

# THE LEAFHOPPERS AND PLANTHOPPERS

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# 3

## External Morphology of Leafhoppers

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### 3.1 INTRODUCTION

The systematics of leafhoppers has long been dependent on a careful study of external morphology. Morphology is herein defined as the study of anatomy plus function, therefore, functional aspects will be considered whenever deemed appropriate. If consistent differences in homologous morphological characters occur in closely related animal taxa at any level of the Linnaean hierarchy, then these characters are probably derived (apomorphic). These characters are the result of evolution, are probably adaptive, and are manifestations of functional change. Subsequently, when properly analyzed, these data furnish evidence for speciation as well as relationships among taxa in a hierarchy. This does not preclude the use of physiological, ecological, zoogeographical, paleontological, and other data, but morphological characters are usually the most useful in constructing keys for identification of specimens. Furthermore, if a systematist is interested in the phylogeny of an animal group, he or she must carefully review comparative morphology so that decisions can be made concerning character polarity (primitive or derived state) and resulting data can be analyzed efficiently.

The objectives of Chapter 3 are to discuss the major morphological terminology used by contemporary leafhopper systematists in their revisionary studies, and to discuss briefly some of the evolutionary aspects of morphological divergence.

Terminology is taken primarily from the published works of North American authors including Beirne (2), Blocker (3–5), Cwikla and Freytag (7), DeLong (10), Freytag (18), Hepner (20), J. Kramer (26–29), S. Kramer (30), Nielson (39–41), Oman (43, 44), Young (52–54), and others. International workers such as Evans (16, 17), Knight (25), Linnavuori (32), and Viraktamath (49, 50) are frequently consulted. The accuracy of terminology is, however, the responsibility of the authors. As much alternative morphology as possible has been included so that the reader can refer to this work for clarification of terms found in current leafhopper literature. Preferred terms have been adopted for structures used in our illustrations but refer to alternative terminology in our discussion and in Table 3.1. The subfamilies recognized by principal leafhopper systematists (2, 44) have been followed rather than the subfamily proposals of Hamilton (19). Bibliographic references for all citations prior to 1956 can be found in Metcalf (36); this is a valuable reference for anyone interested in Cicadellidae.

### 3.2 CHARACTERS OF THE HEAD

Characters of the head are used at all levels of the taxonomic hierarchy including separation of Homoptera from Hemiptera, in separating families of Homoptera, and in separating many taxa within Cicadellidae from subfamily through species. In addition, the relationship of head characters to those of the thorax is widely used. The term *suture* is used in Chapter 3, although this term may encompass structures better defined as a true suture, sulcus, or ecdysial cleavage line (35).

The vertex (or crown, Fig. 3.1a) is defined as the entire dorsal surface of the head excluding the eyes. A coronal suture is usually present on the vertex but is seldom mentioned as a character. The relative length and width (interocular and transocular) of the vertex are used as characters, often in combination with other structures, for example, interocular width compared to median length of the vertex and median length of the vertex to median length of the pronotum separate species of *Xerophloea* (39). Young (53) uses relative vertex length and width, surface contour and texture, and pubescence in separating genera of the Cicadellinae.

Leafhoppers usually have two ocelli that are located near the anterior margin of the head (Fig. 3.1b). Ventrally located ocelli are generally considered plesiomorphic (16) but a dorsal position has also been so considered (19). The position of the ocelli (on the vertex, near the anterior margin of the head, or on the face) was used to separate the subfamilies Ledrinae from Dorycephalinae and their absence is used to characterize some Typhlocybinae (44).

**Table 3.1 Alternative Nomenclature Commonly Used in Leafhopper Systematics**

Preferred Names	Authority	Alternate
<b>Head characters</b>		
Antennal ledge	Young (53)	Antennal ridge
Clypellus	Young (53)	Anteclypeus
Clypeus	Young (53)	Postclypeus
Coronal suture	Linnavuori (32)	Coronal stem, ecdysial cleavage line
Face	Oman (44)	Cephalic aspect
Front	Oman (44)	Clypeus and clypellus
Frons	Oman (44)	Face (in part)
Gena	Oman (44)	Maxillary plate
Lateral frontal suture	Oman (44)	Frontogenal suture, clypeogenal suture
Lorum	Oman (44)	Mandibular plate
Transclypeal suture	Young (53)	Clypeal suture
Vertex	DeLong (10)	Crown
<b>Thoracic characters</b>		
Anteapical cells, FW	Oman (44)	Preapical cells
Anterior margin, FW	Young (53)	Costal margin
Brachial cell, FW	Oman (44)	Cubital cell
Cubital veins, FW	Young (53)	Claval veins
Fore wings (FW)	Kramer (27)	Elytra, tegmina
Hind margin, FW	Young (53)	Commissural margin
Hind wings (HW)	Young (53)	Flying wings
Posterior femoral setal pattern	Young (53)	Hind femoral chaetotaxy
Scutellar Suture	Blocker (3)	Transscutellar suture
Tarsomeres	Blocker (4)	Tarsal segments <sup>a</sup>
Vannal veins, FW	Young (53)	Anal veins
<b>Abdominal characters</b>		
Aedeagus	Oman (44)	Penis, intromittent organ
Anal tube	Oman (44)	Postgenital segments, anal style (in part)
Atrium of aedeagus	Young (53)	Socle
Male genital capsule	Oman (44)	Abdominal segment IX
Paraphyses	Young (53)	Accessory genital structures
Pygofer processes	Oman (44)	Pygofer hooks
Pygofers	Blocker (4)	Genital capsule
Styles	Oman (44)	Parameres, Claspers
Subgenital plates	Evans (14)	Pseudostyles (in part)

<sup>a</sup>Incorrect usage, morphologically.

