The planthopper genus *Stenocranus* in Canada: implications for classification of Delphacidae (Hemiptera)[1]

K.G.A. Hamilton

Agriculture and Agri-Food Canada, Biodiversity, K.W. Neatby Building, Central Experimental Farm, Ottawa, Ontario, Canada K1A 0C6 (e-mail: hamiltona@agr.gc.ca)

Abstract—The Canadian species of *Stenocranus* Fieber are keyed by external characters correlated with species concepts defined by known genitalic characters. *Stenocranus* is differentiated from *Terauchiana* Matsumura (Asian; here reported from the New World for the first time) and *Embolophora* Stål (from Africa) by the remarkable development of the female pygofers, which completely conceal the ovipositor. Based on both head and genitalic characters, the genus is divided into two subgenera: typical *Stenocranus* with many Old World species and two Canadian species, and subgenus *Codex* **nov.** for other New World species. The type of *Delphax dorsalis* Fitch, 1851 is a specimen of *Stenocranus pallidus* Beamer, 1946 **syn. nov.**, and "*S. dorsalis*" *sensu* Beamer is *S. unipunctatus* (Provancher, 1872). A lectotype of *Delphax vittata* Stål, 1862 is designated for the taxon *S. unipunctatus* (*sensu* Beamer, *nec* Provancher); its paralectotypes are specimens of *S. acutus* Beamer. The apparent evolutionary relationships of this fauna to other species of the world Stenocranini and within the superficially similar Saccharosydnini reveal numerous homoplasies and dramatic autapomorphies, contrasted with only a few reliable synapomorphies. A hierarchical classification of Delphacidae, based on the most distinctive synapomorphies, defines subfamily Delphacinae as encompassing at least four tribes: Vizcayini, Stenocranini, Tropidocephalini, and Delphacini, with "Kelisiinae" reduced to subtribe of Stenocranini and "Saccharosydnini" placed within Tropidocephalini.

Résumé—Une clé permet d'identifier les espèces canadiennes de *Stenocranus* Fieber d'après leurs caractéristiques externes qui ont été reliées aux concepts d'espèces définis par les caractères connus des pièces génitales. *Stenocranus* se différencie de *Terauchiana* Matsumura (asiatique; signalé ici pour la première fois dans le Nouveau Monde) et *Embolophora* Stål (africain) par le développement remarquable des pygofères de la femelle qui cachent entièrement l'ovipositeur. D'après les caractères à la fois de la tête et des génitalias, le genre se divise en deux sous-genres, le sous-genre typique *Stenocranus* avec plusieurs espèces de l'Ancien Monde et deux espèces canadiennes et le sous-genre *Codex* **nov.** pour les autres espèces du Nouveau Monde. Le type de *Delphax dorsalis* Fitch, 1851 est un spécimen de *Stenocranus pallidus* Beamer, 1946 **syn. nov.** et « *S. dorsalis* » *sensu* Beamer est *S. unipunctatus* (Provancher, 1872). Un lectotype de *Delphax vittata* Stål, 1862 est désigné pour le taxon *S. unipunctatus* (*sensu* Beamer, *nec* Provancher); ses paralectotypes sont des spécimens de *S. acutus* Beamer. Les relations évolutives apparentes de cette faune avec les autres espèces mondiales de Stenocranini, ainsi qu'à l'intérieur des Saccharosydnini d'apparence superficielle semblable, montrent de nombreuses homoplasies et des autapomorphies remarquables, alors qu'il y a peu de synapomorphies fiables. Une classification hiérarchique des Delphacidae, basée sur les synapomorphies les plus distinctes, définit la sous-famille Delphacinae comme comprenant au moins quatre tribus, les Vizcayini, les Stenocranini, les Tropidocephalini et les Delphacini; les « Kelisiinae » sont réduits à une sous-tribu des Stenocranini et les « Saccharosydnini » sont placés parmi les Tropidocephalini.

[Traduit par la Rédaction]

Received 6 May 2004. Accepted 22 March 2006.

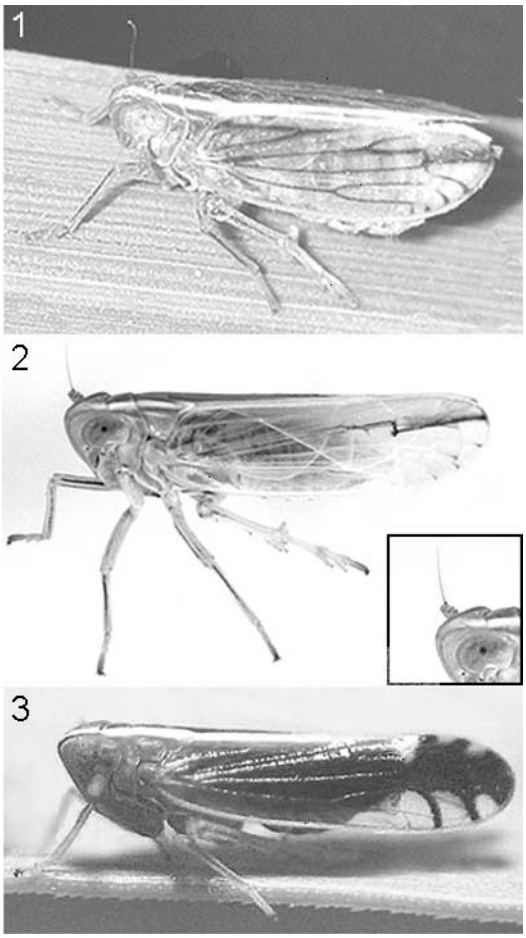
[1]This paper is part of a special issue honouring Geoffrey G.E. Scudder for his significant contributions to entomology in Canada.

