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Leafhoppers (Homoptera: Cicadellidae) that probe human skin: A review of the world literature and nineteen new records, from Panama

Edwin Domínguez Núñez and Annette Aiello

Smithsonian Tropical Research Institute, Apartado 0843-03092 Balboa,
Ancon, Republic of Panama
e-mails: dominguezee@si.edu; aielloa@si.edu
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Summary
We review the world literature on leafhoppers (Cicadellidae) that have probed human skin, update the names presented in those published reports, and sort out which are original accounts and which are citations of previous reports (Table 1). We add 19 new records, representing five subfamilies, and at least 13 genera, all from Panama (Table 2). We speculate as to why these normally phytophagous insects sometimes probe human skin, and provide insight into the possible evolutionary consequences of this behavior.

Keywords
Insecta; Homoptera; Cicadellidae; leafhoppers; aberrant feeding; behavior; bite; blood; entomology; evolution; human skin; probe; medical entomology; new records; Panama

Introduction

Members of the insect orders Homoptera and Heteroptera, sometimes treated collectively as the Hemiptera, have distinctive mouth parts specialized for piercing and sucking that have enabled them to radiate into a variety of niches unavailable to members of most other insect groups. Concomitant with this specialization, essentially all Homoptera and Heteroptera subsist on liquid food alone.

Though the diets of Heteroptera vary from plant juices, to insect prey, to vertebrate blood, the Homoptera are restricted to plant fluids, mainly the xylem and/or phloem of vascular plants. With their high reproductivity and exceptional capacity to transmit plant diseases, the Homoptera include some of the worst agricultural pests. Among the most important in this respect are the leafhoppers (family Cicadellidae), which include highly efficient vectors of plant viruses (Nault and Rodriguez, 1985; Krinsky, 2002).

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Despite their present limitation to feeding on plants, anecdotal evidence suggests that a number of Homoptera, as well as certain plant-feeding Heteroptera, have the potential to diversify onto other food sources. That the switch from herbivory to predation already has occurred within the Heteroptera, *e.g.*, Reduviidae, lends credence to that idea, as does the fact that species representing at least 15 families of herbivorous Heteroptera and five families of Homoptera are known to have bitten humans. These accounts were reviewed by Bequaert (1926), Myers (1929), Usinger (1934), Ryckman (1979), Ryckman and Bentley (1979), and Alexander (1984).

Homoptera known to annoy humans by probing with their mouthparts are found among the leafhoppers (Cicadellidae), treehoppers (Membracidae), spittle bugs (Cercopidae), plant hoppers (Fulgoroidea), and cicadas (Cicadidae).

Over the years, a variety of non-blood-feeding insects, *e.g.*, lacewing larvae (Neuroptera: Chrysopidae), has "bitten" each of us (EDN and AA) and, independently, we began to collect the leafhoppers involved. A chance conversation led to the joint preparation of this paper, with the objectives of investigating the history of this phenomenon in cicadellids and reporting our own experiences.

Methods

We tracked down every published report of leafhoppers biting humans that we could find, updated the names, and organized the original reports chronologically, each followed by the publications that cite them. Thus, the entire history of these reports is laid out in Table 1.

Our own observations (Table 2) were made in three general areas of the Republic of Panama: Panama City (immediately east of the Panama Canal); the town of Arraiján (just west of the Canal watershed); and Cocle Province, which is farther west. Attackers were collected manually and preserved in 70% ethanol or were frozen; later, all specimens were mounted on points and the male genitalia were preserved in vials in glycerin. Vouchers are deposited in MIUP (Museo de Invertebrados G. B. Fairchild de la Universidad de Panamá) and at STRI (Smithsonian Tropical Research Institute) as noted in Table 2.

Nomenclature of the Cicadellidae was updated Cwikla, 1985a; Dietrich and Dmitriev, 2006; Dietrich and Dmitriev, 2008; Dlabola, 1958c; Emeljanov, 1999c; Ghauri, 1971; Ghauri, 1974a; Kramer,1971; Metcalf, 1967a; Metcalf,1967c; Metcalf, 1968a; Ross, 1968; Takiya *et al.* 2006; Young, 1977.

Results

In all, we found 174 records, published from 1911-2006, by 27 authors (authors and co-authors being counted as one), in 33 publications. These reports represent three cicadellid subfamilies, 19 genera, and at least 27 species from various regions of the world, including China, Cuba, England, French Polynesia, India, Japan, North Africa, the Philippines, Trinidad, and the United States (Table 1). Of the 174 records,

Table 1. Cicadellidae reported to have probed human skin world wide. Original reports are highlighted and arranged chronologically, each followed by the publications that cite them. Information in square brackets was added by the authors.

Empoasca fabae (Harris, 1841)	Typhlocybinae	Dallas, Texas [USA]	Tucker (1911, p.29) (as *Empoasca mali*), specimens determined by O. Heidemann. Ingested blood.
Empoasca fabae (Harris, 1841)	Typhlocybinae		Riley & Johannsen (1915, p.33) (as *Empoasca mali*), source not given but most likely Tucker (1911).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Lawson (1926, p.73), citing Riley & Johannson (1915).
Empoasca fabae (Harris, 1841)	Typhlocybinae	North America	Myers (1929, p.475), citing Tucker (1911), Riley and Johannsen (1915).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Ryckman & Bentley (1979, p.37-38) (as *Empoasca mali*), citing Riley & Johannsen (1915).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Ryckman & Bentley (1979, p.42) (as *Empoasca mali*), citing Tucker (1911).
Scaphytopius acutus (Say, 1830)	Deltocephalinae		Riley & Johannsen (1915, p.33) (as *Platymetopius acutus*), source not given.
Scaphytopius acutus (Say, 1830)	Deltocephalinae		Lawson (1926, p.73) (as *Platymetopius acutus*), citing Riley & Johannsen (presumably 1915).
Scaphytopius acutus (Say, 1830)	Deltocephalinae	North America	Myers (1929, p.475) (as *Platymetopius acutus*), citing Riley & Johannsen (1915).
Scaphytopius acutus (Say, 1830)	Deltocephalinae		Riley & Johannsen (1938, p.143) (as *Platymetopius acutus*), source not given, but not doubt their own 1915 record.
Scaphytopius acutus (Say, 1830)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Platymetopius acutus*), citing Myers (1929).
Scaphytopius acutus (Say, 1830)	Deltocephalinae		Ryckman & Bentley (1979, p.37-38) (as *Platymetopius acutus*), citing Riley & Johannsen (1915).
Scaphytopius acutus (Say, 1830)	Deltocephalinae		Ryckman & Bentley (1979, p.38) (as *Platymetopius acutus*), citing Riley & Johannsen (1938).