Flightlessness in the Ulopini and Cephalini is often associated with the absence of ocelli (15). Ocelli on the dorsal surface of the head or loss of ocelli are generally considered derived characters in leafhoppers. The relationship of

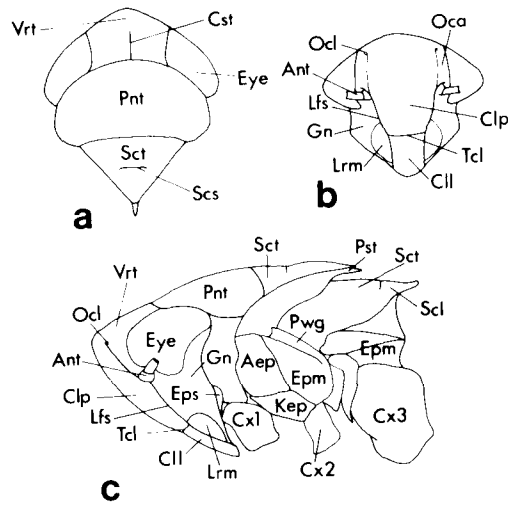


Fig. 3.1 (a) Dorsal surface of head and prothorax. (b) Face. (c) Lateral aspect of head and thorax. Aep, anepisternum; Ant, antenna; Cll, clypellus; Clp, clypeus; Cst, coronal suture; Cx1, procoxa; Cx2, mesocoxa; Cx3, metacoxa; Epm, epimeron; Eps, episternum; Gn, gena; Kep, katepisternum; Lfs, lateral frontal suture; Lrm, lorum; Oca, ocellular area; Ocl, ocellus; Pnt, pronotum; Pst, postnotum; Pwg, pleural wing groove; Scs, scutal suture; Sct, scutellum; Tcl, transclypeal suture; Vrt, vertex.

the lateral frontal (clypeogenal) sutures (Fig. 3.1b) to the ocelli and the distance of the ocelli from the eyes separate groups of subfamilies such as the Iassinae and Agallinae. The ocellocular area (Fig. 3.1b) is located between the eye and the adjacent ocellus; it may be delimited by the lateral frontal suture. The presence of a ledge, or carina, in this area has been used as a generic character in the Cicadellinae and a subfamily character in the Xestocephalinae (44). The compound eyes are generally used as characters only in relationship to other structures of the head.

The antennae (Figs. 3.1b and c) arise anterior to the eyes near the lateral frontal sutures; they consist of a basal scape and pedicel and a long thread-like flagellum that may show marks of segmentation basally (30). They are infrequently used as morphological characters, but Freytag (18) indicates that male antennal disks are distinctive for *Idiocerus* species that possess them. He uses this character to separate several species groups. The character has apparently evolved independently in several species, a condition that can be defined as a homoplasy. According to Oman (44), the length of the antennal filament separates *Sibovia* from *Hordnia* in the Cicadellinae and the ledge above the antennae and antennal pits help separate the subfamilies Neocoelidiinae and Xestocephalinae, respectively. The tentorium (which cannot be seen externally) is complete (16) and the anterior tentorial pits are located adjacent to the antennal bases.

The clypeus and clypellus (or anteclypeus and postclypeus, respectively,

(Fig. 3.1b) are collectively referred to as the *front*. Several characters on these structures are important including the presence of a tubercle on the clypeus of a *Xedreota* species. (29). The shape and degree of protuberance of these structures are important in separating the Cicadellinae from other subfamilies and genera within the subfamily (54). Presence or absence of the transclypeal suture (Fig. 3.1b) is also used as a character in *Xerophloea* and in the subfamily Cicadellinae (44). The face is defined as the entire cephalic aspect of the head. Presence or absence of pubescence on areas of the face is important in the recognition of genera of Cicadellinae. An epistomal suture and subgenal sutures may be present in some primitive groups (16). The gena (Fig. 3.1b) is defined as the *maxillary plate*. It may be entirely concealed in some groups; this condition is considered derived. The expansion of the genae behind the eyes (when visible from the dorsal aspect) is used by Hepner (20) as a character separating the tribe Scaphytopiini from the rest of the Deltocephalinae. The relationship of the clypellus to the margin of the gena separates tribes of Coelidiinae. The apical width compared to the dorsal width of the clypellus separates genus groups in the Deltocephalinae (44). The lorum (Fig. 3.1b) is defined as the *mandibular plate*. It may terminate posteriorly, close to the base of the antenna, or be widely separated from it. The presence of pubescence has been used to characterize some Cicadellinae genera (53).

Combinations of head characters, such as the relationship of the margin of the vertex and face, are valuable characters. As an example, the carinate (keeled) anterior margin of the vertex separates *Draeculacephala* from *Carnocephala* in the Cicadellinae (44). Likewise, differences in the dimensions of the vertex, in relation to the pronotum, can be valuable characters. In the Deltocephalinae, the transocular width of the head, compared to the width of the pronotum, separates species groups of *Balclutha* (3). The relationship of vertex length to pronotal length is used in the genus *Icaia* (5). There is some evidence that this relationship is altered within species, depending on whether they are macropterous (long winged) or brachypterous (short winged).