Introduction

Delphacidae is the largest family of Fulgoroidea (Hemiptera), with a world fauna of well over 2000 species (Denno and Perfect 1994). The number of its described species and genera is rapidly proliferating. Based largely or exclusively on male genitalic characters, well over 283 genera had been described at the last world enumeration (Asche 1985). Many of these are monobasic segregates or comprise only a few closely related species. Yet the process of splitting off generic segregates for "distinctive" species is only just beginning. The delphacids of many faunal areas, including the New World, are little studied. Reliance upon male genitalia has clarified groups of closely related North American species (Muir and Giffard 1924) but leaves the greater number of species without obvious generic affinities. About half of the 125 known species in Canada (Maw *et al.* 2000) and another 75 from the United States are presently placed in *Delphacodes* Fieber (formerly in *Liburnia* Stål or *Megamelus* Fieber) pending assignment to definable genera. Many of these described species in Canada plus numerous undescribed species are without obvious generic affinities. The situation is not improved by including a larger geographic area. The present study is part of a larger project examining all 204 species of Delphacidae north of the Meridional zone (Gulf states and Sonoran subregion). This geographic scope only increases the number of unplaceable species.

Canadian species are particularly valuable in establishing connections between regional faunas, since they inhabit a meeting point of faunas coming east from the Palaearctic region and north from the Neotropics. Few delphacids of the Canadian fauna are larger, more distinctly marked, or more abundant than members of the sedge-feeding genus *Stenocranus* Fieber (Figs. 1–4). Yet despite this, the taxonomy of the genus continues in a highly unsatisfactory state. This is largely due to taxonomic difficulties throughout the family. Traditional characters such as distinctness of surface sculpturing (carinae) and relative production of the head and its processes, including antennae, have proved highly useful in some cases (Fieber 1866) but in many others are so subject to variation within a species, or to homoplasy among unrelated genera, that they have engendered only confusion in the minds of some taxonomists

Figs. 1–3. Habitus of *Stenocranus* spp.: 1, *S.* (s.s.) *felti*; 2, *S.* (*Codex*) *unipunctatus* (inset: enlargement of antenna showing arrangement of pustules); 3, *S.* (*Codex*) *acutus*. Photograph 1 © 2005 Tom Murray, photograph 2 © 2006 Tom Murray, photograph 3 © 2006 Michele Lee, used with permission. For colour versions, see http://bugguide.net/node/view/21612/bgpage, http://bugguide.net/node/view/50770/bgpage, and http://bugguide.net/node/view/59723.

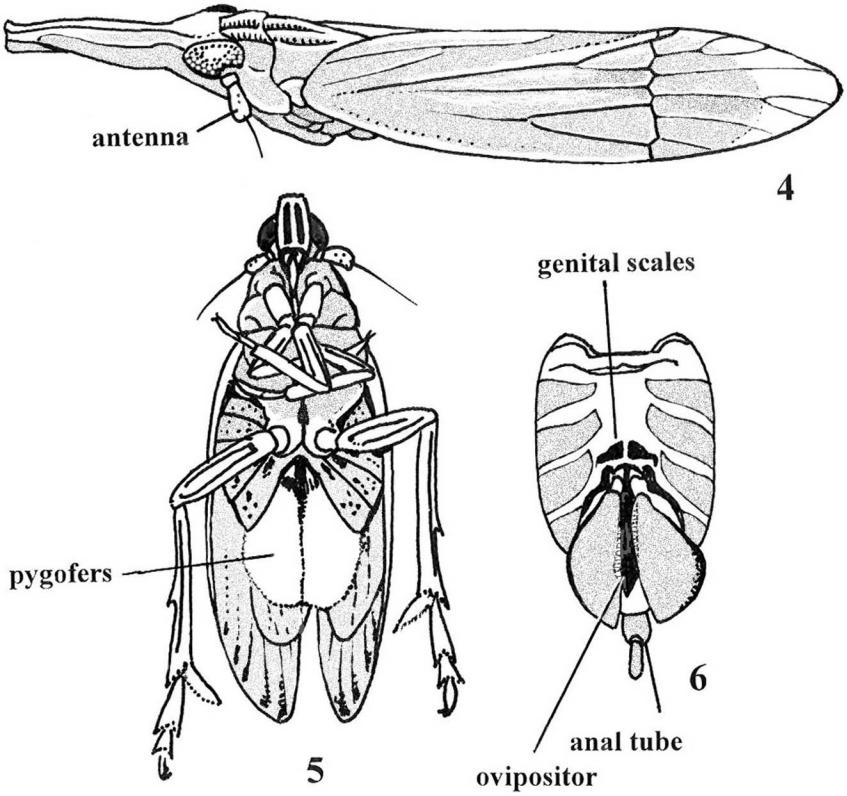


(Crawford 1914). Consequently, many workers restrict their generic definitions to male genitalic characters, which are considered to be more stable than external features.

Stenocranus in North America originally encompassed many unrelated Delphacidae with narrow heads (Van Duzee 1917; Dozier 1922) and narrowed (stenopterous) forewings. These putative synapomorphies have proven unreliable, as the width/length ratio of the head may be variable within genera, and stenoptery is found

https://doi.org/10.4039/n06-805 Published online by Cambridge University Press

Figs. 4–6. *Stenocranus* spp. in dorsolateral aspect (4) and ventral aspect (5–6): 4, undescribed species from Brazil; 5, *S. unipunctatus* female, showing wax-covered pygofers; 6, dissected abdomen of same, showing normally concealed ovipositor and genital scales.



in unrelated genera such as *Kelisia* Fieber and *Kelisoidea* Beamer. Even when *Stenocranus* was reduced to encompass purportedly "naturally related" species (Metcalf 1923), its definition remained vague. Beamer (1946*a*) cited characters to differentiate *Stenocranus* reliably from other Nearctic genera, but these characters are insufficient from a world perspective. He also revised the species using male genitalic characters (Beamer 1946*a*, 1946*b*), but female specimens, including a number of types, could not be identified with confidence. Asche (1985) reviewed the morphology of the world Delphacidae and placed *Stenocranus* in the subfamily Stenocraninae, along with three other Old World genera, using rigorous cladistic methodology and sexual characters to distinguish that subfamily from Kelisiinae. A subsequently described genus from Asia, *Preterkelisia* Yang, bridges this morphological gap (Yang 1989), requiring a reexamination of this part of his classification.

