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Spittlebug nymphs (Homoptera: Cercopidae) in *Heliconia* flowers (Zingiberales: Heliconiaceae): Preadaptation and evolution of the first aquatic Homoptera

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Abstract: Spittlebug nymphs (Homoptera: Cercopidae) have a ventral abdominal breathing tube that evolved as an adaptation to life in semi-liquid spittle masses. Although they are clearly "preadapted" (exapted) to an aquatic existence, only one aquatic spittlebug has been reported and that report has been challenged. Here I present evidence that nymphs of the Costa Rican spittlebugs *Mahanarva insignita* (Fowler) and *M. costaricensis* (Distant) are facultatively aquatic on *Heliconia* (Zingiberales: Heliconiaceae). Some live submerged in the water-filled flower bracts of *Heliconia wagneriana, H. latispatha, H. tortuosa* or *H. bihai*, while some live in drier microhabitats on the leaves, stems or inflorescences of these and other *Heliconia* species. They represent the first well-documented aquatic Homoptera and may be the first well-documented plant-sucking aquatic insects of any kind. By combining positive xylem pressure and easily accessible xylem tissue removed from ordinary terrestrial and aquatic predators, water-filled *Heliconia* flowers may offer an especially attractive microhabitat for these xylem-feeding insects. *M. costaricensis* occurs in three morphological varieties: *costaricensis, quatuordecimnotata* and *semimaculata*, originally described as distinct species.

Key words: Spittlebug, Cercopidae, *Heliconia*, aquatic, xylem-feeding, preadaptation, exaptation.

Natural selection often seizes on "preadaptations" (exaptations) to fashion new ways of life from bits and pieces of an organism's preexisting repertoire of morphological, behavioural and biochemical characteristics (Gould and Vrba, 1982). It would be curious, then, if spittlebug nymphs, seemingly so well equipped for life underwater (see below), had not taken up an aquatic existence. Here I present evidence that two species have done so, in a peculiar microhabitat, in a limited part of Central America. This evolutionary novelty represents the first well-documented instance of aquatic species in the order Homoptera.

Spittlebugs are xylem-sucking insects of the superfamily Cercopoidea (Homoptera). Most spittlebug nymphs live in semi-liquid spittle masses created by adding bubbles and a mucopolysaccharide to excreted xylem fluid. Spittle masses protect nymphs from desiccation and some natural enemies (refs. in Thompson 1994). The nymphs breathe and form bubbles in the spittle fluid by means of a ventral air tube formed by overlapping abdominal plates (Kershaw 1914). The tip of this extensible tube periodically pokes through the surface of the spittle mass and conveys air to abdominal spiracles, permitting spittlebug nymphs to breathe in a manner analogous to mosquito and syrphid fly larvae (Ward 1991, Williams & Feltmate 1992). Adult spittlebugs do not form spittle masses and do not have breathing tubes.

In 1977 Durland Fish found a single spittlebug nymph living submerged in a water-filled *Heliconia bihai* (L.) L. flower bract at the Las Cruces Biological Station near San Vito, Puntarenas Province, Costa Rica. *Heliconia* (Zingiberales: Heliconiaceae) are common neotropical herbaceous monocots (Daniels & Stiles 1979, Stiles 1979, Berry & Kress 1991). They have large, red, orange or yellow, hummingbird pollinated inflorescences composed of multiple flower bracts (Fig. 1a,b,c). In many species these cup-like bracts are erect and hold water (Fig. 1a,c,d). This protects submerged flowers and fruits from herbivores (Wootton & Sun 1990) and attracts aquatic arthropods, primarily fly and beetle larvae (Seifert 1982).

