



## A remarkable new species of spittlebug and a second living New World genus in the Clastopteridae (Hemiptera: Cercopoidea)

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### Abstract

A new species of Neotropical spittlebug (Hemiptera: Cercopoidea: Clastopteridae), *Paraclastoptera erwini* **sp. n.**, is described and illustrated from Orellana, Ecuador. This species exhibits unique features differentiating it from all known *Clastoptera* and serves as the genotype for a new genus *Paraclastoptera* **gen. n.** This is the second extant New World genus for the Clastopteridae, hitherto represented solely by the widespread, abundant and speciose genus *Clastoptera*.

**Key words:** Auchenorrhyncha, taxonomy, morphology, *Clastoptera*, *Iba*, *Prisciba*

### Introduction

The Cercopoidea (Hemiptera: Auchenorrhyncha: Cicadomorpha) includes approximately 2,500 described species classified into approximately 340 genera in five families: Cercopidae, Aphrophoridae, Clastopteridae, Machaerotidae, and Epipygidae (Soulie-Perkins 2020). Commonly called spittlebugs or froghoppers, these insects feed on fluid contained in plant xylem vessels and many species exhibit a preference for nitrogen-fixing plants (Thompson 1994). Spittlebugs are characterized by the nymphal habit of covering themselves with a frothy saliva-like mass composed of small air bubbles incorporated in processed xylem fluid discharged from the alimentary system and supplemented by mucopolysaccharides and proteins produced by the specialized Malpighian tubules of the immatures (Rakitov 2002). Many adults in the Cercopidae exhibit striking warning coloration (Paladini *et al.* 2018) and several species are serious pests of sugarcane and pasture grasses (Holmann & Peck 2002; Thompson 2004). Spittlebugs of the Aphrophoridae have been identified as vectors or potential vectors of the bacterium *Xylella fastidiosa*, an emerging xylem-borne pathogen associated with several important plant diseases (EFSA *et al.* 2019). Both of these large families include several hundred species classified in dozens of genera distributed worldwide, with the exception of Antarctica (Soulie-Perkins 2020).

By contrast, the family Clastopteridae, *sensu stricto* (Metcalf & Wade 1962), is unique among the Cercopoidea for its paucity of genus level diversity. Only two extant genera have been described: the New World genus *Clastoptera*, which ranges from Canada to Argentina (Metcalf & Wade 1962; Soulie-Perkins 2020); and *Iba*, which is restricted to the Philippine islands of Luzon and Mindanao and the island of Borneo (Hamilton 2015).

*Iba* exhibits modest diversity, with three described species (Hamilton 2015) and at least five more undescribed species (VT observations). Aside from collection locales, nothing is known of *Iba* life history or ecology. In comparison to *Iba*, *Clastoptera* is notably speciose, with approximately 85 described species (Metcalf & Wade 1962; Soulie-Perkins 2020) and many more undescribed species. The only well studied fauna is that of America north of Mexico, covered in Doering's thorough 1928 monograph and supplemented since by a handful of new species

descriptions and redescriptions (Hamilton 1977, 1978, 2015; Nguyen *et al.* 2001). A disproportionately large number of all described *Clastoptera* species occur in the United States of America (USA) and Canada, about one third of the total (Metcalf & Wade, 1962). In both countries they constitute a large proportion of the spittlebug fauna, 12 out of 32 native species in Canada (Hamilton 1982) and approximately half of the 60 or so native spittlebug species in the USA. Large numbers of undescribed Neotropical species in museum collections suggest that hundreds more *Clastoptera* species await description (VT & AP observations). The relatively well-collected Costa Rican fauna, for example, includes about a dozen described species and at least 40 additional undescribed morphospecies (VT & Carolina Godoy observations).

The *Clastoptera* are generally easy to recognize. All *Clastoptera* species are small ( $\leq 5.3$  mm) and almost all are globose, broad in relation to length. They are comparatively uniform in morphology and, to a large degree, in coloration. Most are black, brown or gray, sometimes with dorsal markings in white or yellow (or rarely, and mostly subtly, red or pink). As a result, this group is easy to identify to genus, but notoriously difficult to identify to species (Doering 1928). Museum collections typically have the correct generic identification, but few or no species identifications, and, as noted above, south of the USA border with Mexico most species are undescribed. Male genitalia, useful for species level identification in the Cercopidae and Aphrophoridae (see Carvalho & Webb 2005 and Hamilton 2013 for examples), are comparatively simple and relatively uniform in the *Clastoptera* species that have been studied (Doering 1928; Hamilton 2015). On the other hand, differences in internal female genitalia (detailed features of the second valvulae) are useful in separating species (Doering 1928, Hamilton 2015).