The purpose of this study is to place *Stenocranus* in phylogenetic and taxonomic relationship to taxa that are clearly defined and to provide a key to the Canadian species (as well as those in the northern United States), which are defined using characters additional to those of male genitalia.

Methods and morphology

The present study is based on more than 7000 specimens of delphacids in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, of which 350 are members of *Stenocranus*. Types that were not examined in previous revisions were checked, where possible.

Owing to the perceived need to revise the genera of Delphacidae, names used herein for species other than *Stenocranus* species and their relatives

https://doi.org/10.4039/n06-805 Published online by Cambridge University Press

are given in their original combination, regardless of how inappropriate these names may be.

Delphacidae are small to tiny insects with the second antennal segment prominent, bearing distinct sensory pustules, and with a distinctive moveable spur (calcar) on their hind leg adjacent to the tarsus (Fig. 5). The calcar comes in two principal forms: a rigid spur, usually armed with prominent spines (at least one at the tip and often as many as nine along the lower edge), or a flexible flap, either unarmed or with numerous (12–30) tiny serrations on the lower edge. The rigid form is most likely an aid to jumping on a fairly rigid substrate and is usually found on delphacids with woody hosts. The flexible form, found in *Stenocranus*, seems designed to wrap around a slender stem of grasses or sedges or to lie nearly flat against a leaf. Both forms of calcar are sometimes found in a single genus, *e.g.*, *Pissonotus* Van Duzee (Bartlett and Deitz 2000).

Delphacidae of plesiomorphic genera have male terminalia of the cixiid type, in which the aedeagus is composed of a theca and vesica, and have the claspers or "styles" (harpagones, or possibly parameres) directed caudad in an open capsule. Higher forms, including *Stenocranus* species, have the theca reduced to a short conical or tubular structure, into which the terminal part or "endotheca" has been retracted. Most other species (belonging to the subfamily Delphacinae, *sensu* Asche) have the theca reduced to a basal ring around the endotheca, with the endotheca alone projecting past a sclerotized wall or "diaphragm" (formed by fused pygofer lobes) that separates the aedeagal apparatus from the dorsally directed styles.

Female Delphacidae have the ovipositor so long that it divides the sternites almost to the base of the abdomen. The pregenital sternite is pushed back into the abdomen and forms a small plate, the "genital scale", which in some *Stenocranus* is also divided down the middle (Fig. 6). All other structures utilized in this study are common to other groups of Homoptera–Auchenorrhyncha such as Cicadellidae.

Taxonomy

Stenocranus Fieber

Stenocranus Fieber, 1866: 519, 532. Type species by subsequent designation (Oshanin 1912: 118): *Delphax lineola* Germar, 1818: 209 = *Fulgora minuta* Fabricius, 1787: 262.

Synapomorphies

Antennal pustules absent from triangular dorsobasal area of second segment, usually irregularly spaced or forming an oblique band, occasionally closely spaced in several short rows (Fig. 2); ovipositor concealed by pygofer lobes.

Homoplasies

Face usually with black stripes between pale carinae (as in *Liburnia detecta* Van Duzee); eye notch half as deep as eye (as in most Delphacini); tegmen always stenopterous, exposing sides of abdomen (as in flightless *Prokelisia* Osborn); calcar knife-shaped, straight on upper margin, bowed on lower margin (as in *Prokelisia*).

Remarks

Stenocranus exhibits considerable morphological diversity in the head, tegmen, and genitalia (Figs. 1–6). The dark costal crossveins of the tegmina (Fig. 1) and bifurcate anal tube process of *S. felti* Van Duzee (Beamer 1946*a*, Fig. 11) are both autapomorphies (unique specializations). An apparently undescribed Brazilian species has an enormously elongate head (Fig. 4) closely resembling that of the African stenocranine genus *Embolophora* Stål but has genitalia of both sexes nearly identical to those of *S. delicatus* Beamer from the Nearctic region. Its head shape is a homoplasy within the tribe and a dramatic autapomorphy within the genus. This species shares with *S. felti* another homoplasy of a symmetrically pointed tegmen (Figs. 1, 4). Yet another homoplasy is the first Media vein curved towards the margin in *S. felti* (Fig. 1) and *S. vittatus* (Stål), species which otherwise have little in common. The latter is closely allied to the Nearctic species *S. acutus* Beamer (Fig. 3) and *S. lautus* Van Duzee in its venation, tegminal colour pattern, and male genitalia, while *S. felti* has its closest relatives in the Asian fauna (Ishihara 1949).

The genus is demonstrably monophyletic because its species share a dramatic synapomorphy: the female pygofers are ventrally flattened, discoid, and covered with wax-secreting pores, thus completely hiding the ovipositor and genital scales (Figs. 5–6). By contrast, other Stenocranini have the plesiomorphic exposed ovipositor.

https://doi.org/10.4039/n06-805 Published online by Cambridge University Press

Canadian *Stenocranus* species occur in three distinctive forms: one closely resembling the Old World type species of *Stenocranus* (Fig. 2); one in which the tegmen is pointed and the costal crossveins are darkened and reflexed (Fig. 1) as in the leafhopper genus *Flexamia* DeLong; and one with a bold pattern on the tegminal tips that appears to form long costal crossveins (Fig. 3). These species encompass a wide variety of male genitalic forms ranging from nearly symmetric (only the aedeagal sheath being asymmetric, which is plesiomorphic for Delphacidae) to highly asymmetric (as in *Terauchiana* Matsumura, described from Asia).