(*Continued*)

Table 1. (*Cont.*)

Empoasca fabae (Harris, 1841)	Typhlocybinae	Fayetteville, Arkansas [USA]	Becker (1918, p.101) (as *Empoasca mali*), specimens determined by W.D. Gibson.
Empoasca fabae (Harris, 1841)	Typhlocybinae		Lawson (1920, p.20) (as *Empoasca mali*), citing Becker (1918).
Empoasca fabae (Harris, 1841)	Typhlocybinae	North America	Myers (1929, p.475), citing Becker (1918).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Ryckman (1979, p.11) (as *Empoasca mali*), citing Becker (1918).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Ryckman & Bentley (1979, p.33), citing Myers (1929).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Alexander (1984, p.58) (as *Empoasca mali*), citing Becker (1918).
Nephotettix nigropictus (Stål, 1870)	Deltocephalinae	Manila [Philippines]	Banks (1919, p.181) (as *Nephotettix apicalis*).
Nephotettix nigropictus (Stål, 1870)	Deltocephalinae	Philippines	Ryckman (1979, p.11) (as *Nephotettix apicalis*), citing Banks (1919).
Nephotettix nigropictus (Stål, 1870)	Deltocephalinae	Philippines	Alexander (1984, p.58) (as *Nephotettix apicalis*), citing Banks (1919).
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Manila [Philippines]	Banks (1919, p.181) (as *Nephotettix bipunctatus*).
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Brumpt (1922, p.815) (as *Nephotettix bipunctatus*), citing Banks (presumably 1919).
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Bequaert (1926, p.189) (as *Nephotettix bipunctatus*), citing Banks as reported by Brumpt (1922).
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Brumpt (1927, p.952-953) (as *Nephotettix bipunctatus*), citing Banks, as in the 1922 edition.
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Myers (1929, p.474) (as *Nephotettix bipunctatus*), citing Brumpt (1922).
Nephotettix virescens (Distant, 1908)	Deltocephalinae		Martini (1929, p.385) (as *Nephotettix*), source not give, but presumably originating from Banks (1919) or one of those citing him.
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Brumpt (1936, p.1305) (as *Nephotettix bipunctatus*), citing Banks, as in his previous two editions.
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Brumpt (1949, p.1276) (as *Nephotettix bipunctatus*), citing Banks, as in his previous three editions.

(*Continued*)

Table 1. (*Cont.*)

Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Ryckman (1979, p.11) (as *Nephotettix bipunctatus*), citing Banks (1919).
Nephotettix virescens (Distant, 1908)	Deltocephalinae		Ryckman & Bentley (1979, p.31) (as *Nephotettix*), citing Martini (1929).
Nephotettix virescens (Distant, 1908)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Nephotettix bipunctatus*), citing Myers (1929).
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Philippines	Alexander (1984, p.58) (as *Nephotettix bipunctatus*, misspelled as *bipunctata*), citing Banks (1919).
Empoasca fabae (Harris, 1841)	Typhlocybinae	Kansas [USA]	Lawson (1920, p.20) (as *Empoasca mali*).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Lawson (1926, p.73) (as *Empoasca mali*), a repeat of his own report of 1920.
Empoasca fabae (Harris, 1841)	Typhlocybinae	North America	Myers (1929, p.475), citing Lawson (1926).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Riley & Johannsen (1938, p.143) (as *Empoasca mali*), source not given.
Empoasca fabae (Harris, 1841)	Typhlocybinae	Kansas [USA]	Ryckman & Bentley (1979, p.28), citing Lawson (1926).
Empoasca fabae (Harris, 1841)	Typhlocybinae		Ryckman & Bentley (1979, p.38) (as *Empoasca mali*), citing Riley & Johannsen (1938).
Exitianus indicus (Distant, 1908)	Deltocephalinae	Madras [India]	Donovan (1920a, p.220; 1920b, p.212) (as *Phrynomorphus indicus*), based on specimens collected by him, taken to Gahan, and determined by Distant.
Exitianus indicus (Distant, 1908)	Deltocephalinae	l'Inde	Brumpt (1922, p.814) (as *Phrynomorphus indicus*), citing Donovan (presumably 1920).
Exitianus indicus (Distant, 1908)	Deltocephalinae	Madras (India)	Bergevin (1925a, p. 40) (as *Athysanus indicus*), citing personal correspondence from Marshall, who reported that M.E. China found two specimens in the British Museum that were collected by Donovan in Nov. 1919 and annotated as "bloodsuckers." Unknown to him, Donovan (1920) already had published his account of their blood-sucking behavior.

(*Continued*)

Table 1. (*Cont.*)

Exitianus indicus (Distant, 1908)	Deltocephalinae	Madras, India	Bequaert (1926, p.189) (as *Phrynomorphus indicus*), citing Donovan (1920).
Exitianus indicus (Distant, 1908)	Deltocephalinae	India	Brumpt (1927, p.952) (as *Phrynomorphus indicus*), citing Donovan (presumably 1920).
Exitianus indicus (Distant, 1908)	Deltocephalinae	India	Myers (1929, p.474) [as *Athysanus (Phrynomorphus) indicus*], citing Donovan (1920).
Exitianus indicus (Distant, 1908)	Deltocephalinae	Madras (India)	China (1929, p.97) (as *Athysanus indicus*), in note read by E.B. Poulton at 16 Oct. 1929 meeting of the Entomological Society of London, in which he mentions that he "drew Bergevin's attention" to Donovan specimens in the British Museum.
Exitianus indicus (Distant, 1908)	Deltocephalinae	India	Brumpt (1936, p.1305) (as *Phrynomorphus indicus*), citing Donovan (presumably 1920), as in his 1927 edition.
Exitianus indicus (Distant, 1908)	Deltocephalinae	Madras, Inde anglaise	Foley & Audouze (1938, p.526) (as *Athysanus indicus*), reporting observations by Donovan in Nov. 1919.
Exitianus indicus (Distant, 1908)	Deltocephalinae	India	Brumpt (1949, p.1275) (as *Athysanus indicus*), citing Donovan (presumably 1920), as in his previous two editions.
Exitianus indicus (Distant, 1908)	Deltocephalinae	Madras, India	Ryckman (1979, p.16) (as *Phrynomorphus indicus*), citing Donovan (1920a).
Exitianus indicus (Distant, 1908)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Athysanus indicus*), citing Myers (1929).
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Calcutta [India]	Brumpt (1922, p.815) (as *Nephotettix bipunctatus*), citing A. Alcock, with no date or place of publication. We have been unable to locate any Alcock publication that mentions Cicadellidae as biting humans.
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Calcutta [India]	Bequaert (1926, p.189) (as *Nephotettix bipunctatus*), citing Alcock as reported in Brumpt (1922).
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Calcutta (India)	Brumpt (1927, p.952-953) (as *Nephotettix bipunctatus*), citing A. Alcock, as in the 1922 edition.
Nephotettix virescens (Distant, 1908)	Deltocephalinae	India	Myers (1929, p.474) (as *Nephotettix bipunctatus*), citing Brumpt (1922).