In general, many of the unusual shapes of leafhopper heads are adaptive in nature (16). Flattened heads (e.g., *Dorycephalus*) enable the insect to press closely against and blend with a leaf or branch. Long narrow heads (e.g., *Cephaelus*) may also aid in concealment. The unusual head of some, however, seem to lack adaptive features. The principal trends in head shape are to become progressively either narrowly or broadly produced and when broadly produced, then subsequently flattened. There is generally agreement with Evans (16), although it is difficult to accept the suggestion that unusual head shapes are not adaptive.

### 3.3 CHARACTERS OF THE THORAX

Characters of the thorax are used mainly from the subfamily through generic level. The pronotum, scutellum, and scutal (transscutellar) suture of the

mesonotum can be seen from the dorsal view (Fig. 3.1a). The width of the pronotum has been previously discussed in relationship to the head. The shape of the lateral margins (parallel, anteriorly convergent, anteriorly divergent) and the sculpturing and pubescence of the disk (central upper surface) is used to separate genera of Cicadellinae (53) and to separate genera of Agalliinae (44). The shape of the hind margin of the pronotum in relation to the scutellum and the texture of the scutellum have been used as characters. The shape of the scutellum is used to separate the genus *Tuberana* from other Gyponinae (13).

Young (53) states that the proepisternum is never concealed in the Cicadellinae and the posterior margin of the proepimeron bears a digitate projection that partially overlaps the mesepisternum in some genera. A concealed proepisternum is considered a derived state. Young (53) also uses characters of the mesepimeron, metepimeron, and the meron of the hindleg in his classification of the Cicadellinae. This is possible because these leafhoppers tend to be more heavily sclerotized than those of other subfamilies.

Characters of the legs are used extensively in the taxonomy of leafhoppers. The hind legs are adapted for jumping and Evans (16) believes that the ability to take a sudden leap is the leafhopper's main method of protection. The Cicadellidae can be distinguished from other families of Auchenorrhyncha by the posterior tibia armed with many stout setae arranged in rows. According to Davis (8), there are three or four such rows (usually four). In primitive leafhoppers, these setae are only feebly developed with stout setae being developed in higher taxa. In the subfamily Cicadellinae, the anterior tibiae are broadly flattened and dilated in some genera (53). The posterior femur length in relation to the posterior proepimeral margin, and the relative length of the first tarsomere of the hind leg compared to the combined length of the second and third tarsomeres are also used as generic characters. The posterior femoral setal pattern (hind femoral chaetotaxy and other designations, Fig. 3.2c) is also extensively used, although most authors use caution since it is variable within many groups. The setal arrangement is generally expressed by a formula such as 2:2:1, which indicates a pair of apical setae followed by a pair of more proximal setae and a single more proximal seta. An arrangement of 2:1:1:1 indicates a pair of apical setae and three serially arranged, proximal setae.

In the Balcluthini, the basal hind tarsomere (incorrectly referred to by authors as the first hind tarsal segment) is sulcate and diagnostic (3). The absence of two rows of short spines on the basal hind tarsomere separates the subfamilies Bythoniinae and Ledrinae from other Neotropical subfamilies (32). Hamilton (19) makes extensive use of leg characters in his proposed phylogeny of the leafhoppers, including tibial and tarsal setal arrangement (combs or pectens).

The longitudinal veins in the wings are referred to as radial, medial, cubital (claval), and vannal (anal). The radial, medial, and cubital veins delimit the apical and anteapical cells (preapical cells) of the fore wing (Fig. 3.2a). The apices of some longitudinal veins are prolonged in a common submarginal vein in the hind wings of many leafhoppers (Fig. 3.2b). Generally, there is a vannal fold in the fore wing and a vannal and jugal fold in the hind wing.

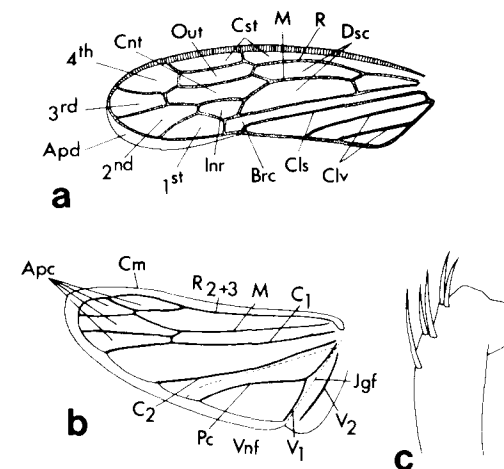


Fig. 3.2 (a) Fore wing. (b) Hind wing. (c) Apex of femur. Apc, apical cells; Apd, appendix; Brc, brachial cell; Cls, claval suture; Clv, claval veins; Cm, costal margin; Cnt, central anteapical cell; Cst, costal cells; C<sub>1</sub>, cubitus 1; C<sub>2</sub>, cubitus 2; Dsc, discal cells; Inr, inner anteapical cell; Jgf, jugal fold; M, media; Out, outer anteapical cell; Pc, postcubitus; R, radius; Vnf, vannal fold; V<sub>1</sub>, first vannal; V<sub>2</sub>, second vannal; 1st, first apical cell; 2nd, second apical cell; 3rd, third apical cell; 4th, fourth apical cell.