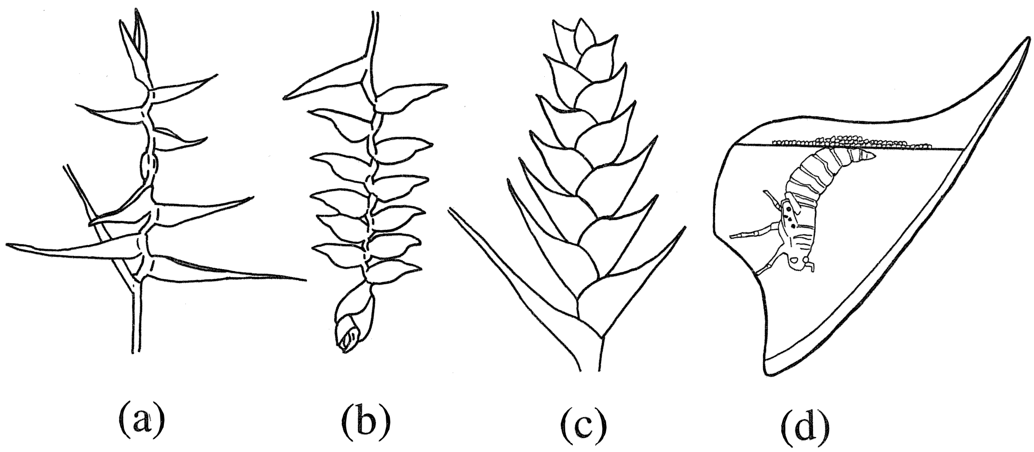

Fig. 1. Characteristic *Heliconia* inflorescences. Each inflorescence consists of a series of flower bracts (red, orange or yellow) linked by a rachis (flower stem). Each bract encloses a series of flowers, which emerge sequentially over several weeks. a. an erect inflorescence with relatively narrow, shallow bracts, characteristic of *H. latispatha* and *H. tortuosa*. b. a pendant inflorescence, characteristic of *H. pogonantha*. c. an erect inflorescence with wider, deeper bracts, characteristic of *H. bihai* and *H. wagneriana*. d. schematic cross section of a water-filled *H. wagneriana* flower bract with a submerged fifth instar *Mahanarva costaricensis* nymph. For purposes of illustration, the nymph is drawn somewhat larger than life size relative to the flower bract, and the flowers and fruits that normally share the bract are omitted. Note the spittle skim on the water surface. Figures a. and b. are drawn after Berry & Kress (1991, Fig. 3).

Fish transferred his spittlebug nymph to a pan of shallow water, where it remained submerged for several days, breathing at the surface through its abdominal tube. He did not observe adults and could not identify the species, but he hypothesized that the nymph was aquatic (Fish 1977).

Kosztarab (1979) visited Las Cruces to follow up on Fish's novel observation. He identified the spittlebug in question as *Tomaspis insignita* Fowler (Homoptera: Cercopidae), reclassified as *Mahanarva insignita* (Fowler) by Fennah (1979), and studied nymphs and adults living in association with *Heliconia tortuosa* Griggs (= *H. villosa* Klotzsch) (Daniels & Stiles 1979). *H. tortuosa* flower bracts are erect but relatively narrow and shallow (Fig. 1a). They hold considerably less water than *H. bihai* bracts (Fig. 1d) and often lack standing water, particularly in older bracts filled with flowers and developing fruits. When Kosztarab transferred nymphs from "nearly dry" *H. tortuosa* bracts to water-filled *H. bihai* bracts they avoided the water, or, when forcibly submerged, moved to the water-air interface, or, overnight, to other parts of the plant. He concluded that *M. insignita* nymphs are not aquatic.

I have reexamined these contradictory conclusions. Below I present evidence that nymphs of two Costa Rican spittlebug species are, in fact, aquatic. But, their aquatic behaviour is facultative, not obligatory. In addition, I present information on their classification and suggest a plausible physiological basis for their occurrence on *Heliconia*.

MATERIALS AND METHODS

Field investigations of spittlebug life habits in relation to *Heliconia* hosts were conducted at four sites: 1) the Organization for Tropical Studies (OTS) Las Cruces Biological Station and Wilson Garden near San Vito, Coto Brus, Puntarenas Province, elevation 1100 m (9-14 June 1993, 28 August-2 December 1994, 22-24 July 1995, 24 June-9 July 1996); 2) the Las Alturas Biological Station northwest of San Vito, Coto Brus, Puntarenas Province, elevation 1300 m (5 December 1994, 4 July 1996); 3) the OTS La Selva Biological Station, Heredia Province, elevation 50 m (9-12 March 1992, 2-7 June 1993, 17-19 September 1994); 4) Monteverde, Puntarenas Province, elevation 1500 m (16-20 June 1993). In addition, casual observations were made at Monteverde 11-13 May 1987.