(*Continued*)

Table 1. (*Cont.*)

Nephotettix virescens (Distant, 1908)	Deltocephalinae	Calcutta (India)	Brumpt (1936, p.1305) (as *Nephotettix bipunctatus*), citing A. Alcock, as in his previous 2 editions.
Nephotettix virescens (Distant, 1908)	Deltocephalinae	Calcutta (India)	Brumpt (1949, p.1276) (as *Nephotettix bipunctatus*), citing A. Alcock (misspelled as Alcok).
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	In Salah [southern Algeria]	Bergevin (1925a, p.38-39) (as *Athysanus* undescribed sp.); described by him in a following paper (1925b, p.42) as *Athysanus vulnerans*, from six specimens (4 males, 2 females) sent to him by Dr. Foley, who reported their biting behavior as communicated in a letter from Dr. Fouque, dated 12 Sept. 1924.
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	In Salah (southern Algeria)	Bergevin (1925b, pp. 42) (as *Athysanus vulnerans* sp. nov.), from specimens collected by Dr. Fouque, and sent to him by Dr. Foley.
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	"Sahara" in error	Bequaert (1926, p.189) (as *Athysanus vulnerans*), citing Bergevin (1925), but he misread Salah as "Sahara."
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	"Sahara" in error	Myers (1929, p.474) (as *Athysanus vulnerans*), citing Bergevin (1925b), though perpetuating Bequaert's error concerning the location; perhaps he did not have access to Bergevin's publication.
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	In Salah (southern Algeria)	China (1929, p.97) (as *Athysanus vulnerans*), citing Bergevin (1925a & 1925b), in letter read by E.B. Poulton at 16 Oct. 1929 meeting of the Entomological Society of London.
Exitianus	Deltocephalinae		Martini (1929, p.385) (as *Athysanus*), source not given, but based on the matching list of genera, presumably originating from Bergevin (1925a).
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	Algeria	Ryckman (1979, p.12) (as *Athysanus* sp.), citing Bergevin (1925).
Exitianus	Deltocephalinae		Ryckman & Bentley (1979, p.31) (as *Athysanus* sp.), citing Martini (1929).
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Athysanus vulnerans*), citing Myers (1929).

(*Continued*)

Table 1. (*Cont.*)

Euscelis curticeps Lindberg, 1927	Deltocephalinae	Khartoum (Soudan Egyptien)	Bergevin (1925a, pp. 39-40) (as *Athysanus* sp.), regarding a specimen collected by H.B. Johnston, 17 Oct. 1924, and sent by Marshall to Bergevin, who passed it on to Lindberg who then described it (1927, p.92-94) as *Euscelis curticeps*.
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Khartoum, Anglo-Egyptian Sudan	Bequaert (1926, p. 189) (as *Athysanus*), citing Bergevin (1925).
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Khartoum (Gouvernement du Soudan)	Lindberg (1927c, p. 92), describing specimens sent to him by Bergevin.
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Sudan	Myers (1929, p.475), citing Lindberg (1927).
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Sudan	China (1929, p.97), citing Bergevin (1925a), in letter read by Poulton at 16 Oct. 1929 meeting of the Entomological Society of London.
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Khartoum (Sudan)	Foley & Audouze (1938, p.526) (as *Athysanus)*, mentioning that Marshall sent 5 undescribed species of blood-sucking "Jassidae" to Bergevin in 1925.
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Sudan	Ryckman & Bentley (1979, p.28), citing Lindberg (1927).
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Khartoum (Sudan)	Lewis (1958, p.45) (misspelled as *curtipes*), citing Lindberg (1927).
Euscelis curticeps Lindberg, 1927	Deltocephalinae	Sudan	Ryckman & Bentley (1979, p.28), citing Lewis (1958).
Euscelis curticeps Lindberg, 1927	Deltocephalinae		Ryckman & Bentley (1979, p.33), citing Myers (1929).
Euscelis curticeps Lindberg, 1927	Deltocephalinae	North Africa	Alexander (1984, p.58) (misspelled as *Athysaurus* sp.), citing Bergevin (1925).
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Khartoum (Soudan Egyptien)	Bergevin (1925a, pp. 39-40) (as *Thamnotettix*, misspelled as *Thamotettiy*), regarding specimens collected by H.B. Johnston, 17 Oct. 1924, and sent by Marshall to Bergevin, who passed them on to Lindberg who then described them (1927, p.88-90) as 5 specimens of *Thamnotettix sanguisuga*. Later, Myers (1929, p.474) reported that according to W. E. China, they correctly belong to *Aconura*.

(*Continued*)

Table 1. (*Cont.*)

Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Khartoum, Anglo-Egyptian Sudan	Bequaert (1926, p. 189) (as *Thamnotettix*), citing Bergevin (1925).
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Khartoum (Gouvernement du Soudan)	Lindberg (1927c, p. 88), describing (as *Thamnotettix sanguisuga*) specimens sent to him by Bergevin. Later, W. E. China said they correctly belong to *Aconura*.
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Sudan	Myers (1929, p.474) (as *Thamnotettix sanguisuga*), citing Lindberg (1927), who described it as a new species, *Thamnotettix sanguisuga*, but in footnote, Myers says W.E. China assured him it belongs to *Aconura* very near *A. prolixa*.
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Sudan	China (1929, p.97) (as *Thamnotettix sanguisuga*), citing Bergevin (1925a), in letter read by E.B. Poulton at 16 October 1929 meeting of the Entomolgical Society of London.
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae		Martini (1929, p.385) (as *Thamnotettix*), source not given, but based on the matching list of genera, presumably originating from Bergevin (1925a).
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Khartoum (Sudan)	Foley & Audouze (1938, p.526) (as *Athysanus*), mentioning that Marshall sent 5 undescribed species of blood-sucking "Jassidae" to Bergevin in 1925.
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae		Brumpt (1949, p.1276) (as *Thamnotettix*, misspelled as *Tamnotettix*), citing Bergevin (1925).
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Khartoum (Sudan)	Lewis (1958, p.45) (as *Aconura* nr. *prolixa:* as "a bug which may be an Aconura"), citing Lindberg (1927) and Myers (1929).
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae	Sudan	Ryckman & Bentley (1979, p.28) (as *Thamnotettix sanguisuga*), citing Lindberg (1927).
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Thamnotettix sanguisuga*), citing Myers (1929).
Aconurella near *prolixa* (Lethierry, 1885)	Deltocephalinae		Ryckman & Bentley (1979, p.31) (as *Thamnotettix*), citing Martini (1929).

(*Continued*)

Table 1. (*Cont.*)

Orosius cellulosus (Lindberg, 1927)	Deltocephalinae	Khartoum (Soudan Egyptien)	Bergevin (1925a, pp. 39-40) (as *Deltocephalus*), regarding specimens collected by H.B. Johnston, 17 Oct. 1924, and sent by Marshall to Bergevin, who passed them on to Lindberg, who described them (1927, p.90-92) as three specimens of *Thamnotettix cellulosus* (misspelled as *cellulosa*).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae	Khartoum, Anglo-Egyptian Sudan	Bequaert (1926, p. 189) (as *Deltocephalus*), citing Bergevin (1925).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae	Khartoum (Gouvernement du Soudan)	Lindberg (1927c, p. 90), describing (as *Thamnotettix cellulosa*) a specimen sent to him by Bergevin.
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae	Sudan	Myers (1929, p.475) (as *Thamnotettix cellulosa*), citing Lindberg (1927).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae	Sudan	China (1929, p.97) (as *Thamnotettix cellulosa*), citing Bergevin (1925a), in letter read by E.B. Poulton at 16 Oct. 1929 meeting of the Entomological Society of London.
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae		Martini (1929, p.385) (as *Deltocephalus*), source not given, but based on the matching list of genera, presumably originating from Bergevin (1925a).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae		Brumpt (1949, p.1276) (as *Deltocephalus*), citing Bergevin (1925).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae	Khartoum (Sudan)	Lewis (1958, p.45-46) (as *Thamnotettix cellulosa*), citing Lindberg (1927).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae	Sudan	Ryckman & Bentley (1979, p.28) (as *Thamnotettix cellulosa*), citing Lindberg (1927).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae		Ryckman & Bentley (1979, p.28) (as *Thamnotettix cellulosa*), citing Lewis (1958).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae		Ryckman & Bentley (1979, p.31) (as *Deltocephalus*), citing Martini (1929).
Orosius cellulosus (Lindberg, 1927)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Thamnotettix cellulosa*), citing Myers (1929).
Eratoneura basilaris (Say, 1825)	Typhlocybinae		Lawson (1926, p.73) (as *Erythroneura basilaris*), citing unpublished experience of Raymond H. Beamer.

(*Continued*)

Table 1. (*Cont.*)

Eratoneura basilaris (Say, 1825)	Typhlocybinae		Myers (1929, p.475) (as *Erythroneura basilaris*), citing Lawson (1926).
Eratoneura basilaris (Say, 1825)	Typhlocybinae		Riley & Johannsen (1938, p.143) (*Erythroneura basilaris*), citing Lawson (1926).
Eratoneura basilaris (Say, 1825)	Typhlocybinae	Kansas [USA]	Ryckman & Bentley (1979, p.28) (as *Erythroneura basilaris*), citing Lawson (1926).
Eratoneura basilaris (Say, 1825)	Typhlocybinae		Ryckman & Bentley (1979, p.33) (as *Erythroneura basilaris*), citing Myers (1929).
Eratoneura basilaris (Say, 1825)	Typhlocybinae		Ryckman & Bentley (1979, p.38) (as *Erythroneura basilaris*), citing Riley & Johannsen (1938).
Paraphlepsius irroratus (Say, 1830)	Deltocephalinae		Lawson (1926, p.74) (as *Phlepsius irroratus*), citing unpublished experience of E.M. Becton.
Paraphlepsius irroratus (Say, 1830)	Deltocephalinae	North America	Myers (1929, p.475) (as *Phlepsius irroratus*), citing Lawson (1926).
Paraphlepsius irroratus (Say, 1830)	Deltocephalinae		Riley & Johannsen (1938, p.143) (as *Phlepsius irroratus*), citing Lawson (1926).
Paraphlepsius irroratus (Say, 1830)	Deltocephalinae	Kansas [USA]	Ryckman & Bentley (1979, p.28) (as *Phlepsius irroratus*), citing Lawson (1926).
Paraphlepsius irroratus (Say, 1830)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Phlepsius irroratus*), citing Myers (1929).
Paraphlepsius irroratus (Say, 1830)	Deltocephalinae		Ryckman & Bentley (1979, p.38) (as *Phlepsius irroratus*), citing Riley & Johannsen (1938).
Endria inimica (Say, 1830)	Deltocephalinae		Lawson (1926, p.74) (as *Deltocephalus inimicus*).
Endria inimica (Say, 1830)	Deltocephalinae	North America	Myers (1929, p.475) (as *Deltocephalus inimicus*), citing Lawson (1926).
Endria inimica (Say, 1830)	Deltocephalinae		Riley & Johannsen (1938, p.143) (as *Deltocephalus inimicus*), citing Lawson (1926).
Endria inimica (Say, 1830)	Deltocephalinae	Kansas [USA]	Ryckman & Bentley (1979, p.28) (as *Deltocephalus inimicus*), citing Lawson (1926).