Characters of the fore wings (tegmina or elytra, Fig. 3.2a) are used for distinguishing most leafhopper taxa. The number and length of the apical cells, the presence or absence of a membrane, of supernumerary crossveins, and of closed anteapical cells are characters used to separate genera of Cicadellinae (54). The indistinct basal veins and absence of crossveins anterior to the apical cells characterizes the Typhlocybinae, and the absence of an outer anteapical cell characterizes the Balcluthini and Macrostelini. A closed anteapical cell is used to characterize the genus *Ciminius* in the Cicadellinae (44); this character is also used to separate groups of the Deltocephalinae indicating homoplasy within distantly related subfamilies. The vein separating the appendix and first apical cell denotes stages of evolutionary change in the Iassinae (4). The absence of an appendix characterizes the Typhlocybinae, except the Alebrini. The fore wing may be truncate or tapered apically in genera of the subfamily Neoballinae (32). The straight hind margin (commissural margin) is characteristic of the tribe Acinopterini (subfamily Deltocephalinae). Fore wings are commonly described as macropterous, brachypterous, or subbrachypterous (intermediate between brachypterous and macropterous). In primitive groups (e.g., some Iassinae) the membrane of the fore wing is irregularly and closely filled with setiferous punctures; in advanced groups, punctation decreases in the middle of cells so that the bristle punctures only remain along the vein margin (51).

The hind wings (flying wings, Fig. 3.2b) contain characters, such as the interrupted R 2+3 vein, that characterize generic groups within the Cicadellinae. The submarginal vein of the hind wing and its relationship to vein R+M

separates tribes of Typhlocybae (52). The presence or absence of vein 1V also separates tribes of Typhlocybae. The hind wings are often reduced or virtually absent, especially in such short-winged groups as *Athysanella* and other genera in the Deltocephalinae (44).

### 3.4 CHARACTERS OF THE ABDOMEN

The abdomen of Auchenorrhyncha consists of 11 distinct segments; the first eight (pregenital segments) bear spiracles. The male abdominal segment IX (genital segment, Fig. 3.4a) will be discussed in detail. The female genital segments are VIII and IX (Fig. 3.3c). The postgenital segments are X and XI (anal tube, Fig. 3.4a). The postgenital segments may be reduced in size and are variously sclerotized.

Pregenital abdominal segments contain several major characters. Knight (25) uses variation in the size of the abdominal apodemes of segment II (Fig. 3.3a) as specific characters in the typhlocybine genus *Dikraneura*. The apodemes of the muscles in the base of the abdomen are used in sound production (6). Apodemes are valuable characters for separating *Macrosteles* males in the subfamily Deltocephalinae and for *Zygina* and *Alebra* in the subfamily Typhlocybae where the male genitalia are too simple for taxonomic use. The female abdominal sternum VII (Fig. 3.3b) is often a valuable character at the

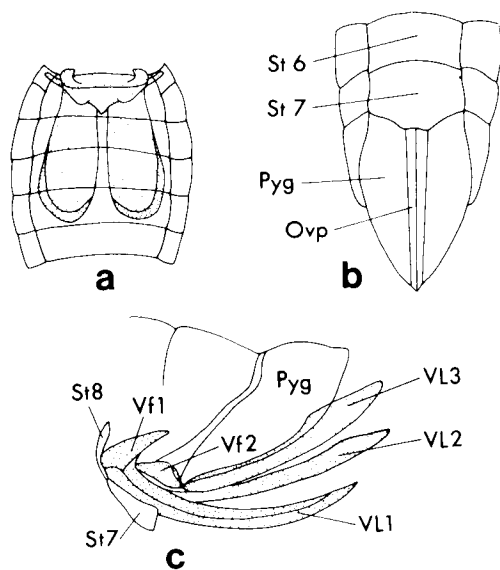


Fig. 3.3 (a) Abdominal apodeme. (b) Ventral aspect of female genital segments. (c) Lateral aspect of female genitalia. Ovp, ovipositor; Pyg, pygofer; St6–7, sterna 6–7; VL1–3, first, second, and third valvulae, Vf1–2, first and second valvifer.

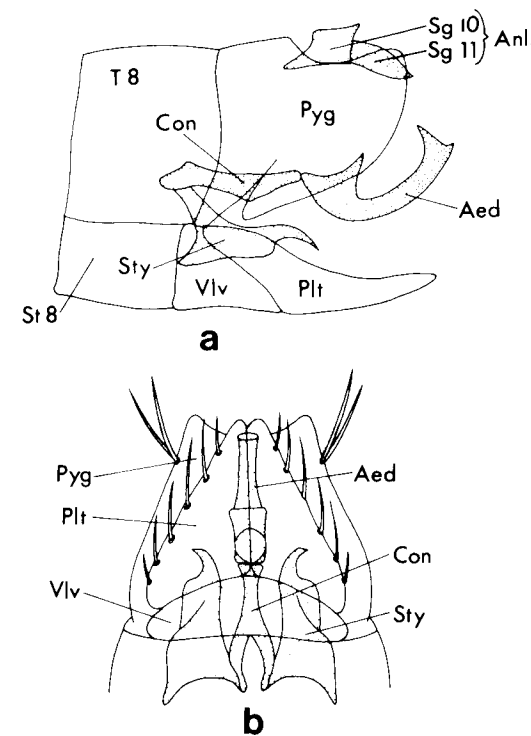


Fig. 3.4 (a) Lateral aspect of male genitalia. (b) Ventral aspect of male genitalia. Aed, aedeagus; Anl, anal tube; Con, connective; Plt, plate; Pyg, pygofer; Sg 10, tenth segment; Sg 11, eleventh segment; Sty, style; St 8, eighth sternum; T 8, eighth tergum; Vlv, valve.