While *Iba* is known only from museum specimens, several *Clastoptera* species have been studied in nature or in agricultural contexts. Natural history studies include Garman (1923) on *C. obtusa* (Say), Wheeler (1984) and Kuenzi & Coppel (1985) on *C. arborina* Ball, and Thompson (2011) on *C. distincta* Doering. A few species have been associated with economic damage, including *C. undulata* Uhler on *Casuarina* plantings (Dustan 1960, Bennett & Hughes 1963), *C. achatina* Germar on pecan (Teddars 1995), *C. laenata* Fowler, *C. globosa* Fowler and *C. ochropila* Jacobi on cacao (Lozano 1980; Mendes & Garcia 1985; López *et al.* 2013), and an undetermined *Clastoptera* sp. on grape in Brazil (Azevedo *et al.* 2009). Recently, a new species of *Clastoptera* in Florida has achieved nuisance levels on oaks (Thompson *et al.* In press). Two species, *Clastoptera brunnea* Ball and *C. achatina*, are experimentally demonstrated vectors of the disease-causing bacterium *Xylella fastidiosa* (Severin 1950; Sanderlin & Melanson 2010) and others are suspected in *Xylella* transmission in coffee (Garita-Cambronero *et al.* 2008). One species, *C. xanthocephala* Germar, has been introduced into Hawaii (Nishida 2002).

*Clastoptera* species also have been studied for their associations with larvae of drosophilid flies of the genus *Cladochaeta*, which live in spittles in association with *Clastoptera* nymphs (Thompson & Mohd-Saleh, 1995; Grimaldi & Nguyen 1999; Sánchez-Monge & Segura-Wang 2006). In addition, many *Clastoptera* live on actinorhizal host plants (Thompson 1999), a distinctive subset of nitrogen-fixing plants. Overall, the genus *Clastoptera* is abundant and widespread in the New World, ecologically diverse, speciose but morphologically homogeneous, and geographically remote from its closest known relatives in the Philippines and Borneo.

In this paper, we report the discovery of an extraordinary new Neotropical clastopterid. This species, represented by nine individuals, was discovered in canopy fogging samples collected in 1979 and 1994–1999 by Terry Erwin and his collaborators at two rain forest sites in Ecuador and one in Brazil (see Lucky *et al.* 2002 and Erwin *et al.* 2005 for a description of methods and the Ecuadoran sites, and Holzinger *et al.* 2013 and Barringer *et al.* 2019 for analyses of other Auchenorrhyncha from the same locales). Described below, this new clastopterid has unique morphological features that distinguish it at the generic level from *Clastoptera* and *Iba*. Its discovery doubles the number of extant New World Clastopteridae genera from one to two and, using Clastopteridae *sensu stricto*, increases the world total from two to three.

## Materials and methods

Morphological terminology follows Doering (1928) and Hamilton (2015), including the use of the term ‘tegmina’ which refers to the forewings. All observed specimens are reported; label information for all specimens is listed, with line breaks within a label indicated by “/”. The holotype is deposited in the USNM. Paratypes are deposited in the USNM and AMNH, as indicated in “Material examined”. Collection abbreviations (Evenhuis 2019) are as follows, which also include abbreviations for collections surveyed for the presence of the new taxon described here:

- AMNH: American Museum of Natural History, New York, NY, USA  
BMNH: The Natural History Museum, London, UK  
CAS: California Academy of Sciences, San Francisco, CA, USA  
DZUP: Museu de Entomologia Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.  
EMEC: Essig Museum of Entomology, Berkeley, CA, USA  
FMNH: Field Museum, Chicago, IL, USA  
FSCA: Florida State Collection of Arthropods, Gainesville, FL, USA  
MCZC: Museum of Comparative Zoology, Cambridge, MA, USA  
MCTP: Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil.  
MZUSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.  
NCSU: North Carolina State University Insect Collection, Raleigh, NC, USA  
NYSM: New York State Museum, Albany, NY, USA  
UCDC: Bohart Museum of Entomology, Davis, CA, USA  
USNM: US National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Multiple digital photographs were taken of each specimen, at different focal lengths, using a Leica Z16 APO microscope with attached JVC KY-F75U digital camera. These ‘source’ images were electronically combined to yield a single, pan-focal image using the software package Auto-Montage Pro version 5.04.0013 (Synoptics Ltd., 2006). Exceptions: Figs. 5 and 6 were produced using a Leica MZ16 in conjunction with a Canon EOS Rebel T6 digital camera and processed as photomontage images using CombineZM software. Measurements were taken in millimeters (mm) using a calibrated ocular micrometer in a Leica MZ16 microscope. Genitalia were prepared with aqueous super saturated KOH solution. Line vector drawings were made over photographs taken under light microscopy and double-checked by comparison with specimens.