Included Nearctic species

The following species have been removed from *Stenocranus*: *Stenocranus breviceps* Dozier, 1922 = *Liburnia slossoni* [sic] Ball, 1903 (Metcalf 1923); *Kelisia crocea* Van Duzee, 1897 = *Stenocranus crocea* (Osborn and Ball 1897) = *Prokelisia crocea* (Oman 1947); *Stenocranus hinei* Dozier, 1922 = *Megamelus aurantii* Crawford, 1914 (Muir and Giffard 1924); and *Stenocranus rostrifrons* Crawford, 1914 = *Saccharosydne rostrifrons* (Metcalf 1943). This leaves 12 widespread Nearctic species. Two of these species belong to the typical subgenus, which includes all the Old World species (Asche 1985; Yang 1989). The other 10 Nearctic species belong to an exclusively New World subgenus, described below. Two Neotropical species, *S. angustus* Crawford from Belize and *S. maculipes* Berg from Argentina, are not known to me.

Typical subgenus

Synapomorphies

"Genital scale" bilobed or medially divided; theca asymmetric with short, ventrally curved apical process.

Homoplasies

Clasper tips straight (Asche 1985), as in many Delphacini.

Included Nearctic species

Two Nearctic species that are not closely related to each other and that are quite different in both the form of their wings and the details of the male genitalia. Both are found in Canada, but this does not necessarily imply a recent spread from the Old World to the New.

Stenocranus (s.s.) *felti* Van Duzee

Stenocranus (s.s.) *sandersoni* Beamer

Codex subgen. nov.

Type species: *Delphax vittata* Stål, 1862: 315.

Etymology: *codex*, bound volume.

Synapomorphies

Face unusually narrow, with parallel-margined facial carinae, reminiscent of the edges of a closed hardcover book; male theca usually elongate.

Homoplasies

Females lack a strongly sclerotized "genital scale" (as in many Delphacini), genital clasper tips are turned outwards (as in *Prokelisia*); strongly asymmetric processes of the anal tube are common in this subgenus but do not define related groups of species.

Included Nearctic species

Half of the 10 described species do not occur in Canada (*). Several synapomorphies define groups of species within this subgenus. The distinctive tegmen, with marginal pale spots and the first branch of Media curved perpendicular to the costal margin, groups *S. acutus*, *S. lautus*, and *S. vittatus*, and these species in turn are united with *S. brunneus* Beamer, *S. delicatus*, and the long-headed undescribed species from Brazil (Fig. 4) in having the aedeagal endotheca arched at the base.

**Stenocranus* (*Codex*) *acutus* Beamer

**Stenocranus* (*Codex*) *arundineus* Beamer

**Stenocranus* (*Codex*) *brunneus* Beamer

Stenocranus (*Codex*) *delicatus* Beamer

Stenocranus (*Codex*) *dorsalis* (Fitch)

Stenocranus (*Codex*) *lautus* Van Duzee

**Stenocranus* (*Codex*) *ramosus* Beamer

**Stenocranus* (*Codex*) *similis* Crawford

Stenocranus (*Codex*) *unipunctatus* (Provancher)

Stenocranus (*Codex*) *vittatus* (Stål)

Remarks

Genitalic characters shared with *Terauchiana*, including strongly asymmetric processes of the

https://doi.org/10.4039/n06-805 Published online by Cambridge University Press

anal tube, are presumably plesiomorphic in this subgenus. The following identification key uses such characters to distinguish the Canadian species of *Stenocranus* plus (for comparison) species as far southeast as Pennsylvania.

Key to *Stenocranus* from Canada to Pennsylvania

1. Tegmen symmetrically pointed, with two black-tipped costal crossveins defining bases of apical cells (Fig. 1) . . . . . *felti* Van Duzee (B.C. to N.S.)
— Tegmen rounded (Fig. 2); dark costal crossveins absent, or longitudinal veins curved to costa beyond transverse crossvein row defining bases of apical cells 2
2. Tegminal vein tips darkened, strongly curved towards costa, crossvein-like 6
— Tegminal vein tips nearly straight, either pale or with dark spot only at junction of costa; not appearing like crossveins 3
3. Face 2.5 times as long as wide, nearly uniformly tan . . . . . *sandersoni* Beamer (Sask. to Maine)
— Face 3 times as long as wide, black with contrastingly pale carinae 4
4. Smaller, front tibia 0.6 mm long in male, 0.7 mm in female; genital capsule entirely pale; male anal tube armed with symmetrical spines . . . . . *delicatus* Beamer (Ont. to Kansas)
— Larger, front tibia 0.7 mm long in male, 0.8 mm in female; genital capsule dark or with dark markings; male anal tube with strongly asymmetrical spines 5
5. Smaller, length of female 5 mm; male abdomen with dark markings on venter, genital capsule brown to tan with darker markings . . . . . *dorsalis* (Fitch) (B.C. to P.E.I.)
— Larger, length of female 6 mm; male abdomen yellow except for contrasting black genital capsule . . . . . *unipunctatus* (Provancher) (B.C. to Maine)
6. Dorsomedial length of hind tibia as long as hind tarsus; aedeagal tip straight . . . . . *lautus* Van Duzee (Ont. to Kansas)
— Dorsomedial length of hind tibia greater than hind tarsus; aedeagal tip strongly bent downwards . . . 7
7. Head rounded in lateral aspect, with the crown exceeding the eyes by a length equivalent to half its width before the eyes; size larger, male 4.5 mm or longer, female 5.0 mm or longer . . . . . *vittatus* (Stål) (Ont. to Que.)
— Head angled in lateral aspect, more strongly produced, crown exceeding eyes by a length equivalent to its width before the eyes; size smaller, male less than 4.5 mm, female less than 5.0 mm . . . . . *acutus* Beamer (Pennsylvania to Florida)

Stenocranus acutus Beamer

Delphax vittata Stål, 1862: 315 (in part).