Mahanarva identifications are based on Distant (1879, 1900), Fowler (1897-1898), Fennah (1979), and direct comparisons with type material in the entomological collections of the British Museum (Natural History). *Mahanarva* specimens in the entomological collections of the Museo de Insectos of the Universidad de Costa Rica and the Instituto Nacional de Biodiversidad (INBio) of Costa Rica were also examined. Genitalia of representative male specimens were dissected and compared. Voucher specimens of the varieties denoted below have been deposited with INBio and the Museo de Insectos. *Heliconia* identifications are based on Daniels & Stiles (1979). *Heliconia* species names follow Berry & Kress (1991).

RESULTS

Heliconia spittlebug taxa in Costa Rica: At least two spittlebug species, both of the genus *Mahanarva* (Distant 1909, Fennah 1979), live on *Heliconia* plants in Costa Rica (Fig. 2). *M. insignita* (Fowler) (Fig. 2a), the spittlebug studied by Fish (1977) and Kosztarab (1979), occurs near the Costa Rica-Panama border.

Three other Costa Rican heliconia spittlebug taxa appear to belong to a single polytypic species. Two forms occur at Monteverde. The majority form (Fig. 2b), wich has been collected recently only around Monteverde, corresponds to *Mahanarva semimaculata* (Fowler 1897-1898). The other Monteverde form (Fig. 2c), which has been collected widely elsewhere in the northwestern mountain ranges of Costa Rica but accounts for less than five percent of the Monteverde specimens, corresponds to *Mahanarva costaricensis* (Distant 1879). Because the Monteverde forms occur together on the same host plants (*H. tortuosa*), have been observed to mate on two occasions and have indistinguishable male genitalia, I propose that they represent color varieties of a single species, *M. costaricensis* (Distant).*M. costaricensis* also occurs in a smaller, more pubescent morphological form (Fig. 2d), originally described as *Tomaspis quatuordecimnotata* (Fowler 1897-1898, p. 177). This form has been collected from lower elevations in the Atlantic regions of Costa Rica and adjacent parts of Panama and Nicaragua. No definitive male genitalic characteristics separate this form from the two forms at Monteverde and their morphological characteristics seem to intergrade. I propose that all three forms (Fig. 2b,c,d) represent morphological varieties of one species. Fowler (1897-1898, p. 206) and Distant (1900) reached a similar conclusion but did not designate varieties. Based on direct visual comparison to type specimens in the British Museum (Natural History) I designate the smaller, more pubescent 14-spotted form as *M. costaricensis* var. *quatuordecimnotata* (Fig. 2d), the larger, less pubescent 14-spotted form as *M. costaricensis* var. *costaricensis* (Fig. 2c) and the

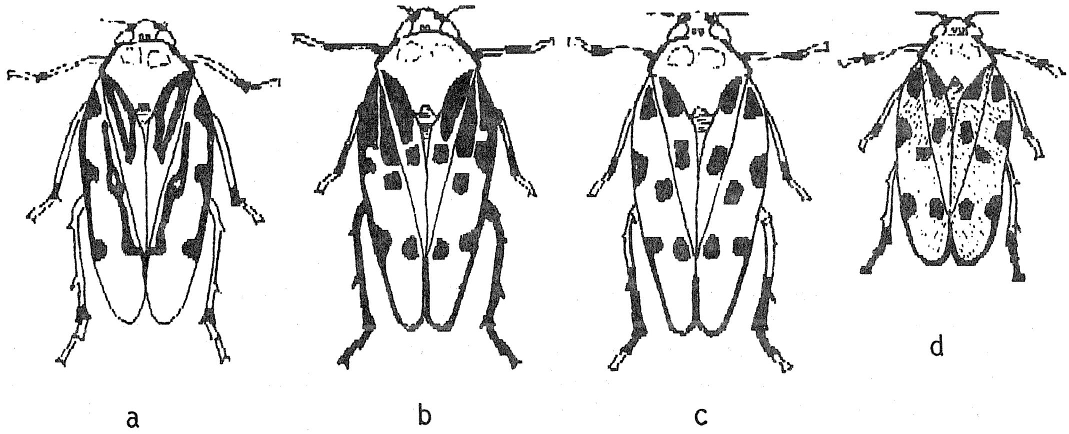

Fig. 2. Spittlebugs of the genus *Mahanarva* living in association with *Heliconia* in Costa Rica. The ground colour of each form is black. The markings are orange. The length of specimens ranges from 15 to 20 mm. a. *M. insignita*, the species found at Las Cruces. b. *M. costaricensis* var. *semimaculata*, the characteristic form at Monteverde. c. *M. costaricensis* var. *costaricensis*, the minority form at Monteverde. d. *M. costaricensis* var. *quatuordecimnotata*, the form at La Selva (note the pubescent forewings).