During this investigation the authors searched among undetermined Clastopteridae in several collections for additional specimens. Among thousands of specimens examined, only two more were found, both in the USNM, and both, like the original canopy samples, collected by Terry Erwin and his collaborators (these are included among the nine specimens treated here). This does not preclude the possibility that other specimens exist in unexamined collections or were overlooked in collections we did examine, but it does underline their rarity. Collections examined included: AMNH, BMNH, CAS, DZUP, EMEC, FMNH, FSCA, MCZC, MCTP, MZUSP, NCSU, NYSM, UCDC and USNM.

## Classification

### Clastopteridae

#### *Clastoptera* Germar

*Clastoptera* Germar, 1839. Type species: *Clastoptera achatina* Germar, by subsequent designation (Van Duzee 1917).

**Diagnosis:** Globose, small insects, variable in size and color markings. Head wider than long; vertex narrow; postclypeus without a median carina, inflated; antennae inserted in deep cavities between eyes and postclypeus; pronotum broader than long, transversely wrinkled; scutellum triangular, much longer than wide; tegmina deflected posteriorly, clavus with apex rounded, corium terminating in a hyaline membrane; male pygofer higher than wide with a prominent process just below anal tube, subgenital plates fused to posterior edge of pygofer; paramere (style) strongly hooked dorsally.

## *Paraclastoptera* gen. n.

Type species: *Paraclastoptera erwini* by original designation

**Diagnosis:** Globose, small insects. Head convex, moderately pilose, wider than long; vertex narrow; postclypeus hexagonal, inflated, without a median carina; pronotum hexagonal with rounded humeral angles and median carina well marked; male pygofer higher than wide with a bilobed process below the anal tube, subgenital plates fused at base and to posterior edge of pygofer; paramere (style) subrectangular with an elongate apex, aedeagus globose and curved.

**Description:** Head subrectangular, wider than long, convex, moderately pilose; eyes rounded; ocelli closer to each other than to eyes; tylus rectangular; vertex rectangular; antennae inserted in a deep pit on the middle of the eye, basal body of flagellum cylindrical; postclypeus hexagonal, inflated, without a median carina, rostrum not reaching mesocoxae, pronotum hexagonal with rounded humeral angles and a median carina well marked; scutellum triangular, with a pair of rounded carina on the anterior portion; tegmina rounded with an apical reticule of closed cells, basal portion of second anal vein with a pronounced elevation; tibia with two lateral spines, basal spine smaller, apical spines of tibia disposed in a single row. Male pygofer higher than wide; subgenital plates fused at base, paramere (style) subrectangular with an elongate apex; aedeagus stout with a globose apex, curved dorsally in lateral view. Female pygofer higher than wide; first valvulae of ovipositor long and slender tapering toward apex, basal process inconspicuous, rounded and turned backwards, second valvulae of ovipositor short and wide with dorsal margin undulate.

**Etymology:** The genus is named for its resemblance to *Clastoptera*, hitherto the only New World genus of the Clastopteridae.

## *Paraclastoptera erwini* sp. n.

(Figs 1–18)

**Type locality.** Ecuador, Orellana Province, 1 km south of Onkone Gare Camp, Reserva Etnica Waorani, 00°39'25.7"S, 076°27'10.8"W.

**Diagnosis.** Head creamy white with five black markings; postclypeus black, without a median carina; pronotum hexagonal, multicolored, with pronounced wrinkles, transverse on anterior, longitudinal on posterior; tegmina black, pilose, costal margin cream white, apical reticulate cells cream white; hind wing with closed preapical cell; pygofer short and stout; parameres (styles) subrectangular with a bifid elongated apex; aedeagus stout with a globose apex, curved dorsally.