Stenocranus acutus Beamer, 1946*a*: 6.

Remarks

Examination of the types of *Delphax vittata* shows that this species was incorrectly synonymized with *Stenocranus lautus* by Van Duzee (1917). Three of the four syntypes of *D. vittata* in the Swedish Museum of Natural History, Stockholm, ("Mus. Holm.") are not conspecific with the "Typus". One of these is a male, even though the type series was originally stated to be entirely females. There is no reason to doubt that the entire series is original type material; the specimens are all labelled correctly and consistently with the localities mentioned in the description. Metcalf (1923) must have seen this series, and may actually have added the type labels, since he illustrated both the "Typus" female and the "Allotypus" male. The latter is 3.9 mm long with the characteristic genitalia of *S. acutus* (Metcalf 1923, Fig. 642; Beamer 1946*a*, Figs. 7, 7*a*). Both "Paratypus" females are 4.2–4.4 mm long and appear to be conspecific although they are from two different states ("Carolina meridionalis et Pennsylvania"). Thus, *S. acutus* is found as far north as Pennsylvania. For comments on the "Typus" female, see *S. vittatus*, below.

Stenocranus dorsalis (Fitch)

Delphax dorsalis Fitch, 1851: 46.

Stenocranus pallidus Beamer, 1946*a*: 3, **new synonymy.**

Remarks

This synonymy is based on examination of the Fitch type in the New York State Museum collection at Albany. Unfortunately, this

https://doi.org/10.4039/n06-805 Published online by Cambridge University Press

specimen's male genitalia were improperly preserved, but the anal tube remains in the microvial and was found to have the distinctive shape of that of *S. pallidus*, which was illustrated by Beamer (1946*a*). The correct name for "*S. dorsalis*" of Beamer (1946*a*) is discussed below, under *Stenocranus unipunctatus* (Provancher).

Stenocranus pallidus Beamer is not the same species as *Stenocranus pallidus* Linnavuori, which is a junior homonym corrected by Asche (1985) to *S. linnapallidus*.

Stenocranus unipunctatus (Provancher)

Delphax unipunctatus Provancher, 1872: 319.

Stenocranus dorsalis: Beamer, 1946*a*: 2 (*nec* Fitch).

Remarks

The identity of this species is based on the large size of the female Provancher type (".23 pce." = 6 mm) and the characteristic tegminal marking: "a black spot on the fifth cell [counting] from the costa, which continues as a brown line to the wing tip" (as in Fig. 2).

Stenocranus vittatus (Stål)

Delphax vittata Stål, 1862: 315.

Stenocranus unipunctatus: Beamer, 1946*a*: 5 (*nec* Provancher).

Remarks

The redefined species is based on a syntype female of *D. vittata*, bearing a "Typus" label, in the Swedish Museum of Natural History, Stockholm. This specimen is considerably bigger (5.2 mm) than the other syntypes, with a blunter head (Metcalf 1923, Fig. 101). It is here designated **lectotype** of *Delphax vittata* to replace the misapplied name *Stenocranus unipunctatus* (*sensu* Beamer).

Discussion

Character states and evolutionary relationships already mentioned reveal numerous apparent homoplasies, dramatic autapomorphies, and a few synapomorphies of considerable reliability. Based on these characters, it is concluded that cladistics based on data sets chosen by the probability of their having been evolved only once (measured by the complexity of individual structures) provides "key" (clarifying) groupings against which it is possible to correlate other characters of doubtful significance. Such complex apomorphies are generally ones that correlate best, *i.e.*, provide the maximum number of supplementary synapomorphies, and can be used with greater assurance in areas of phylogeny where data is conflicting. This is the technique first used by Hansen (1890), who used "unique" (*i.e.*, synapomorphic) characters to demonstrate that treehoppers (Membracidae) and leafhoppers (Cicadellidae) are closely related, despite abundant differences.

The "key" character defining *Stenocranus* is the highly modified female genitalia. This character embraces species that differ considerably in head length, pustule patterns of the antennae, wing venation, and even genitalic characters in both sexes. This redefinition of *Stenocranus* maintains existing species combinations, includes an autapomorphous species, and also results in a genus of considerable but not unwieldy size (>60 species) that is identifiable in both sexes and has a maximum probability of being monophyletic. A comparable situation exists in *Saccharosydne* Kirkaldy, which is probably paraphyletic to two autapomorphic species that have been described as monobasic genera: *Neomalaxa flava* Muir, with elongate antennae (Muir 1918), and *Pseudomacrocorupha wagneri* Muir, with pectinately toothed calcars (Muir 1930). These are united by the clearly synapomorphic "key" characters of curious head shape, black-striped antennae, a bizarrely elongated and coiled endothecal shaft deeply retracted into the abdomen, and a hook-like process on the dorsal side at the base of the shaft (Asche 1985, Figs. 643–658), while the autapomorphies of elongate antennae and pectinate calcars are comparable to those encountered in *Stenocranus* and *Pissonotus*.

"Key" characters in the phylogeny of Delphacidae are here used to define the subfamily Delphacinae and the tribes Delphacini, Stenocranini, and Tropidocephalini. Supplementary (probably homoplastic) characters that correlate with genera in these taxa but are seldom used in delphacid taxonomy include the following: distinctive colour patterns of face, antenna, thorax, tegmen; arrangement and spacing of antennal pustules; depth of eye notch; shape of tegmen; shape of calcar. These are confirmed as stable characters in the most

https://doi.org/10.4039/n06-805 Published online by Cambridge University Press

distinctive genus of the Delphacini, *Megamelus* (synapomorphy: male genital capsule with inflated lateral lobes). Absolute lengths of antennal segments, rostrum, and leg segments (including calcar length) are useful characters at the species level and their relative lengths are useful also at the generic level.