Monteverde majority form as *M. costaricensis* var. *semimaculata* (Fig. 2b).

Heliconia spittlebug nymphs are facultatively aquatic: I found *M. costaricensis* or *M. insignita* nymphs living submerged in water-filled *Heliconia* flower bracts at all four study sites (Table 1). They typically covered the water surface with a skim of spittle and occurred at densities as high as a dozen mixed instars per bract, though one to three nymphs per occupied bract was more common. Early instar nymphs were limited to the air-water interface by their small size, but many larger nymphs were completely submerged, with only the tip of the ventral air tube breaking the surface (Fig. 1d). Occasionally, submerged nymphs of both species reacted to my shadow by withdrawing completely into the recesses of water-filled bracts. Nymphs rarely occupied dry parts of inflorescences when water was present inside bracts.

On the other hand, neither species was obligately aquatic. At La Selva, *M. costaricensis* var. *quatuordecimnotata* nymphs sometimes occurred on *Heliconia* stems, leaves and drier flower bracts, as well as in the pendant, water-free inflorescences of *H. pogonantha* (Fig. 1b, Table 1). At Las Cruces and Las Alturas some *M. insignita* nymphs occurred on leaves or "dry" inflorescences of *H. tortuosa*. In November and December, when *H. tortuosa* was not in bloom, they occurred only on leaves.

To test the affinity of nymphs for submergence, I transferred three *M. insignita* nymphs from relatively dry *H. tortuosa* bracts to water-filled *H. bihai* bracts. All three spontaneously immersed themselves, took up an aquatic existence and began to make spittle, two within a few minutes, one by the next day. Likewise, four of seven *M. costaricensis* var. *quatuordecimnotata* nymphs transferred from water-free *H. pogonantha* bracts to water-filled *H. wagneriana* bracts immersed themselves within a few minutes, the rest by the next day. In each case I used rooted, intact *Heliconia* plants. Kosztarab's (1979) apparently contradictory results may be attributable to his use of cut inflorescences. Spittlebug nymphs of other species often avoid or abandon cut or wilting plants, probably because they find xylem fluid difficult to extract or nutritionally unrewarding as the xylem stream diminishes or dilutes. Like Fish (1977), I found that nymphs can remain suspended without apparent harm in water-filled laboratory dishes for at least 48 hours.

TABLE 1

Heliconia *hosts and associated spittlebugs by species, locality, life stage and season.* H. tortuosa *was the only* Heliconia *species observed at Monteverde and Las Alturas. At Las Cruces and La Selva other* Heliconia *species were in bloom during the study but spittlebugs were observed only on the species listed. Spittlebugs have been collected year round at each study site (present work and museum labels), suggesting that heliconia spittlebugs find suitable local hosts in every season (likely but not necessarily* Heliconia, *see text). At La Selva and Las Cruces, adults reard from representative nymphs confirmed the taxonomic identity of nymphs. Months in which nymphs of a given spittlebug-*Heliconia *association were living submerged in water-filled flower bracts are represented in* **bold** *type. Numbers represent months (3=March, 4=April, etc.).*

Spittlebug and (locality)	*Heliconia* host	Nymphs	Adults
M. costaricensis	*H. irrasa*	9	None
var. *quatuordecimnotata*	*H. latispatha*	6, **9**	6, 9
(La Selva)	*H. mathiasiae*	9	6[a]
	H. pogonantha	3, 6, 9	3, 6, 9
	H. wagneriana	**3**	3
M. costaricensis	*H. tortuosa*	**5**, 6, 7[c]	5, 6, 7[c], 9[c]
var. *semimaculata*[b]			
(Monteverde)			
M. insignita	*H. bihai*	**3**[d], **6**	None
(Las Cruces)	*H. latispatha*	6[a]	9[a]
	H. tortuosa	3d, **6-9**, 10, 11	3d, 6-11
(Las Alturas)	*H. tortuosa*	**7**, 12	7

[a] N=1-2.
[b] A few of the adults on *H. tortuosa* at Monteverde were *M. costaricensis* var. *costaricensis*. Monteverde nymphs were not determined to variety.
[c] D. Peck (pers. comm.).
[d] Fish (1977) or Kosztarab (1979).