**Description.** *Head* (Figs 1–4, 14–15), in dorsal view creamy white with five black markings: three on the anterior margin and one mark starting between the ocelli and forward to anterior margin of tylus, posterior margin with two black stripes located on the middle portion, elevated like a flap over anterior margin of pronotum; head moderately pilose with about 20 hairs between each ocellus and eye and a row of comb-like hairs located posterior to eye overlapping posterior margin of head continuing ventrally but not reaching the inner margin of eye; eyes greyish, rounded with a slight teardrop shape toward bottom; ocelli closer to each other than to eyes; tylus rectangular with anterior margin slightly curved, two thirds of central area black, lateral portions creamy white; vertex rectangular, creamy white, pilose; antennae brownish inserted on a deep pit with basal body of flagellum cylindrical and a long arista; postclypeus black with ventral portion and lateral ridges creamy white, hexagonal, without a median carina, dorsal margin straight, ventral margin concave in the middle portion, twelve lateral ridges on each side, anteclypeus black with cream spots on posterior margin, anterior margin cream white, pilose; rostrum with second article cream and third one black brown, not reaching the mesocoxae. *Thorax* (Figs 1–2, 4–5, 14–15): blackish; pronotum hexagonal, multicolored: a blackish band extending across the anterior margin with two small symmetrical extensions toward the median portion, one creamy white band extending across the pronotum in a shallow curve toward the humeral angles, posterior to this band are two triangular black areas to either side of median carina separated by a vertical white cream band in the middle, posterior region with a gold orangish luminescent canoe-shaped band about one fifth the length of pronotum, posterior margin creamy white, median carina strongly marked, anterior half slightly sinuous, becoming one of many longitudinal wrinkles in posterior half, pronotum covered in

pronounced wrinkles, disposed transversally in the anterior half, longitudinally in the posterior half, with some individual wrinkles forming a right angle, anterior margin markedly convex, lateral margins slightly concave toward posterior, posterior margin deeply concave in the middle raising like a flap toward the anterior margin of scutellum; scutellum black, triangular with a cream apex and two small cream spots at midpoint, pilose with a pair of rounded lateral carina on anterior portion delineating a rounded cavity covering about half the length of scutellum; tegmina black, pilose, costal margin cream white, apical reticulate cells cream white, four closed cells located above apical callus, veins R2 and R3 creamy white, basal portion of second anal vein with a pronounced elevation, adjacent to pronounced cavity; pro and metathoracic legs black brown, hind legs black brown with a cream lateral area at point of articulation with tibia, tibia with two lateral spines, basal spine smaller, both tipped with black, apical spines of tibia disposed on a single row. *Abdomen* plain black.

*Genitalia: Male:* Pygofer short and stout, higher than wide with a bilobate process between the anal tube and subgenital plates (Figs. 7–8); subgenital plates turned upward, fused at base, apex bilobate with round lobes (Figs. 7–8); parameres (styles) subrectangular with a bifid elongated apex, upper lobe with a small spine located approximately on the middle portion in external view, dorsal process curved and well developed with a subapical spine in external view (Figs. 9–11), aedeagus stout with a globose apex, curved dorsally in lateral view, apex slightly bilobate and gonopore oval, subapical; shaft covered by scale-like spines. (Figs. 12–13); *Female:* Morphologically similar to the male, pygofer higher than wide (Fig. 16); first valvulae of ovipositor (Fig. 17) long and slender tapering toward apex, basal process inconspicuous, rounded and turned backwards, second valvulae of ovipositor (Fig. 18) short and wide with dorsal margin undulate.

*Tegminal color variation:* The single male specimen from Brazil differs slightly from the Ecuadorian specimens in tegminal coloration. Markings by costal margin, near apex and straddling claval suture whiter and a bit more pronounced, with net effect of making the white tegminal markings more conspicuous.

**Measurements (mm) mean/sd/range, ♀ N=4, ♂ N=4 for forewing length and 5 for all other measurements.** Body length: ♂ 3.69/0.27/3.40–4.20, ♀ 3.75/0.31/3.30–4.15; head length: ♂ 0.28/0.02/0.25–0.3, ♀ 0.28/0.02/0.25–0.30; head width: ♂ 1.66/0.11/1.46–1.75, ♀ 1.75/0.13/1.60–1.95; pronotal length: ♂ 0.91/0.07/0.82–1.00, ♀ 1.04/0.04/0.98–1.10; pronotal width: ♂ 1.69/0.10/1.52–1.78, ♀ 1.83/0.10/1.73–1.95; scutellum length: ♂ 1.18/0.08/1.03–1.25, ♀ 1.20/0.07/1.1–1.30; scutellum width: ♂ 0.83/0.08/0.70–0.95, ♀ 0.86/0.03/0.83–0.90; forewing length: ♂ 3.02/0.14/2.84–3.20, ♀ 3.03/0.16/2.85–3.25; forewing width: ♂ 1.43/0.03/1.40–1.45, ♀ 1.6/0.09/1.50–1.75.