(*Continued*)

Table 1. (*Cont.*)

Endria inimica (Say, 1830)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Deltocephalus inimicus*), citing Myers (1929).
Endria inimica (Say, 1830)	Deltocephalinae		Ryckman & Bentley (1979, p.38) (as *Deltocephalus inimicus*), citing Riley & Johannsen (1938).
Draeculacephala mollipes (Say, 1840)	Cicadellinae		Lawson (1926, p.74).
Draeculacephala mollipes (Say, 1840)	Cicadellinae	North America	Myers (1929, p.474) (misspelled as *Draculaecephala mollipes*), citing Lawson (1926).
Draeculacephala mollipes (Say, 1840)	Cicadellinae		Riley & Johannsen (1938, p.143), citing Lawson (1926).
Draeculacephala mollipes (Say, 1840)	Cicadellinae	Kansas [USA]	Ryckman & Bentley (1979, p.28), citing Lawson (1926).
Draeculacephala mollipes (Say, 1840)	Cicadellinae		Ryckman & Bentley (1979, p.33), citing Myers (1929).
Draeculacephala mollipes (Say, 1840)	Cicadellinae		Ryckman & Bentley (1979, p.38), citing Riley & Johannsen (1938).
Exitianus obscurinervis (Stål, 1859)	Deltocephalinae		Lawson (1926, p.74) (as *Euscelis obscurinervis*).
Exitianus obscurinervis (Stål, 1859)	Deltocephalinae	North America	Myers (1929, p.475) (as *Euscelis obscurinervis*), citing Lawson (1926).
Exitianus obscurinervis (Stål, 1859)	Deltocephalinae		Riley & Johannsen (1938, p.143) (as *Euscelis obscurinervis*), citing Lawson (1926).
Exitianus obscurinervis (Stål, 1859)	Deltocephalinae	Kansas [USA]	Ryckman & Bentley (1979, p.28) (*Euscelis obscurinervis*), citing Lawson (1926).
Exitianus obscurinervis (Stål, 1859)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Euscelis obscurinervis*), citing Myers (1929).
Exitianus obscurinervis (Stål, 1859)	Deltocephalinae		Ryckman & Bentley (1979, p.38) (as *Euscelis obscurinervis*), citing Riley & Johannsen (1938).
Psammotettix lividellus (Zetterstedt, 1840) or near	Deltocephalinae	Hsuchowfu, Kiangsu, China	Lawson (1926, p.74) (as *Deltocephalus striatus* or near), citing correspondence from Marshal Hertig.
Psammotettix lividellus (Zetterstedt, 1840) or near	Deltocephalinae	Kiangsu, China	Myers (1929, p.475) (as *Deltocephalus*), citing Lawson (1926).

(*Continued*)

Table 1. (*Cont.*)

Psammotettix lividellus (Zetterstedt, 1840) or near	Deltocephalinae	Kiangsu, China	Ryckman & Bentley (1979, p.28) (as *Deltocephalus*), citing Lawson (1926).
Psammotettix lividellus (Zetterstedt, 1840) or near	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Deltocephalus*), citing Myers (1929).
Exitianus exitiosus (Uhler, 1880)	Deltocephalinae	St. Louis, Missouri [USA]	Crosby (1926, p.812) (as *Euscelis exitiosus*), determined by W.L. McAtee.
Exitianus exitiosus (Uhler, 1880)	Deltocephalinae	North America	Myers (1929, p.475) (as *Euscelis exitiosus*), citing Crosby (1926).
Exitianus exitiosus (Uhler, 1880)	Deltocephalinae	St. Louis, Missouri [USA]	Ryckman (1979, p.15) (as *Euscelis exitiosus*), citing Crosby (1926).
Exitianus exitiosus (Uhler, 1880)	Deltocephalinae		Ryckman & Bentley (1979, p.33) (as *Euscelis exitiosus*), citing Myers (1929).
Exitianus exitiosus (Uhler, 1880)	Deltocephalinae	USA	Alexander (1984, p.58) (as *Euscelis exitiosus*), citing Crosby (1926).
Empoasca fabae (Harris, 1841), a false record	Typhlocybinae		Readio (1927) published "Studies on the biology of the Reduviidae of America North of Mexico," but as far as we can determine didn't mention Cicadellidae.
Empoasca fabae (Harris, 1841), a false record	Typhlocybinae		Ryckman & Bentley (1979, p.36) (as *Empoasca mali*), citing Readio (1927) in error; Readio never published on biting cicadellids.
Empoasca fabae (Harris, 1841), a false record	Typhlocybinae		Alexander (1984, p.58) (as *Empoasca mali*), citing Readio (1927), a false record perhaps based on misinterpretaton of confusing text in Ryckman & Bentley (1979, p. 36).
Hortensia similis (Walker, 1851)	Cicadellinae	Trinidad	Myers (1929, p.474) (as *Kolla similis*) reporting communication with H.A. Ballou.
Hortensia similis (Walker, 1851)	Cicadellinae		Ryckman & Bentley (1979, p.33) (as *Kolla similis*), citing Myers (1929).

(*Continued*)

Table 1. (*Cont.*)

Typhlocyba quercus (Fabricius, 1777), but Myers had doubts about the identification	Typhlocybinae	Japan	Myers (1929, p.475) [He had doubts about the identification], reporting unpublished observation by T. Esaki.
Typhlocyba quercus (Fabricius, 1777)	Typhlocybinae		Ryckman & Bentley (1979, p.33), citing Myers (1929), but Myers had doubts about the identification.
Eratoneura maculata (Gillette, 1898)	Typhlocybinae	Japan	Myers (1929, p.475) [as *Erythroneura (Zygina) maculata?*], reporting unpublished observation by T. Esaki.
Eratoneura maculata (Gillette, 1898)	Typhlocybinae		Ryckman & Bentley (1979, p.33) (as *Erythroneura maculata*), citing Myers (1929).
Empoasca?	Typhlocybinae	no locality given, but likely to have been Cinnamara, Assam, India	Andrews (1929, p.96), personal experience reported in letter read by E.B. Poulton at 16 Oct. 1929 meeting of the Entomological Society of London.
Kybos smaragdula (Dlabola, 1958c:51)	Typhlocybinae	England	Myers (1929, p.475 & 477), reporting the as yet unpublished experience of W.E. China.
Kybos smaragdula (Dlabola, 1958c:51)	Typhlocybinae	Esther, Surrey [England]	China (1929, p.96-97) (as *Empoasca smaragdula*), his personal experience reported in note read by E.B. Poulton at 16 Oct. 1929 meeting of the Entomological Society of London, wherein he mentions that "Myers has recently published a note on this subject, but I have had no time to trace it."
Kybos smaragdula (Dlabola, 1958c:51)	Typhlocybinae		Ryckman & Bentley (1979, p.33), citing Myers (1929).
Neoaliturus tenellus (Emeljanov, 1999c:56)	Deltocephalinae	University of California [USA]	Usinger (1934, p.97) (as *Eutettix tenellus*), reporting unpublished experience of Julius Freitag.