Heliconia spittlebugs are not confined to *Heliconia*: Kosztarab (1979) observed three *M. insignita* nymphs on banana (*Musa sapientum* L.) at Las Cruces. R. Garrigues (personal communication) has observed *M. costaricensis* var. *quatuordecimnotata* nymphs and adults on *Calathea zebrina* at Selva Verde near La Selva. I observed a single adult *M. costaricensis* var. *semimaculata* feeding on a *Calathea* species at Monteverde. *M. costaricensis* var. *quatuordecimnotata* adults have been collected on sugar cane (Vargas Picado 1970), but they are not common (F. Badilla, personal communication). By comparison, I have observed hundreds of nymphs and dozens of adult heliconia spittlebugs on *Heliconia* plants, which were clearly the main hosts at each site during this study.

Heliconia spittlebug distribution is patchy: *Heliconia* grow in clumps of one to several hundred stems (Stiles 1979, Seifert 1982). At the sites studied, spittlebugs were absent from a majority of suitable looking clumps. For example, at Las Cruces in 1993 only five of sixty-nine suitable *H. tortuosa* clumps along the Sendero Rio had spittle or *M. insignita* adults present (clumps averaged three healthy inflorescences, with a maximum of twelve). In the Wilson garden only seven of twenty *H. bihai* clumps had spittle present (none had adult spittlebugs). Relative scarcity and patchy distributions may explain the curious paucity of references to these conspicuous insects in the *Heliconia* insect literature (*cf.* Seifert 1982).

DISCUSSION

The heliconia spittlebugs *M. insignita* and *M. costaricensis* exhibit a unique adaptation, submerged xylem sap feeding in the water-filled bracts of *H. wagneriana*, *H. latispatha*, *H. tortuosa* and *H. bihai*. They represent the first well-documented aquatic Homoptera, supporting Fish's (1977) original proposal for *M. insignita*. The commonly held view that there are no truly aquatic Homoptera (*cf.* Gaevskaya 1969, Polhemus 1984, Ward 1991, Williams & Feltmate 1992) will have to be modified. On the other hand, the heliconia spittlebug nymphs described above are not obligately aquatic. They can undergo complete nymphal development on *Heliconia* parts free of standing water, where, like ordinary spittlebug nymphs, they inhabit a semiaquatic spittle microhabitat of their own creation. Their facultative aquatic behavior is not surprising. Developmental plasticity is characteristic of insects inhabiting small, transient aquatic habitats (Barton & Smith 1984).

Note that heliconia spittlebug nymphs differ fundamentally from previously described "semiaquatic" salt marsh leafhoppers, planthoppers, coccids and aphids (Polhemus 1984). While these insects survive periodic salt water inundation, there is no evidence that they can remain submerged indefinitely or develop for a substantial portion of a life cycle underwater.

In retrospect, it is not surprising that spittlebugs have evolved aquatic nymphs. They are clearly preadapted to do so, with ventral tubes eminently well suited to surface breathing in shallow aquatic environments (Fish 1977). *Aeneolamia flavilatera* (Urich) nymphs, for example, use their breathing tubes to survive temporary flooding (Pickles 1945) and spittlebugs of the Old World family Machaerotidae spend most of their nymphal existence head down in narrow dwelling tubes filled with excreted xylem fluid (Marshall & Marshall 1966). In heliconia spittlebugs a simple behavioral shift has transformed a tube evolved for breathing in semi-liquid spittle masses into a snorkel for breathing underwater. This is a classic example of exaptation. Natural selection has coopted a pre-existing morphological feature to serve a new use, leading to functional change in the context of structural continuity (Gould & Vrba 1982).