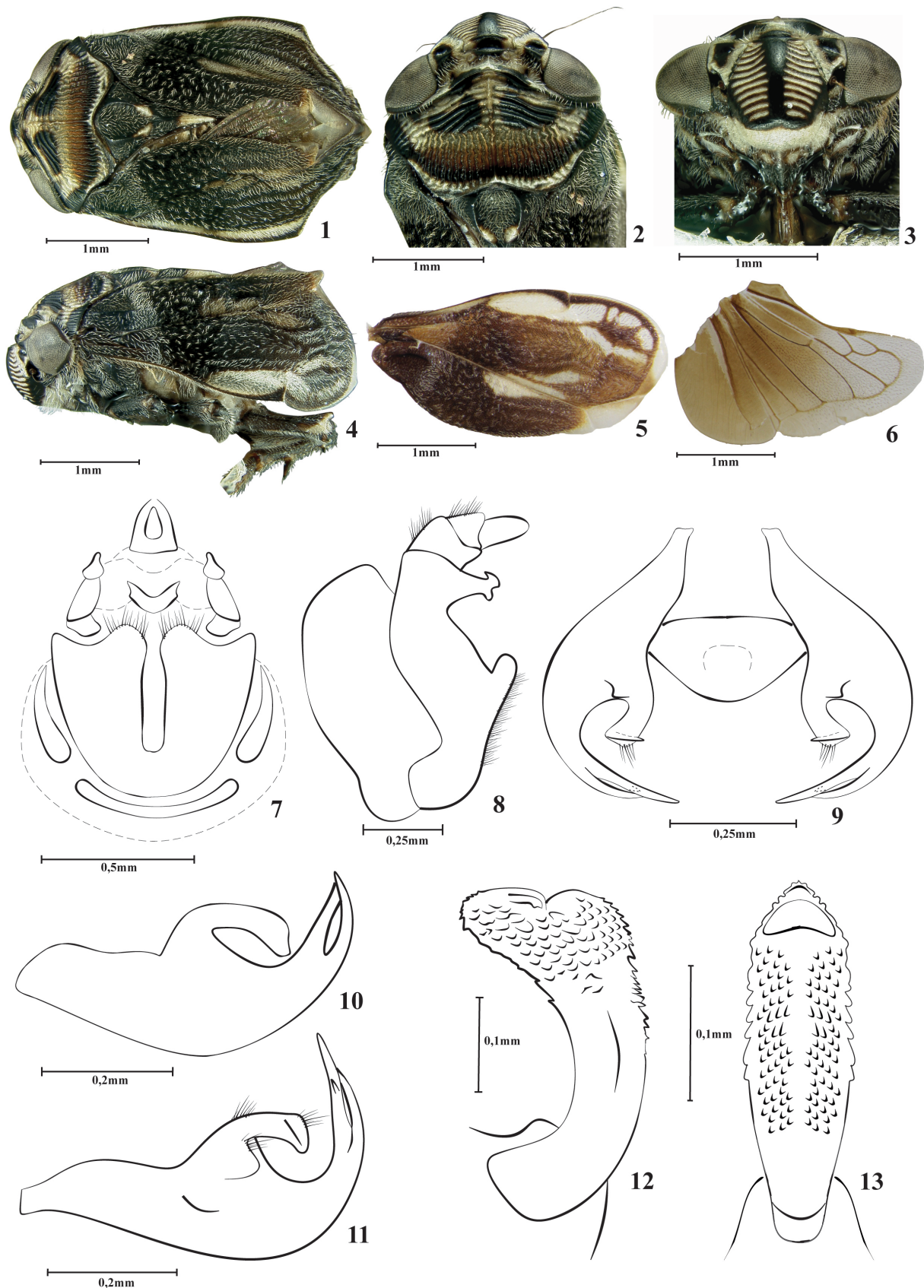
**Distribution.** Ecuador, Brazil (Fig. 19).

**Remarks.** The single specimen from Brazil was taken about 1,800 km east of the Ecuadorian specimens. It appears to differ only in tegminal markings. Dorsal coloration is variable in many *Clastoptera* species (see examples in Doering 1928, plates I–II; Hamilton 1982, pp. 83–84). Given the geographical distance, we cannot exclude the possibility that the Brazilian specimen represents a distinct species but, based on its otherwise indistinguishable morphology, we include it in *P. erwini*.