(*Continued*)

Table 1. (*Cont.*)

Neoaliturus tenellus (Emeljanov, 1999c:56)	Deltocephalinae		Herms (1950, p.574) (as *Eutettix tenellus*), citing Usinger (1934).
Neoaliturus tenellus (Emeljanov, 1999c:56)	Deltocephalinae		Ryckman & Bentley (1979, p.42) (as *Eutettix tenellus*), citing Usinger (1934).
Neoaliturus tenellus (Emeljanov, 1999c:56)	Deltocephalinae	California [USA]	Alexander (1984, p.58) (as *Eutettix tenellus*), citing Usinger (1934).
Erythroneura comes (Say, 1825)	Typhlocybinae	Fresno, California [USA]	Usinger (1934, p.97-98), reporting unpublished experiences of Calvert E. Norland and Gordon L. Smith.
Erythroneura comes (Say, 1825)	Typhlocybinae		Herms (1950, p.574), citing Usinger (1934).
Erythroneura comes (Say, 1825)	Typhlocybinae		Ryckman & Bentley (1979, p.42) (as *Erythroneura comes*), citing Usinger (1934).
Erythroneura comes (Say, 1825)	Typhlocybinae	California [USA]	Alexander (1984, p.58) (misspelled as *Erythronema comes*), citing Usinger (1984).
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	In Salah [southern Algeria]	Foley & Audouze (1938, p.526) (as *Athysanus vulnerans*), reporting observations by Fonque in Sept. 1924.
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	sud algerien	Brumpt (1949, p.1276) (as *Athysanus vulnerans*), reporting observation made by Dr. Fouque (misspelled as Fonque).
Neoaliturus tenellus (Emeljanov, 1999c:56)	Deltocephalinae	Logan, Utah [USA]	Knowlton (1951, p.112) (as *Circulifer tenellus*), observations by him and M.F. Bowen.
Erythroneura	Typhlocybinae	Wad Medani [Sudan]	Lewis (1958, p.45), apparently an independent report.
Erythroneura	Typhlocybinae	Sudan	Ryckman & Bentley (1979, p.28), citing Lewis (1958).
Deltocephalus	Deltocephalinae	Wad Medani [Sudan]	Lewis (1958, p.45), apparently an independent report.
Deltocephalus	Deltocephalinae	Sudan	Ryckman & Bentley (1979, p.28), citing Lewis (1958).

(*Continued*)

Table 1. (*Cont.*)

Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	Khartoum [Sudan]	Lewis (1958, p.45) (as *E. vulnerans* Bergevin). There is confusion here: the genus name is not spelled out and the preceding genus is *Euscelis*, although *vulnerans* Bergevin was described in *Athysanus*. Regardless, apparently this is an independent report because all previous records are for Salah.
Exitianus fasciolatus (Melichar, 1911)	Deltocephalinae	Sudan	Ryckman & Bentley (1979, p.28) (as *E. vulnerans*), citing Lewis (1958).
Exitianus?	Deltocephalinae	Wad Medani [Sudan]	Lewis (1958, p.45), apparently an independent report.
Thamnotettix 2 spp.	Deltocephalinae	Wad Medani [Sudan]	Lewis (1958, p.46), apparently an independent report.
Empoasca decipiens (Paoli, 1930) or *Empoasca solani* (Curtis, 1846)	Typhlocybinae	Oxford [England]	McCrae (1974, 238). Specimen determined by W. J. Le Quesne as as a female of either *Empoasca decipiens* or *E. pteridis*, the females of which "cannot be differentiated."
Hortensia similis (Walker, 1851)	Cicadellinae	Cuba	Novoa & Alayo (1986, p.80).
Hortensia similis (Walker, 1851)	Cicadellinae	Republic of Panama	Guerra V. (2002, p.38-39), unpublished thesis.
Homalodisca vitripennis Germar, 1821	Cicadellinae	French Polynesia	Grandgirard *et al.* (2006, p.435) (as *Homalodisca coagulata*).

we surmise that only 37 are original, and the rest are citation upon citation of those 37. Not included in the 174 are three false records that were based upon a misreading of Readio (1927).

We add 19 new records, all from Panama, representing 13 genera, and at least 13 species to the list of Cicadellidae known to have attacked humans (Table 2). These new records represent five subfamilies, two of which, Gyponinae and Xestocephalinae, have not been reported previously. Eleven are first records for their genera: *Dilobopterus, Tylozygus, Balclutha, Chlorotettix, Hecalapona, Planicephalus, Plesiommata, Portanus, Xestocephalus, Xyphon*, and *Zyginama*. Two attacks were to the back of the neck, but the other 17 were to the extremities, mostly the forearm, and in each case caused itching or mild stinging lasting several seconds to several minutes.

Fifteen of the attacks took place at night or at dusk, usually on people reading or watching television. One of the four daytime attacks was by an individual of *Dilobopterus stolli* that alighted on EDN's leg and probed repeatedly for some three minutes but did not pierce the skin. It was then captured in a vial and placed on the leg of EDN's wife (LV). The insect immediately pierced her skin, causing pain and itching. A second incident involved a lab researcher who was attacked upon reaching into a brightly lighted chamber containing his study subjects, *Hortensia similis* (Guerra, 2002). A third daytime attacker was a typhlocybine that alighted on EDN while he was waiting at a bus stop. The fourth daytime attack took place in a patio. A fifth daytime attack is not included in our data because the specific insect individual was not captured; it was to a person (LV) who was watering a garden, and thus disturbed a large number of *Dilobopterus stolli* on their plant, *Pseuderanthemum reticulatum* (Hooker *f.*) Radlkofer (Acanthaceae). Including our own contributions, we calculate that now there are 193 published records of Cicadellidae having bitten humans, of which 56 are the original observations, and that they represent 30 genera and at least 39 species in five subfamilies.

In addition to our experiences, Pierre Jolivet has been probed by various species near rice fields and the Awash River in Ethiopia; and by *Nephotettix*, probably *virescens*, during a typhoon in Hong-Kong (personal communication). As well, William Eberhard (in the Neotropics) has been probed occasionally by leafhoppers (personal communication). Neither of them captured their attackers.