generic level, but rarely gives good specific characters (31). This character can, however, be used to separate several New World *Balclutha* species (3) and is diagnostic at the species level in the closely related genus *Dalbulus* (11). The length of the female sternum VII, compared to VI, has been used as a generic character in the Iassinae and other groups. The length of the male abdominal sternum VIII is used to separate several genera of Iassinae (4).

The postgenital segments, anal tube (X and XI) or anal tube (X) and anal style (XI), also contains characters of value (44). Segment X may be simple or collar-like; it is sometimes almost completely membranous. There are rarely one or more processes that may be modified for clasping. The heavily sclerotized segment X separates *Elymana* from *Deltocephalus* and other closely related genera of Deltocephalinae. Characters of Segment XI mainly concern its size in relation to other segments. Cwikla and Freytag (7) describe segment XII as part of the anal tube in *Xestocephalus*, but Cwikla (personal communication) indicates that this was an error.

The genital capsule of the male (abdominal segment IX) contains numerous characters. The tergum is usually deeply incised dorsally for reception of

segment X and consists of two lateral plates called the pygofer. Other authors refer to the entire dorsum as the pygofer, but the plural form is used here. Each pygofer may be modified and can serve as a clasper during copulation. Young (54) uses dorsal processes of the pygofer to separate *Amphigonalia* from closely related genera of Cicadellinae; the presence of pygofer processes (hooks) are important in separating genera of Iassinae (4). Presence or absence of pygofer processes in *Athysanella* help separate subgenera and their various configurations can be species level characters (1).

Ventrally, the genital capsule is differentiated into the basal “valve” and the paired distal subgenital plates (Fig. 3.4b). The subgenital plates (17) serve the dual function of protecting the aedeagus and acting as accessory clasping organs. The valve is not often used in classification but it can be valuable in some groups such as the Iassinae (4). The valve is fused with the pygofer in the Iassinae (33); this also occurs in the Idiocerinae and Agallinae. The absence of the valve is a character in the genus *Goblinaja* (28). Characters of the plates are numerous. In the Deltocephalinae, the uniseriate arrangement of macrosetae helps to differentiate certain genera (44). Length of the plates, compared to the apex of the pygofer, separates genera of the Cicadellinae. The plates may be absent in some Iassinae or modified into structures that Kramer (27) terms *pseudostyles* in the genus *Grunchia*. In some groups, the plates are bisegmented (e.g., *Agalliopsis* and *Idiocerus*); Evans (16) considers this an ancestral state. The plates may be fused into a single structure as in *Tichocoelidia*, a condition considered as derived (51). This condition is apparently derived from that found in *Sorhoanus* where the inner margins are straight and lie close together. The primitive state is seen in *Doratura* where the inner margins are widely separated (51). The entire genital capsule is withdrawn into the pregenital abdominal segments in most Iassinae genera (4).

Characters of the female genital segments (Fig. 3.3c—VIII and IX) are not used extensively in leafhopper classification but are diagnostic in some groups. Structures involved include the first and second valvifers and the associated three pairs of valvulae that are part of the ovipositor. These characters are used (8) to separate selected higher categories of Auchenorrhyncha. Nielson (40) uses characters from sternum VIII, although they are usually reduced in size, to distinguish species groups of *Cuerna*. The form of female abdominal tergum IX (the pygofer) and its chaetotaxy furnish useful characters in the Cicadellinae. The form of the apices of the second valvulae of the ovipositor and their armature of primary teeth and secondary denticles on the dorsal margin help relate genera. Young and Beirne (55) use characters of the ovipositor, especially the base of the first valvulae, to separate species of the deltocephaline genus *Flexamia*.

In males, the so-called internal genitalia is ectodermal in origin and consists of a pair of styles (parameres), a connective, which has been regarded as a basal piece of the intromittent organ (aedeagus) by morphologists, and the aedeagus (penis). Accessory genital structures, paraphyses, are of frequent occurrence. They are believed to have arisen independently in many leafhopper groups. In

the Cicadellinae, they commonly occur between the connective and the base of the aedeagus and are usually paired (54).