Diagnostic characters separating *P. erwini* from *Clastoptera* and *Iba* are its pronounced and uniquely configured pronotal wrinkles (Figs 1–2, 4, 14–15) and the closed preapical cell on the hind wing (Fig. 6). Most *Clastoptera* have wrinkles covering the pronotum, always transverse, sometimes fine and indistinct, sometimes more pronounced, and serving as an important character differentiating species (Doering 1928). In *Iba*, the wrinkles are inconspicuous and “obliquely striate” (Hamilton 2015, fig. 6B) or absent (VT observations on several species). The pronounced and partly longitudinal wrinkles of *P. erwini* immediately distinguish it from every known species of *Clastoptera* and *Iba*. The closed hind wing preapical cell also distinguishes it from these genera. Hindwing venation is invariant in *Clastoptera* (Doering 1928, p. 15) and includes an open preapical cell that is also characteristic of *Iba* (Hamilton 2015, figs. 3C and 4C). In addition, *P. erwini*’s scaly aedeagus (Figs. 12–13) is markedly distinct from the aedeagi of all 28 *Clastoptera* species illustrated in Doering (1928, plates XXV–XXVII).

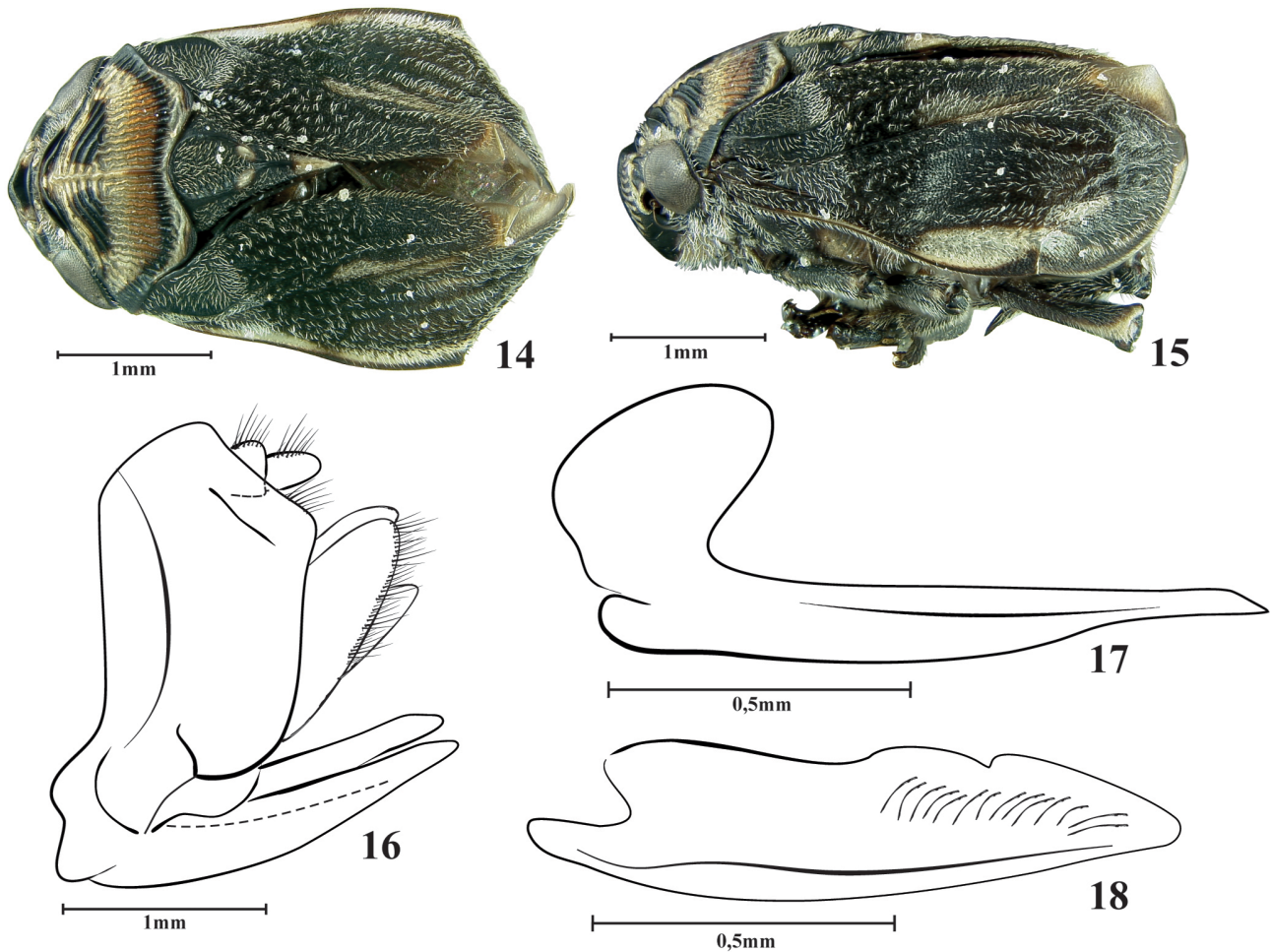
**Etymology.** The Latin species name “*erwini*” honors the late Terry Erwin, whose pathbreaking canopy work made this study possible.