Discussion

Several authors doubted that leafhoppers showed interest in humans until they experienced it themselves. Donovan (1920a, 1920b) commented "Several people used to complain to me of being stung by these insects, but, not being cognizant at the time of such habits among the Homoptera, I discountenanced these tales of the presumed aggressors. It was only when I was myself a victim of the insects' action that I was disillusioned." Lawson (1920) stated "The writer has had several people tell him about being bitten by little green leafhoppers, but not till a short time ago did he have any personal proof of the fact. One night, while collecting under a light, he felt a little prick on his hand, and on looking down saw a little green leafhopper [*Empoasca fabae*

Table 2. Cicadellidae that have probed human skin in the Republic of Panama

Name	Subfamily	Gender	Day/night	Date	Locality, victim, and part of body attacked	Deposition
Dilobopterus stolli Signoret, 1850	Cicadellinae	male	D	2011 Nov. 13	Panamá: San Isidro, El Valle, in patio: probed EDN's leg with no success, but probed Linette Vega's (LV) leg after being transferred there	MIUP
Hortensia similis (Walker, 1851)	Cicadellinae	female	N	2009 Dec. 23	Panamá: San Isidro, El Valle, in living room: probed LV's forearm	MIUP
Hortensia similis (Walker, 1851)	Cicadellinae	female	D	2001	Panamá: Universidad de Panamá, in Lab. de Estudios Biológicos de Plagas Agrícolas, in lab: "attacked" Ismael Guerra [Unpublished thesis]	MIUP
Tylozygus geometricus (Signoret, 1854)	Cicadellinae	female	N	2008 Oct. 23	Panamá: Arraiján, Loma del Río, 8.9407 -79.6568, in living room: probed AA's forearm	STRI
Xyphon reticulatum (Signoret 1854)	Cicadellinae	male	dusk	2012 Feb. 4	Panamá: Canal Area, near Canal Administration Building: probed LV's forearm	MIUP
Plesiommata sp.	Cicadellinae	male	dusk	2012 Nov. 15	Panamá: Chiriquí, David, Doleguita, 8th Street: probed Indira Simon's leg	STRI
Plesiommata sp.	Cicadellinae	female	N	2012 Nov. 29	Panamá: Arraiján, Puerta de Hierro: probed Jeraldín Vergara's left ring finger	MIUP
Balclutha sp.	Deltocephalinae	female	N	2009 Oct. 26	Panamá: San Isidro, El Valle, in living room: probed LV's forearm	MIUP
Chlorotettix minimus Baker, 1898	Deltocephalinae	male	N	2012 Mar. 14	Panamá: Arraiján, Loma del Río, 8.9407 -79.6568, under reading lamp: probed the back of AA's hand (02: 52 H)	STRI
Planicephalus flavicosta (Stål, 1862)	Deltocephalinae	male	N	2012 Mar. 5	Panamá: San Isidro, El Valle, in living room: probed LV's forearm	MIUP
Hecalapona brevisens DeLong and Freytag, 1975	Gyponinae	female	N	2008 Aug. 19	Panamá: Arraiján, Loma del Río, 8.9407 -79.6568, under reading lamp: probed AA's forearm	STRI
Solansaca stevensi (Ghauri, 1974a)	Typhlocybinae	male	D	2009 Feb. 25	Panamá: Santa Librada, Policlinica, at bus stop: probed EDN's forearm	MIUP

(*Continued*)

Table 2. (*Cont.*)

Solanasca stevensi (Ghauri, 1974a)	Typhlocybinae	dam-aged	N	2009 June 2	Panamá: San Isidro, El Valle, in living room: probed the back of EDN's neck	MIUP
Solanasca stevensi (Ghauri, 1974a)	Typhlocybinae	male	D	2012 May 3	Panamá: San Isidro, El Valle, in living room: probed the back of LV's hand	MIUP
Zyginama sp.	Typhlocybinae	female	N	2007 Aug.	Panamá: San Isidro, El Valle, in living room: probed LV's forearm	MIUP
Unidentifiable to genus, but none of the above.	Typhlocybinae	female	N	2009 Oct. 26	Coclé: Antón, El Valle, in hotel restaurante: probed LV's forearm	MIUP
Xestocephalus desertorum (Berg)	Xestocephalinae	female	N	2011 Feb. 4	Panamá: Arraiján, Loma del Río, 8.9407 -79.6568, while watching TV: probed AA's neck (22: 15 H)	STRI
Xestocephalus desertorum (Berg)	Xestocephalinae	male	N	2013 Jan. 7	Panamá: Arraiján, Loma del Río, 8.9407 -79.6568, while working at a computer: probed AA's left wrist (22: 14 H)	STRI
Portanus sp.	Xestocephalinae	female	N	2012 Aug. 25	Panamá: Villa de las Fuentes N°2, adyacente al Río Curundú, in bedroom: probed Carmen Galdames' forearm	MIUP

(Harris, 1841)] at work." Lawson later (1926) published his personal encounters with leafhoppers belonging to three additional species, and reported correspondence from Marshal Hertig, from Hsuchowfu, Kiangsu, China who wrote "Several times I thought I felt a pricking, but believing that Jassids wouldn't do such a thing, dismissed the idea as imagination. The apparent pricking whenever these insects rested on my arm, however, continued, and so I watched them with my hand lens. In practically every case, (half a dozen or so) after alighting, the proboscis appeared, they braced themselves for the thrust and the prick was felt."

The fact that leafhoppers do probe human skin is well-documented, however, though a number of writers speak of their cicadellid attackers as "blood suckers," there is no evidence that the purpose of the probing is to obtain blood, and only Tucker (1911) gives proof that blood actually was obtained—when he crushed a leafhopper that bit him, he produced a bloody smear. In none of our own cases do we know whether the attackers actually obtained blood. Our first priority was to capture and identify the leafhoppers that probed us. To have waited to see whether they engorged would have risked losing the specimens. Perhaps the authors of previous reports made the same decision, or they simply assumed that the insects were seeking blood.

What induces these normally phytophagous insects to seek human fluids? Though no one has answered that question convincingly, we tend to agree with Myers (1929) and Schaefer (2000) who speculate that, in most cases, the insects found themselves in water-stressed situations and, in the absence of plants, sought moisture by probing human skin. Such tiny insects attracted to light and unable to escape from it and the heat it produces might be particularly prone to water-stress. Similarly, Chris Dietrich (personal communication) notes, "Most species spend much of their time feeding, so it's possible that when they probe human skin they are trying to determine whether they have landed on a suitable host plant."