The traditional subdivision of Delphacidae into one small, primitive subfamily, Asiracinae, and the apomorphic Delphacinae was based solely on the shape of the calcar (moveable tibial spur), which defines the family (Muir 1915). Our present knowledge of the relationships of Delphacidae as a family rests largely on the superlative comparative studies of Asche (1985, 1990) and Emeljanov (1996). The general outline of the phylogeny is now clear, although some of the details, and hence classification, are still debatable (Bartlett 2005). This uncertainty is due largely to the extraordinary degree of homoplasy in the family. Very few generic or even subfamilial characters correlate well with any others. The most severe difficulties in determining phylogenetic relationships occur in the basal lineages (the traditional Asiracinae) and in the great proliferation of most derived genera (Delphacini), which includes more than 80% of all delphacid genera (Asche 1985). The following taxonomy best meets the phylogenetic data presented here. Delphacidae has two distinctive subfamilies, Asiracinae (possibly paraphyletic) and Delphacinae (monophyletic). The latter encompasses at least four tribes: Vizcayini, Stenocranini, Tropidocephalini, and Delphacini, with "Kelisiinae" reduced to subtribe of Stenocranini and "Saccharosydnini" placed within Tropidocephalini.

Family Delphacidae

Delphacidae Leach, 1815: 125.

Araeopidae Metcalf, 1939: 247.

Synapomorphies

Large antennae notching ventral margin of eyes; calcar at apex of hind tibia; medially divided abdominal sternites in both sexes; ovipositor extending nearly to base of abdomen.

Homoplasies

Median ocellus suppressed (as in all other Fulgoroidea except Cixiidae).

Remarks

This family was renamed Araeopidae owing to homonymy of its type genus (Metcalf 1943). This nomenclatorial controversy was resolved when the International Commission on Zoological Nomenclature (1961) placed Delphacidae on its official list of family-group names and fixed the type genus as *Delphax* Fabricius. It had earlier ruled that the older name *Delphax* Walbaum (a porpoise genus) was not an available name.

The modern family is probably derived from the Cretaceous family Lalacidae, subfamily Protodelphacinae (Hamilton 1990).

Included taxa

Haupt (1929), Wagner (1963), and Asche (1985) recognized multiple subfamilies, but other taxonomists prefer only the traditional two, or at most three, subfamilies: Asiracinae, Delphacinae, and Stenocraninae (Yang and Yang 1986; Yang 1989) or Asiracinae, Delphacinae, and Ugyopsinae (Emeljanov 1996: "Ugyopinae", but based on *Ugyops* Guérin-Méneville). The traditional two subfamilies is best supported by "key" characters and seems most advisable until phyletic relationships among the basal taxa are established conclusively.

Subfamily Delphacinae

Synapomorphies

Nymphs with facial pits mostly grouped in pairs, in characteristic pattern (Emeljanov 1996, Figs. 3:11–16), those of mesothorax of fifth instar reduced to two adjacent to mesonotal carina, one at base of mesothoracic wing pad and two much further distad on its disc, and one just below metanotal carina (Emeljanov 1996, Figs. 4:4–9), pits of abdomen not continuing onto laterotergites; adult calcar rigid and coarsely toothed to pectinate ("cultrate" of Muir 1915) or foliaceous and flexible ("laminate") with marginal teeth small or absent; sound-producing abdominal apodemes elongate, forming large and elaborate framework that surrounds basal part of abdomen (Asche 1990, Figs. 65–70); aedeagus without vesica, theca reduced to basal ring or tube around endotheca; genital opening largely sclerotized as a "diaphragm" formed by fused pygofer lobes separating aedeagal apparatus from genital claspers, the latter usually directed dorsolaterad.

Included taxa

The number of tribes in the subfamily varies considerably among various treatments. Asche (1990) added a new subfamily, Vizcayinae (for one Oriental genus), to his earlier delineation of the most primitive members of the lineage leading to Delphacinae: subfamilies Kelisiinae, Stenocraninae, and Plesiodelphacinae and tribes Tropidocephalini, Saccharosydnini, and Delphacini (Asche 1985). However, the bulk of the "key" characters of all these taxa are those of Delphacinae, to which subfamily Emeljanov (1996) relegated them as separate tribes. One possible exception is the Neotropical Plesiodelphacinae, which Bartlett (2005) assigned to the primitive subfamily Asiricinae [sic]. The following is a synopsis of the other New World tribes of subfamily Delphacinae *sensu lato*.

Tribe Delphacini

Synapomorphies

First branch of Media on forewing briefly connected to preceding vein, forming a three-branched pectinate system (Crawford 1914, plate 49, Fig. P), or veins in this region more extensively fused, producing irregular cells near the "stigma"; genital claspers vertical or oblique, attached to base of aedeagus by long, flexible connective; theca ring-like around aedeagus or incomplete.

Tribe Tropidocephalini

Tropidocephalini Muir, 1915: 269.

Synapomorphies

Theca with stout process on short base or withdrawn into base of anal tube.

Homoplasies

Antennae large, deeply notching eyes (convergent with some Asiracini and Delphacini).

Remarks

The "subfamily Saccharosydninae" (Vilbaste 1968) was reduced to tribal level by Asche (1985). This taxon may be an autapomorphic subtribe of Tropidocephalini containing a single genus, *Saccharosydne* (see remarks on this genus, above). Phylogenetic studies are needed to demonstrate whether or not Tropidocephalini minus Saccharosydnina is paraphyletic.

Tribe Stenocranini

Stenocraninae Wagner, 1963: 165.

Kelisiinae Wagner, 1963: 164, **stat. nov.** (subtribe).

