeal region of *Tabanus* sp. (approximate position indicated by dashed lines in B). Note lateral and median "patches" of sensory sensilla, in epipharynx. Oval indicates position of "functional mouth", or opening into cibarium. Legend: c, cibarium; fc, food canal. Again, epipharyngeal sensilla are similar in *Chrysops* sp.

F. Review (Terms and Sample Quizzes)

Structures / terms underlined throughout the previous narrative may be used for testing purposes. Quizzes will be presented in two formats: (1) multiple choice; and (2) lab identification (as PowerPoint slides). For the multiple choice format you should be prepared to match those terms with their descriptions, and for the lab identification you need to learn, and be able to identify, all labeled structures shown in accompanying PowerPoints. Examples of both quiz types are given below.

Multiple choice (choose the one correct answer for each statement).

1. The food canal of a tabanid fly is associated with the:
a. labrum b. epipharynx c. labium d. cibarium

2. Mouthpart in female tabanid that does not penetrate the skin during feeding.
a. labrum b. hypopharynx c. labium d. mandible

3. The stomodaeum is an opening at the:
a. proximal end of food canal b. distal end of food canal
c. posterior cibarium d. posterior epipharyngeal region

4. An ocellar triangle is present in:
a. *Hybomitra difficilis* b. *Tabanus atratus*
c. *Chrysops exitans* d. none of these species

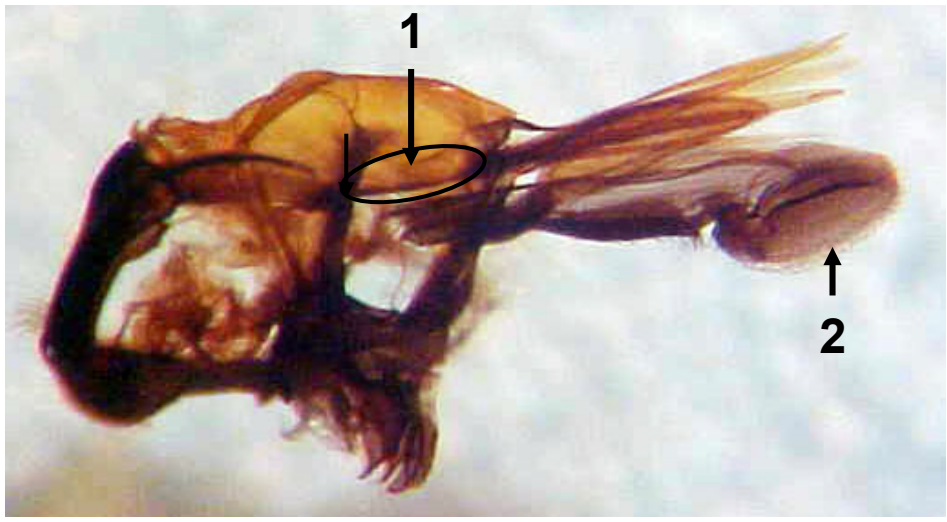
5. Flagellomeres are associated with (found on) the:
a. antenna b. palps c. arista d. cibarium

6. In zoological nomenclature the –idae ending denotes a:
a. generic name b. family name c. subfamily name d. order name

LAB QUIZ*

*one of several examples that may appear on exam

Match the term (A through G) with its appropriate number on accompanying photos. Two terms will not be used.



A. labium

B. vestibule

C. pharyngeal pump

D. labellum

E. epipharynx

F. clypeus

G. cibarium