The styles (Fig. 3.5a) are essentially structures for clasping during copulation. The distal part may be variously modified and these differences may be diagnostic. Shape of the style apex separates the deltocephaline genus *Athysanella* from *Icaia* (5) and sculpting on the apophysis is useful in separating species groups of *Dalbulus* (Triplehorn, unpublished). A ventral arm, a preapical lobe, and an apophysis may occur in the style and these are often used as characters. Characters of the connective are used in numerous groups. The amorphous (without apparent sclerotization) condition separates several Iassinae genera and is a derived condition (4). The connective may be fused or articulate with the base of the aedeagus and is a diagnostic character in groups of genera in the Deltocephalinae (44); the fused condition is considered derived. A Y-shaped, versus a linear, configuration of the anterior arms separate species groups within the Deltocephalinae and is associated with host preference. Deltocephaline leafhoppers with a linear connective are primarily grass feeders. Those with a Y-shaped connective, for the most part, are not grass feeders. The linear connective is probably a specialization of the Y-type when the arms of the Y have become contiguous and fused. Several genera (e.g., *Driotura* and *Athysanella*) appear to be intergradations between the two types (44). The apex of the connective may be bifid or truncate at its point of connection with the aedeagus and is a character used to separate species groups in the deltocephaline genus *Balclutha* (3). The length of the connective, compared to the length of the styles, is used as a character in *Icaia* with the longer connective being considered apomorphic or derived (5).

The aedeagus (intromittent organ or penis, Fig. 3.5b) is probably the most consistently used character in leafhopper species differentiation. DeLong used the aedeagus and other characters of the external male genitalia early in his career and shared this discovery with his colleagues; this has been one of his important contributions to insect systematics. The aedeagus is typically articulated with but may be fused with the apex of the connective; the latter condition

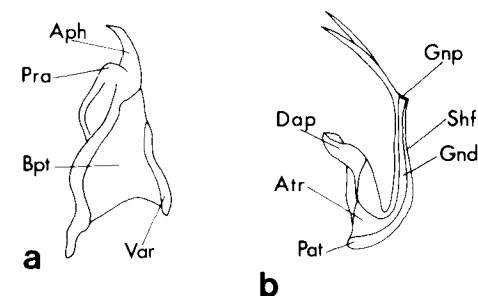


Fig. 3.5 (a) Dorsal aspect of style. (b) Lateral aspect of aedeagus. Aph, apophysis; Atr, atrium; Bpt, basal part; Dap, dorsal apodeme; Gnd, gonoduct; Gnp, gonopore; Pat, preatrium; Pra, preapical lobe; Shf, aedeagal shaft; Var, ventral arm.



is considered derived. The aedeagus is free at its apex. It is typically composed of a preatrium, an atrium (socle), a dorsal apodeme, and the shaft (stem) that contains the gonoduct. A gonopore is present on the shaft and its position may be diagnostic in such groups as the deltocephaline genus *Flexamia* (55). The double gonopore of *Circulifer* is diagnostic; the terminal processes of the shaft containing the gonopores form a semicircle. There may be various processes found on the aedeagus especially associated with the shaft. Such processes, or their absence, can be diagnostic in genera such as *Icaia* (5). Aedeagal processes are commonly referred to as appendages but this terminology is not acceptable to morphologists. The male and female external genitalia are, however, considered to be of appendicular origin by some morphologists. The aedeagus is typically symmetrical but may be asymmetrical in various groups such as the deltocephaline genus *Flexamia* (55). The asymmetrical condition, according to authors, is clearly derived. Comparative length and width of the aedeagus can be diagnostic in many groups.

### 3.5 COLOR PATTERN AND SIZE

Size and coloration are considered variable characters, therefore, caution is advised in their use (32). Nevertheless, these characters are widely used in many groups at all taxonomic levels and are diagnostic in many instances. Le Quesne (31) uses the term *external characters* for all aspects of coloration as well as morphology, therefore, it is discussed here.

In Auchenorrhyncha, visual courtship signals may have resulted from the development of species-specific color patterns and structures (6). Fore wing pattern and other color characteristics are used to separate genus groups in the Deltocephalinae, for example, *Norvellina* and associated genera from *Scaphoideus* and other genera (44). These characters are apparently examples of convergent evolution within the subfamily. Color and facial pattern (banding) are likewise used to separate genera of the deltocephaline tribe Cochlorhini.

Subgenera and species of the gyponine genus *Ponana* are separated using color (12). Extensive use of color is made in separating genera and species of economically important Indian leafhoppers (49). Examples are general body color to separate genera of Typhlocybinae, black spots on the head to separate species of *Cofana*, and the degree of fuscous on the clypellus to separate species of *Idioscopus*. A combination of head characters and the presence of a black submarginal band on the vertex separates males of the Asian species of the genus *Nephotettix* (21).

According to Freytag (18), color pattern of the pronotum, scutellum, and fore wings may be useful and diagnostic in separating species of the genus *Idiocerus*. He describes the development of the female color pattern in males parasitized by pipunculid flies and indicates that this is a sex reversal character. Color is used as a supporting character in the genus *Dikraneura* (25) and color of the vertex and stripes on the pronotum is used to separate *Neobala* species in

the subfamily Neobaliinae (32). Subgenera of the agallian genus *Aceratagallia* can be separated on color characteristics, although corroborative non-color characters are also helpful.

Color characters are generally used to separate genus groups and lower categories. Many of the subfamilies, such as Cicadellinae and Typhlocybinae, have many very colorful taxa but there is so much variation that this information is seldom used in diagnostic keys. Wagner (51) considers dark and light brown basic pigmentation as ancestral; green, yellow, and white basic coloration is advanced (with or without red or black marking). He uses *Balclutha* and *Idiocerus* as examples of derived groups. According to Evans (14), the predominant color of the most primitive groups is brown, followed by green, orange, yellow, red, black, and white.

Parasitism by Pipunculidae reportedly causes color changes in *Nephotettix* resulting in males assuming female coloration and vice versa (22). Parasitized specimens, in general, are almost always paler in color than unparasitized ones.