Other explanations have been offered including the idea that a virus transmitted by these insects affects their behavior and disorientates them (McCrae, 1974); the possibly that the insects are stimulated by substances in solution, such as salt or urea—a speculation based on the observation that often they appear to be attracted to perspiration (Lindberg, 1927; Lewis, 1958; Schaefer, 2000); or simple thirst or hunger (Myers, 1929). Rakitov *et al.* (2005) reviewed the literature on leafhopper aggregations (males in most cases) on moist ground. Their analysis of the excreta produced at a site in Peru indicated "significant sodium retention." Mammalian blood contains many of the sugars, proteins, and salts also found in plants, but it is much richer in nitrogen compounds and the protein is rather different from that found in [cell sap] (Usinger, 1934). Whether cicadellids are able to utilize the protein component of mammalian blood is not known, however, Usinger (1934), using mammalian blood serum, carried out experiments on a herbivorous heteropteran, *Leptocoris trivittatus* (Say) (Rhopalidae), and learned that at least that plant feeder could survive on it to some degree.

Whatever the explanation for biting behavior in cicadellids, it is common and widespread in the group, and one can imagine the phenomenon as an indicator of the potential for dietary diversification within the Homoptera. Though no adventitious biter has been shown to transmit any disease (Schaefer, 2000), the detection of

Filovirus-like particles in a leafhopper (Lundsgaard, 1997) further expands the possibilities, as does the intriguing finding that a recently evolved bacterial symbiont harbored by a leafhopper, *Euscelidius variegatus* (Cicadellidae), is closely related to a bacterial symbiont found in bedbugs (*Cimex lectularius*), insects whose sole source of nourishment is mammalian blood (Hypsa and Aksoy, 1997; Degnan *et al*, 2011).

Comments on the literature

The published records of leafhoppers piercing human skin began a century ago with Tucker (1911), who reported having been bitten by *Empoasca fabae* (as *E. mali*) in Dallas, Texas, in July of 1909. Two additional cases involving the same species of leafhopper occurred elsewhere in the United States: one in Arkansas (Becker, 1918), the other in Kansas (Lawson, 1920).

From then on the literature on biting leafhoppers becomes confusing at times, perhaps thanks to the enthusiasm generated by the novelty of the subject. Authors cited each other frequently, often quite informally as letters read into the minutes (proceedings) of society meetings, and they sent specimens back and forth from one museum to another. As a result, in a number of cases several authors published independently, based on the same specimen and biting event. In some cases the leafhoppers were identified only to genus and later described elsewhere, or incorrectly identified and later corrected by someone else, or the source of the record is not given. We have followed the threads of these records to try and determine which are original and which are citations and, assuming that those identifcations were correct, to update the nomenclature. An unsolved mystery involves Alfred William Alcock (1859-1933), a British naturalist who worked in India and was Superintendent of the Indian Museum. Though principally a fish specialist he had a broad interest in all things natural. He is cited by Brumpt (1922, 1927, and 1936; and again in 1949, misspelled as Alcok) as the source of a record of *Nephotettix virescens* (Distant, 1908) (as *N. bipunctatus*) biting humans in Calcutta, but not in the earlier Brumpt editions (1910, 1913). However, the Alcock publications that we have seen (1900, 1903, 1911, 1920) do not mention biting leafhoppers. In fact, in the insect pests section of the 1900 and 1903 "Indian Museum Notes," for which he was the editor, leafhoppers are not mentioned at all, and in "Entomology for Medical Officers" (1911, 1920) he states that Homoptera are "of no particular interest to the medical officer." It seems most likely that Brumpt was referring to a letter or other communication received directly from Alcock between the years 1920 and 1922.

Bergevin (1925a, pp. 40) was a communication hub for observations and specimens: *e.g.*, citing personal correspondence from Marshall, he reported that M.E. China found two specimens of *Exitianus indicus* (Distant, 1908) (as *Athysanus indicus*) in the British Museum that were collected in Madras, India, by Donovan in November 1919 and annotated as "bloodsuckers." Unknown to Bergevin, Donovan (1920a, 1920b) already had published his account of the blood-sucking behavior. In another instance, Bergevin (1925a, pp. 39-40), reported that specimens of *Eucelis curticeps* Lindberg, 1927 (as *Athysanus* sp.), collected by H.B. Johnston in Khartoum, Sudan on 17 Oct

1924, were sent to him by Marshall, and that he passed them on to Lindberg for description.

Myers (1929) contains a numerical error that caused us confusion when analyzing the list of biting leafhoppers he attributes to various authors. In the second paragraph of his text, he credits eight to Bequaert (1926), instead of three. Another confusion appears to have originated due to a reorganization of his list of published biting incidents. He uses *l.c.* three times: the first time immediately after a citation of Crosby (1926), who never published on the species indicated, and the second and third times after citations of Lawson (1926). At first we thought the three *l.c.* referred to the three records by Bequaert (1926), who is quoted extensively in the previous section of the paper, but the taxa turned out not to match. Without a doubt the three are citations of Lawson (1926), a conclusion supported by the fact that Lawson is the only other source for the record from Kiangsu, China.

On 16 October 1929, at a meeting of the Entomological Society of London, E. B. Poulton read a letter from E. A. Andrews and a note by W.E. China describing their encounters with biting cicadellids. That information was published on 31 December of the same year in the proceedings of the society as "Jassidae as blood-sucking insects." However, because Myers (1929) already had published news of the W. E. China incident, shortly before the meeting took place, he is listed as the original source in our Table 1, and Mr. China is listed as having cited his own record.

In Ryckman and Bentley (1979, pp. 36), the entry for Readio (1927) is confusing for lack of a clear break after quoting him, and initially that misled us to believe that Readio reported *Empoasca fabae* (as *E. mali*) as biting. In fact Readio wrote only of Heteroptera and did not report biting by any cicadellid. Apparently Alexander (1984) was equally misled and did not consult Readio (1927) directly; he incorrectly credits him for a report of biting by *Empoasca fabae* (as *E. mali)*.

McCrae (1974) was in error when he stated, "I can find no records of leafhoppers biting or attempting to bite man in Britain, and Dr. W. J. LeQuesne who I have consulted also knows of no such instances." In truth, separate accounts of the experience of W.E. China, in Surrey were published in 1929 by China and by Myers. The claim by Guerra (2002) that his laboratory study subjects, *Hortensia similis*, attacked him in defense of their eggs has little credibility.

As shown in Table 1, we have attempted to sort out the confusing network of reports of leafhoppers probing human skin. We would welcome additions and corrections to those efforts.

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