If the ventral breathing tube shared by all spittlebug nymphs is an exaptation for submerged living, why haven't aquatic spittlebugs evolved more often? I suggest that the main impediment is the need for suitable host plant substrates near the air-water interface. *Heliconia* plants, which wrap small, dependable aquatic habitats in well-vascularized terrestrial plant tissue, happen to fill an aquatic nymph's need for safe, accessible xylem resources uncommonly well. Submerged nymphs should escape terrestrial predators and parasites that cannot penetrate an aqueous environment, just as the plants' own submerged fruits and flowers escape corresponding herbivores (Wootton & Sun 1990). The nymphs will also escape predators limited to larger or more permanent aquatic habitats.

Heliconia probably offer a second major attraction to spittlebugs, energetically inexpensive xylem sap. Xylem feeders spend large amounts of energy pumping dilute sap against negative pressure (Raven 1983, Press & Whittaker 1993). In some spittlebugs this challenge has led to a predilection for nitrogen-fixing hosts, which apparently have more nutritious xylem sap (Thompson 1994). It is unlikely that *Heliconia* fix nitrogen. Their nitrogen content is relatively low (Seifert 1982). But, *Heliconia* sometimes exhibit positive xylem pressure. Stems can spurt water when cut (Berry & Kress 1991, p. 316) and at least two species (*H. wagneriana* and *H. imbricata*) actively transport water into fluid-filled bracts, maintaining water levels regardless of rainfall or other external factors (Seifert 1982, Bronstein 1986, Wootton & Sun 1990). *Heliconia* may offer spittlebugs xylem sap that is energetically inexpensive to extract, an advantage that should apply to both nymphs and adults on various plant parts, particularly water-filled flowers.

The apparent scarcity of suitable aquatic host plant substrates is not peculiar to xylem-feeding bugs. Almost all known aquatic Heteroptera are predaceous (Gaevskaya 1969). Phloem-feeding Heteroptera and Homoptera are conspicuously absent in submerged aquatic habitats, which seem to discourage the direct utilization of living angiosperms as an insect food source (Ward 1991, Newman 1991). Williams and Feltmate (1992) omit sap-sucking as a recognized nutritional mode among aquatic insects. *M. insignita* and *M. costaricensis* nymphs may be the only well-documented, truly aquatic sap-sucking insects in the world insect fauna.

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RESUMEN

Las ninfas de cercópidos (Homoptera: Cercopidae) tienen un tubo respiratorio ventral que evolucionó como una adaptación para vivir en espumas semi-líquidas. Aunque es claro que ellas están preadaptadas (exaptadas) a una existencia acuática, solamente un cercópido acuático ha sido identificado y este relato ha sido disputado. Aquí, presento pruebas de que las ninfas de los cercópidos costarricenses *Mahanarva insignita* (Fowler) y *M. costaricensis* (Distant) son facultativamente acuáticas en *Heliconia* (Zingiberales: Heliconiaceae). Algunas viven sumergidas en agua en las brácteas de flores de *Heliconia wagneriana, H. latispatha, H. tortuosa* o *H. bihai,* mientras otras viven en los microhábitats más secos sobre los hojas, los tallos o las floresecencias de éstas y otras especies de *Heliconia.* Estos cercópidos representan los primeros homópteros acuáticos bien documentados, y tal vez representan el primer caso bien documentado de insectos acuáticos que chupan la savia de plantas. Es posible que la combinación de la presión positivo del xilema y el tejido de xilema muy accessible y lejano a los depredadores terrestres y acuáticos ordinarios explique porque las flores de *Heliconia* presentan un microhábitat especialmente atractivo para estos insectos que chupan la savia del xilema. *M. costaricensis* tiene tres variedades morfológicas: *costaricensis, quatuordecimnotata* y *semimaculata,* descritas originalmente como tres especies distintas.

REFERENCES

Barton, D. R. & S. M. Smith. 1984. Insects of extremely small and extremely large aquatic habitats, p. 456-483. *In* V.H. Resh & D.M. Rosenberg (eds.). The Ecology of Aquatic Insects. Praeger Scientific, New York.

Berry, F. & W. J. Kress. 1991. Heliconia: An Identification Guide. Smithsonian Institution, Washington, D.C. 334 p.

Bronstein, J. L. 1986. The origin of bract liquid in a neotropical *Heliconia* species. Biotropica 18: 111-114.