Size characters are more difficult to assess than color (leafhopper size reportedly varies from 2 to 30 mm in length). There is tremendous variation within a subfamily and even within lower categories. Size can be diagnostic, however, in separating taxa at all levels of the hierarchy. The Cicadellinae contain the largest individuals but many are as small as the largest Typhlocybinae. Ranges of size are useful and the terms *robust* versus *slender* are often used in keys. Linnavuori (32) uses these terms to separate the subfamily Neobaliinae from Xestocephalinae. Likewise, the slender habitus (overall appearance) also characterizes genera of the tribe Balcluthini and body length separates the deltocephaline genus *Stenometopiellus* from other genera (44).

### 3.6 ADAPTATIONS AND HOMOPLASIES

Head width, compared to pronotal width, is a variable character in leafhoppers. This relationship was used to separate Balcluthini genera until it was interpreted as a homoplasy, probably an independent development in closely related taxa (a parallelism) and used as evidence to suppress the genus *Nesosteles* (3). We have observed the same relationship in other groups such as *Paraphlepsius*. Likewise, medial length of the vertex as compared to the medial length of the pronotum also varies. In *Athysanella*, this character varies within presently designated subgenera (Blocker, unpublished). Many examples can be observed in other genera of Deltocephalinae, including *Pendarus*. Wagner (51) considers a shorter (rounded) head an apomorphy (ancestral character). He uses a comparison of nymphs to adults as evidence and the genera *Fieberiella* and *Paramesus* as examples. Also, nymphs in the typhlocybinae genera *Eurhadina* and *Typhlocyba* have an acute vertex edge that has disappeared in the adult. Presence or absence of fuscous spots on the vertex is also a variable character within *Athysanella* subgenera and within species of *Aceratagallia*. Differences in the punctuation of the vertex and pronotum appears in different subfamilies such as the Cicadellinae (53) and Iassininae (4).

On the thorax, the margins of the pronotum have been used to characterize groups of Cicadellinae (54). In dorsal view, the lateral margins may be parallel, convergent anteriorly, or divergent anteriorly. These characters have been observed in other subfamilies, such as the Deltocephalinae. The relationship of the femoro-tibial “knee” is variable within genera of Cicadellinae (54) and the presence of tibial spurs in various subgenera of *Athysanella* is apparently an example of parallel evolution (Blocker, unpublished). The absence of the outer antepical cell in the fore wing has long been used within the subfamily Deltocephalinae to characterize the Macrostelini and Balcluthini (44). It was recently noted, however, that this condition occurs in some of the *Aconurella*. If present classification is correct, this would suggest an example of convergent evolution since the latter genus is currently placed in the Doraturini. A careful examination will be necessary to elucidate the relationship of these groups.

Development of the abdominal apodemes of abdominal sternum II appears to occur independently in genera such as *Macrosteles* in the Deltocephalinae and *Dikraneura* in the Typhlocybiinae (6). Armature of the male pygofer also occurs independently in such genera as *Athysanella*, *Balclutha*, *Aconurella*, and many others (Blocker, unpublished). These are often considered adaptations for grasping and therefore examples of convergent evolution. The male subgenital plates are fused into a single sclerite in some groups of Deltocephalinae, Neocoelidiinae, and Typhlocybiinae. This condition is illustrated for the genus *Goniagnathus* by Wagner (51), for *Lampridius* by Viraktamath and Viraktamath (50), for *Tichocoelidia* by Kramer (26), and for Typhlocybiinae by Mahmood (34). All of these are apparently examples of convergent evolution. A unique development apparently occurs in the closely related genera of *Balclutha* and *Cicadulina*; these genera share a plumose condition of setae located on the genital plates (47). *Balclutha* and the closely related genus *Agelina* share plumose macrosetae on the pygofer. The length of the connective, compared to the length of the styles, appears to be diagnostic in the non-related genera, *Icaia* and *Psammotettix*. This character is apparently another example of convergent evolution. Double gonoducts are present in the aedeagus of many groups of Deltocephalinae, such as *Circulifer*, *Opsius*, and *Ascius* (44). This condition also occurs in the subfamily Mukariinae (32). Asymmetry of structures, particularly in the aedeagus, also occurs in genera of various subfamilies including Deltocephalinae and Coelidiinae.

According to Claridge (6; Chapter 5) acoustic signals are important in interspecific interactions in most groups of Auchenorrhyncha. Leafhoppers produce vibrational sound patterns that are transmitted via the substrate. The pulse patterns of calls may be complicated and are usually distinct for sympatric species. Ossiannilsson (45) demonstrated that most groups of Auchenorrhyncha produce low intensity acoustic signals and use them in communication. The variation in size of abdominal apodemes in the pregenital segments of the abdomen in some leafhopper genera such as the typhlocybinae genus *Dikraneura* is responsible for differences in the mating call and for reproductive isolation of species (25). These apodemes of muscles (usually associated with segment II) are prominently involved in sound production.

### 3.7 ABNORMALITIES IN THE EXTERNAL GENITALIA

Modifications in leafhopper genital structures range from slight changes in shape to complete absence of development of normal structures, which has often led to erroneous classifications and misidentification of species. These modifications occur in both sexes. Genital abnormalities may be commonly caused by parasites of the order Strepsiptera, the dipteran family Pipunculidae, the hymenopteran family Dryinidae, and by nematodes. For a discussion of parasites, the reader is referred to Freytag (Chapter 18).