Synapomorphies

Endotheca long and nearly straight (except sometimes at base), armed with at most a small, reflexed tip; theca tubular or flat with one or two elongate processes, intermediate in size between plesiomorphic elongate shape (in Asiracinae *sensu lato*) and ring-like shape of Delphacini.

Included taxa

Two subtribes with seven genus-group taxa: Holarctic genera *Stenocranus* and *Terauchiana* and the African genus *Embolophora* in Stenocranina, and *Kelisia* (weakly distinguished from the Old World genus-group taxon *Anakelisia* Wagner) in Kelisiina; *Stenokelisia* Ribaut (Ribaut 1934) and *Preterkelisia* form a link between these two groups of genera. These two genera have characteristically modified stenopterous venation (with Media continuing straight through the subapical crossvein row) as in *Kelisia*, but with genital asymmetry as in *Stenocranus* (Yang 1989). *Preterkelisia* has the strongly asymmetric anal tube of *Stenocranus*, while *Stenokelisia* has the lobate anal tube of *Kelisia*; *Stenokelisia* has the asymmetric theca of *Stenocranus*, while *Preterkelisia* has a bilaterally symmetric theca as in *Kelisia*, but with a tubular base. Apparently the asymmetry of theca and anal tube is plesiomorphic for the tribe as a whole. If so, Kelisiina encompasses *Kelisia*, *Preterkelisia*, and *Stenokelisia*, while *Anakelisia* is best treated as a subgenus of *Kelisia*.

Kelisiina appears to be a sister lineage of Stenocranina, although Asche (1985) considered it to be a sister taxon to higher tribes (Stenocraniini + Plesiodelphacini + Delphacini) based on how the egg ruptures in hatching. Since this can happen only in one of two ways (transversely or longitudinally), it seems virtually impossible to demonstrate synapomorphy with this character.

Canadian Stenocranini (including Kelisiina) all feed on sedges, whereas Delphacini are mostly grass-feeders. There are at least 12 Nearctic species of Kelisiina (Beamer 1945, 1951) and

https://doi.org/10.4039/n06-805 Published online by Cambridge University Press

13 of Stenocranina (Beamer 1946*a*, 1946*b*), plus the following new record.

Terauchiana Matsumura, new Nearctic record

Terauchiana Matsumura, 1915: 178. Type species by monotypy: *T. singularis* Matsumura, 1915.

Synapomorphy

Widely spaced antennal pustules in three rows on second segment (Ishihara 1949, Fig. 16).

Homoplasies

Crown exceeding eyes by at least one eye length, with median carina furcating only near tip (in *Embolophora* the furcation extends to between the eyes). There are genitalic characters that separate these two genera in the Old World (Asche 1985), but unfortunately the only New World specimen I have seen is a female.

Included Nearctic species

The only specimen I have examined from the New World is of an apparently undescribed species from Illinois (in Canadian National Collection). It differs from the type species of the genus (Ishihara 1949, Figs. 15–19) in its shorter furcation of the median facial carina and in its larger calcar. There are four other species in Asia (Asche 1985).

Conclusions

The phylogenetic relationships of *Stenocranus* and its relatives provide a good basis for classification principles appropriate to the taxonomic difficulties encountered in this family. "Key" synapomorphies clearly define the family Delphacidae, the subfamily Delphacinae, and genera such as *Stenocranus* and *Saccharosydne* (*sensu lato*), although both of these genera include species with striking autapomorphies.

References

Asche, M. 1985. Zur Phylogenie der Delphacidae Leach, 1815 (Homoptera Cicadina Fulgoromorpha). Marburger Entomologische Publikationen, **2**(1), teil 1–2: 1–910.

Asche, M. 1990. Vizcayinae, a new subfamily of Delphacidae with revision of *Vizcaya* Muir (Homoptera: Fulgoroidea) — a significant phylogenetic link. Bishop Museum Occasional Papers, **30**: 154–187.

Bartlett, C.R. 2005. Progress in the phylogeny of the Delphacidae using molecular and morphological tools. *In* Abstracts of talks and posters, 12th International Auchenorrhyncha Congress, University of California, Berkeley, 7–12 August 2005, S[ymposia]: 29–30.

Bartlett, C.R., and Deitz, L.L. 2000. Revision of the New World delphacid planthopper genus *Pissonotus* (Hemiptera: Fulgoroidea). Thomas Say Publications in Entomology: Monographs. Entomological Society of America, Lanham, Maryland.

Beamer, R.H. 1945. The genus *Kelisia* in America north of Mexico (Homoptera–Fulgoridae–Delphacinae). Journal of the Kansas Entomological Society, **18**(3): 100–108.

Beamer, R.H. 1946*a*. The genus *Stenocranus* in America north of Mexico (Homoptera–Fulgoridae–Delphacinae). Journal of the Kansas Entomological Society, **19**: 1–11.

Beamer, R.H. 1946*b*. A new species of *Stenocranus* and notes on a *Bakerella* (Homoptera–Fulgoridae–Delphacinae). Journal of the Kansas Entomological Society, **19**: 137–138.

Beamer, R.H. 1951. A review of the genus *Kelisia* in America north of Mexico, with four new species (Homoptera–Fulgoridae–Delphacinae). Journal of the Kansas Entomological Society, **24**: 117–121.

Crawford, D.L. 1914. A contribution towards a monograph of the Homopterous insects of the family Delphacidae of North and South America. Proceedings of the United States National Museum, **46**: 557–640.

Denno, R.F., and Perfect, T.J. 1994. Introduction: planthoppers as models for ecological study and effective pest management. *In* Planthoppers: their Ecology and Management. Chapman & Hall, New York. pp. 1–4.

Dozier, H.L. 1922. A synopsis of the genus *Stenocranus*, and a new species of *Mysidia* (Homoptera). The Ohio Journal of Science, **22**(3): 69–83.