**Material examined. Type material: Holotype** (♂, dissected, deposited at USNM), with labels: “1232, Ecuador, Orellana / Transect Ent. 1 km S. / Onkone Gare Camp / Reserva Etnica Waorani; 216.3m, 7-Oct-1995 / 00°39’25.7”S, 076°27’10.8”W / T.L. Erwin *et al.*, t-7....2 / Fogging terre firme forest”; and “HOLOTYPE / *Paraclastoptera erwini* / Paladini, Thompson, Bell, Cryan”; **Paratypes**, each including the additional label “PAPATYPE / *Paraclastoptera erwini* / Paladini, Thompson, Bell, Cryan”: (♂, deposited at AMNH) with same label information



**FIGURES 1–13.** *Paraclastoptera erwini* n. sp., male. 1. Habitus, dorsal view. 2. Head, dorsal view. 3. Head, ventral view. 4. Habitus, lateral view. 5. Tegmina, lateral view. 6. Hindwing, lateral view. 7. Pygofer, ventral view. 8. Pygofer, lateral view. 9. Parameres (styles), dorsal view. 10. Paramere, lateral internal view. 11. Paramere, lateral external view. 12. Aedeagus, lateral view. 13. Aedeagus, dorsal view.

as holotype, except: “6-Oct-94” and “t-10....5”; (♀, deposited at USNM) with same label information as holotype except: “22-Jun-96” and “t-5...3”; (2♀, 1 dissected and deposited at AMNH, 1 deposited at USNM) with labels: “2059, Ecuador, Orellana / Tiputini Biodiversity Sta. / nr Yasuni Nat. Park / Erwin Transect—T/6; 220–250m, 7-Feb-1999 / 00°37’55”S, 076°08’39”W / T.L. Erwin *et al.*, t-6....10 / Fogging terre firme forest”; (♂, deposited at USNM) with same label information, except: “t6....3”; (♀, deposited at USNM) with same label information except: “5-Feb-99” and “t9....1”; (♂, USNM), with label information: “ECUADOR: NAPO Res. Ethnica / Waoroni, 1km S. Onkone Gare / Camp, Trans.Ent. 20 Jan 1994 / 220m, 00° 38’S 076° 36’W / T.L. Erwin, et. Al; Insecticidal fogging of the mostly bare / green leaves, some with covering / of lichenous or bryophytic plants / Project MAXUS at x-trans 7,58 m / Lot 615”; **Other material:** (♂, USNM), with label information: “BRASIL: / Amazonas / Hwy BR174/ N of Manaus, km 20/ 19 August 1979/ Terra firme; CANOPY FOGGING PROJECT / TRS #101 Tray 736 / Adis, Erwin, Montgomery, / et. al. collectors; Terra firme forest / canopy fogged with / Pyrethrum”.



**FIGURES 14–18.** *Paraclastoptera erwini* n. sp., female. 14. Habitus, dorsal view. 15. Habitus, lateral view. 16. Pygofer, lateral view. 17. First valvula of ovipositor. 18. Second valvula of ovipositor.