Daniels, G. S. & F. G. Stiles. 1979. The *Heliconia* taxa of Costa Rica, keys and descriptions. Brenesia 15, Supl.: 1-150.

Distant, W. L. 1879. Descriptions of some new species of *Hemiptera-Homoptera* from Central America. Entomol. Mon. Mag. 16: 61-63.

Distant, W. L. 1900. Contributions to a knowledge of the Rhynchota. II. Rhynchota of Central America. Trans. Entomol. Soc. London 1900: 687-697.

Distant, W. L. 1909. Rhynchotal notes.--XLVI. Ann. Mag. Nat. Hist. Series 8 3: 187-213.

Fennah, R. G. 1979. Revisionary notes on the New World genera of cercopid froghoppers Homoptera: Cercopoidea). II. Bull. Entomol. Res. 69: 267-273.

Fish, D. 1977. An aquatic spittle bug (Homoptera: Cercopidae) from a *Heliconia* flower bract in southern Costa Rica. Entomol. News 88: 10-12.

Fowler, W. W. 1897-1898. Biologia Centrali-Americana. Insecta: Rhynchota: Hemiptera-Homoptera. Vol. 2, p. 174-206.

Gaevskaya, N. S. 1969. The Role of Higher Aquatic Plants in the Nutrition of the Animals of Fresh-water Basins. National Lending Library for Science and Technology, Boston Spa, Yorkshire, England. 231 p.

Gould, S. J. & E. S. Vrba. 1982. Exaptation a missing term in the science of form. Paleobiology 8: 4-15.

Kershaw, J. C. 1914. The alimentary canal of a cercopid. Psyche 21: 65-72.

Kosztarab, M. 1979. Observations on the spittlebug, *Tomaspis insignita* Fowler (Homoptera: Cercopidae). Florida Entomol. 62: 396-401.

Marshall, A. T. & P. M. Marshall. 1966. The life history of a tube-dwelling cercopoid: *Machaerota coronata* Maa (Homoptera: Machaerotidae). Proc. Royal Entomol. Soc. London (A) 41: 17-20.

Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. J. N. Am. Benthol. Soc. 10: 89-114.

Pickles, A. 1945. Observations on *Tomaspis flavilatera* Urich, an insect pest of sugar cane in British Guiana. Proc. 1945 Meeting British West Indies Sugar Technologists, p. 46-52.

Polhemus, J. T. 1984. Aquatic and semiaquatic Hemiptera, p. 231-260. *In* R.W. Merritt & K.W. Cummins (eds.). An Introduction to the Aquatic Insects of North America, Second Edition. Kendall/Hunt Publishing Co. Dubuque, Iowa.

Press, M. C. & J. B. Whittaker. 1993. Exploitation of the xylem stream by parasitic organisms. Phil. Trans. Roy. Soc. London Series B 341: 101-111.

Raven, J. A. 1983. Phytophages of xylem and phloem: a comparison of animal and plant feeders. Adv. Ecol. Res. 13: 135-234.

Seifert, R. P. 1982. Neotropical *Heliconia* insect communities. Q. Rev. Biol. 57: 1-27.

Stiles, F. G. 1979. Notes on the natural history of *Heliconia* (Musaceae) in Costa Rica. Brenesia 15, Supl.: 151-180.

Thompson, V. 1994. Spittlebug indicators of nitrogen-fixing plants. Ecol. Entomol. 19: 391-398.

Vargas Picado, O. 1970. Estudio sobre la baba de culebra, *Prosapia distanti* (Homoptera: Cercopidae) y un esayo sobre su combate en el pasto Kikuyo *P. clandestinium* Hochst.). Tesis presentada a la Facultad de Agronomía como requisito parcial para optar al grado de Ingeniero Agrónomo. Universidad de Costa Rica, San José.

Ward, J. V. 1991. Aquatic Insect Ecology. 1. Biology and Habitat. J. Wile, New York. 438 p.

Williams, D. D. & B. W. Feltmate. 1992. Aquatic Insects. C.A.B. International, Wallingford, Great Britain. 358 p.

Wootton, J. T. & I.-F. Sun. 1990. Bract liquid as a herbivore defense mechanism for *Heliconia wagneriana* inflorescences. Biotropica 22: 155-159.