Parasitism not only affects the styles, aedeagus, and other structures of the genital segments, but also affects non-genital structures such as the sternal apodemes of abdominal segment II and color patterns. DeLong (9) described a parasitized *Chlorotettix* as a gynandromorph. A sex mosaic of *Arthaldeus* and specimens of *Eupteryx* with suppressed secondary female genitalia and a sex mosaic have been described by Kathirithamby (22–24). Specimens with suppressed genitalia were parasitized by Dryinidae. Sex mosaics may or may not be caused by parasites. Kathirithamby (22–24) reported that parasitism cannot reverse the formation of the male and female genitalia, only gradually reduce them; all parasitized specimens have some form of reduced genitalia, however, sex mosaics are most probably caused by genetic imbalance.

The genus *Errastunus* has varying degrees of male and female genitalia reduction when parasitized by Pipunculidae. Oman (44) reports that various Typhlocybiinae are attacked by Strepsiptera and several authors have observed Deltocephalinae parasitized by all the major insect parasites, including nematodes. In the genus *Athysanella*, a large number of specimens have genitalia that are underdeveloped (Blocker, unpublished). These range from total suppression to nearly normal development with many stages between these two states. The styles, connective, and aedeagus are undifferentiated in some specimens. After they differentiate, the anterior arms of the connective usually appear Y-shaped in contrast to the linear shape seen in normal specimens where the anterior arms are fused. Various intermediate conditions can be observed in underdeveloped specimens; the styles and aedeagus are almost always reduced in size. Characters of the genital segment and legs may also be reduced in size. Undeveloped genitalia are bilaterally symmetrical and there is no present evidence of parasitism as a cause for abnormal size and shape. It has been suggested that nematodes may be responsible, but no evidence of this has been obtained. There is no apparent alteration of structures in some parasitized specimens examined but when alteration does occur, structures usually assume a bizarre or asymmetrical shape. This phenomenon is currently being investigated. At least one described species has been based on undeveloped genitalia and there may be others.

### 3.8 INTRASPECIFIC AND SPECIFIC VARIATION

It is difficult to determine whether differences between individuals and populations are infraspecific or specific in nature. Often genetic information and data

from interbreeding experiments are not available to the reviser. To help solve this dilemma, systematists must examine as many specimens from as many locations as possible. Le Quesne (31) and Nielson (41) discuss this situation in depth and offer good suggestions for future research effort, especially for economically important groups.

High temperature decreases body size of *Nephotettix* species; growth was retarded at 35°C whereas 30°C was optimum (46). Differences in body and wing length in *Empoasca* were found at different temperatures (48). Le Quesne (31) offers numerous examples of infraspecific variation involving color. Different color morphs of *Oncopsis flavicollis* (L.) females were originally described as separate species. Teneral specimens of the genus *Kybos* show an attractive red color that disappears in mature specimens; specimens of *Zygina* show seasonal color change (31).

The male genitalia in some *Edwardsiana* exhibit much infraspecific variation (31). In the genus *Eupteryx*, a stronger development of aedeagal processes occurs in more southern populations and specimens of *Euscelis* show similar tendencies as the climate becomes warmer. The spring and summer generations of *Euscelis* exhibit differences in genitalia and this condition can be artificially induced by alteration of day length; other differences were shown to be temperature dependent (37, 38). A previously described species of *Gypsonana* was suppressed after infraspecific variation was determined in the progeny of a single female that spanned two generations (42). Nielson (41) discusses problems found in many economically important genera (e.g., *Macrostes*, *Circulifer*, and *Empoasca*.) such as how data from interspecific crosses (taxa now considered separate species) can be of value in determining correct systematic position of polymorphic groups that are now classified as species complexes.

### 3.9 SUMMARY

The morphological characters of the external structure of leafhoppers most used by North American workers have been reviewed and a standardized system of nomenclature for the major structures has been proposed. Alternative nomenclature has also been listed. The examples are, for the most part, from groups familiar to us but some examples of unfamiliar groups are also used. The numerous examples of homoplasy that occur are impressive and a few are discussed. There are many other examples that could have been substituted.

In this concluding discussion it is emphasized that one must carefully examine as many characters, from as many specimens, from as many locations as possible before arriving at taxonomic conclusions. As an example (51), if one evaluates the genera *Doratura* and *Eupelix* by morphological characteristics of the head, *Doratura* will appear more highly evolved but if one evaluates characters of abdominal segment IX, *Eupelix* will appear to be evolutionarily advanced.

It is just as evident, in leafhoppers as in other insects, that one must use caution in describing a species or other taxon as “primitive” or “advanced” since all have varying degrees of derived character evolution. A careful analysis of the chronological sequence of occurrence of major (weighted) characters helps establish a useful classification. Such an analysis is needed for subfamilies and lower categories in Cicadellidae.

Caution must also be used in the assessment of infraspecific variation as well as variation in higher taxa. It is probable that species of *Balclutha* and *Macrostes* have been recently “split” due to error in the assessment of infraspecific variation (Blocker, unpublished). These problems will continue to occur, however, as long as more than one person studies the same group. It is hoped that these differences of opinion will strengthen our future classifications.

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