Emeljanov [Ymel'yanov], A.F. 1996. On the question of the classification and phylogeny of the Delphacidae (Homoptera, Cicadina), with reference to larval characters. Entomological Review, **75**(9): 134–150.

Fieber, F.X. 1866. Grundzüge zur generischen Theilung der Delphacini. Verhandlungen der Kaiserlich-Königlichen Zoologisch-botanischen Gesellschaft in Wein, **16**: 497–516.

Fitch, A. 1851. Catalogue with references and descriptions of the insects collected and arranged for the State Cabinet of Natural History. Annual Report of the State Cabinet of Natural History, **4**: 44–69.

Hamilton, K.G.A. 1990. Homoptera. *In* Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Edited by* D.A. Grimaldi. Bulletin of the American Museum of Natural History, **195**: 82–122.

Hansen, H.J. 1890. Gamle og nye hovedmomenter til Cicadariernes morphologi og systematik. Entomologisk Tidskrift utgifven af Entomologiska Föreningen i Stockholm, **11**: 19–76. [English translation in Entomologist, **33** (1900).]

Haupt, H. 1929. Neueinteilung der Homoptera–Cicadina nach phylogenetisch zu wertenden Merkmalen. Zoologische Jahrbücher, Abteilung für Systematik, Okologie und Geographie der Tiere, **58**: 173–286.

International Commission on Zoological Nomenclature. 1961. Opinion 602. *Delphax* Fabricius, 1798 (Insecta, Hemiptera); interpretation under the plenary powers. Bulletin of Zoological Nomenclature, **18**(4): 246–248.

Ishihara, T. 1949. Revision of the Araeopidae of Japan, Kyukyu Islands and Formosa (Hemiptera). Scientific Reports of the Matsuyama Agricultural College, **2**: 1–102 + 17 pl.

Leach, W.E. 1815. Entomology. *In* Edinburgh Encyclopaedie, **9**: 57–172.

Matsumura, S. 1915. Neue Cicadinen Koreas. Transactions of the Sapporo Natural History Society, **5**: 154–184.

Maw, H.E.L., Foottit, R.G., Hamilton, K.G.A., and Scudder, G.G.E. 2000. Checklist of the Hemiptera of Canada and Alaska. NRC Research Press, Ottawa, Ontario.

Metcalf, Z.P. 1923. A key to the Fulgoridae of eastern North America with descriptions of new species. Journal of the Elisha Mitchell Society, **38**: 139–230 + pl. 38–70.

Metcalf, Z.P. 1939. Hints on bibliographies. Journal of the Society of Bibliographers of Natural History, **1**: 241–248.

Metcalf, Z.P. 1943. Fascicle IV: Fulgoroidea, Part 3: Araeopidae (Delphacidae). *In* General catalogue of the Hemiptera. *Edited by* W.E. China. Smith College, Northampton, Massachusetts.

Muir, F. 1915. A contribution towards the taxonomy of the Delphacidae. The Canadian Entomologist, **47**: 208–212, 261–270, 296–302, 317–320.

Muir, F. 1918. Homopterous notes. II. Proceedings of the Hawaiian Entomological Society, **3**: 414–429.

Muir, F. 1930. On some South American Delphacidae (Homoptera, Fulgoroidea). Entomologiske Tidskrift utgifven af Entomologiska Föreningen i Stockholm, **51**: 207–215.

Muir, F., and Giffard, W.M. 1924. Studies on North American Delphacidae. Bulletin of the Hawaiian Sugar Planters' Association, Division of Entomology, **15**: 1–53.

Oman, P.W. 1947. The types of Auchenorrhynchous Homoptera in the Iowa State College Collection. Iowa State College Journal of Science, **21**(2): 161–228.

Osborn, H., and Ball, E.D. 1897. Contributions to the Hemipterous fauna of Iowa. Proceedings of the Iowa Academy of Sciences, **4**: 172–234.

Oshanin, V.T. 1912. Katalog der paläarktischen Hemipteren (Heteroptera, Homoptera–Auchenorrhyncha und Psylloideae). R. Friedländer & Sohn, Berlin.

Provancher, L. 1872. Description de plusieurs Hémiptères nouveaux (continuée). Le Naturaliste Canadien, **4**: 319–320.

Ribaut, H. 1934. Nouveaux delphacides (Homoptera–Fulgoroidea). Bulletin de la Société d'Histoire naturelle de Toulouse, **66**: 281–301.

Stål, C. 1862. Novae vel minus cognitae Homopterorum formae et species. Berliner Entomologische Zeitschrift, **6**: 479–504.

Van Duzee, E.P. 1897. A preliminary review of the North American Delphacidae. Bulletin of the Buffalo Society of Natural Sciences, **5**: 225–261.

Van Duzee, E.P. 1917. Catalogue of the Hemiptera of America north of Mexico, excepting the Aphididae, Coccidae and Aleurodidae. University of California Publications, Technical Bulletins, College of Agriculture, Agricultural Experiment Station, Entomology, **2**: 557–558.

Vilbaste, J. 1968. Über die Zikadenfauna des Primorje Gebietes. Izdatel'stvo "Valgus", Tallin[n, Estonia]. [In Russian with German summary.]

Wagner, W. 1963. Dynamische Taxionomie, angewandt auf die Delphaciden Mitteleuropas. Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut, **60**: 111–180.

Yang, C.T. 1989. Delphacidae of Taiwan (II) (Homoptera: Fulgoroidea). National Science Council, Republic of China, Special Publication 6, Taipei.

Yang, J.T., and Yang, C.T. 1986. Delphacidae of Taiwan (I), Asiracinae and the tribe Tropidocephalini (Homoptera: Fulgoroidea). *In* Collected papers on Homoptera of Taiwan. Taiwan Museum Special Publication Series No. 6.