## Discussion

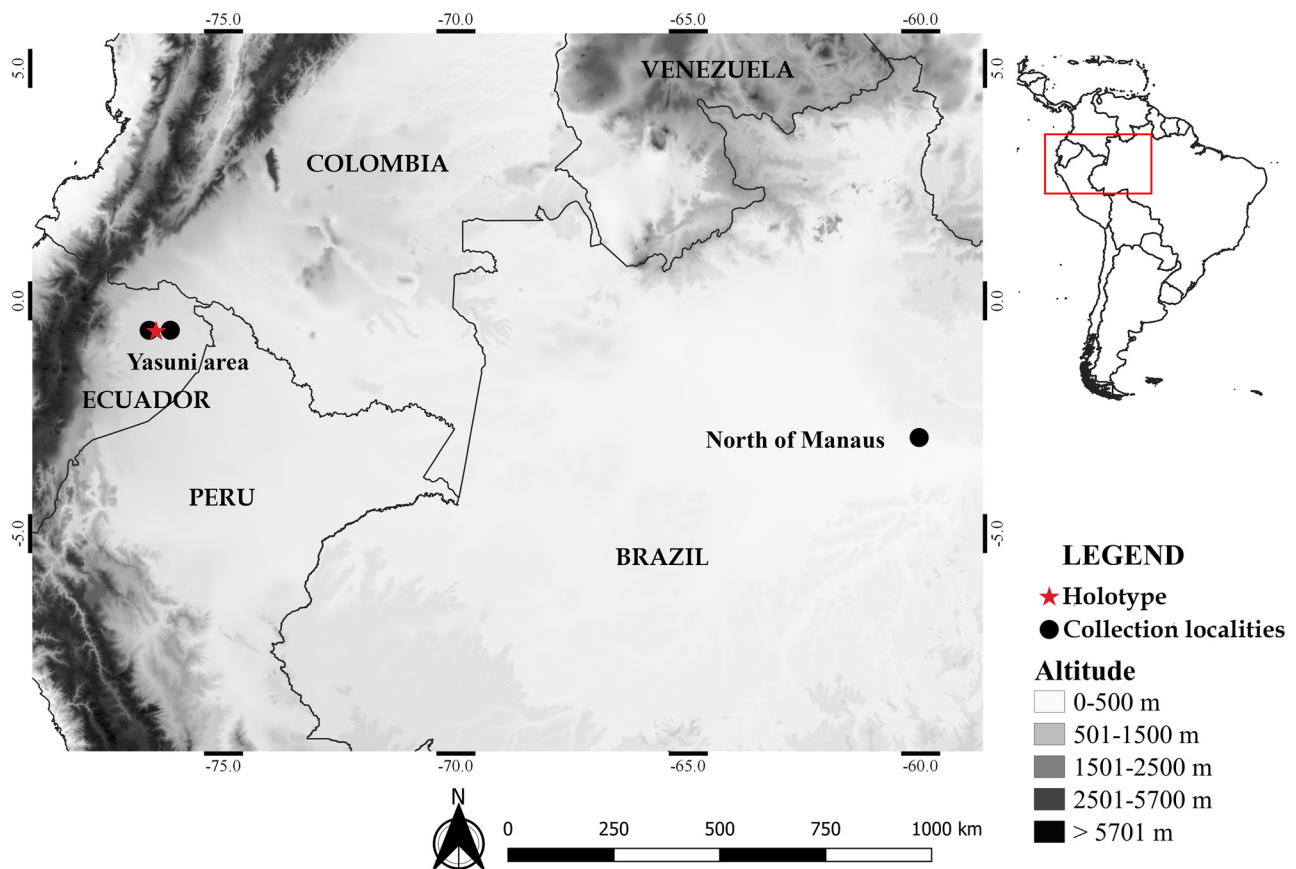
*Paraclastoptera erwini* is unique among the Clastopteridae for its striking longitudinal posterior pronotal wrinkles, coloration of the pronotum, distinctive hind wing venation and aedeagal form. It is also, except for the pronotum and parts of the head, robustly pilose, more so than any known clastopterid. On the other hand, similarity in size, form, and many details of morphology may place this genus in Hamilton’s proposed tribe Clastopterini (Hamilton 2015), along with *Clastoptera*, *Iba* and the fossil clastopterid genus *Prisciba* (see below). The proposal to include *Clastoptera* and *Iba* in a single tribe Clastopterini dates to Jacobi (1928).

In addition to the living genera, there are two well-documented fossil species of Clastopteridae, *Prisciba serrata* Poinar and Brown and *Prisciba dominicana* Poinar and Brown, each known from single specimens in 15–20

million-year-old Dominican amber (Poinar *et al.* 2013; age determination from Iturralde-Vinent & MacPhee 1996). There is also a single compression fossil described as *Clastoptera comstocki* Scudder from the Florissant Formation in Colorado, dating to about 34 million years (Scudder, 1890). Its morphology is consistent with inclusion in the Clastopteridae, but its poor state of preservation, at least as represented in the published illustration and description, precludes more detailed comparative analysis.

The three living genera are characterized by small size, globose form, and many of a series of characters that Hamilton (2015) uses to define the Clastopterini. They differ most conspicuously in the form of the grooves or wrinkles on the pronotum, transverse where they occur in *Clastoptera*, anteriorly transverse and posteriorly longitudinal in *Paraclastoptera*, inconspicuous or absent in *Iba*. Notably, *Paraclastoptera* differs from *Clastoptera* and *Iba* in the absence of an open preapical cell at the tip of the hind wings (compare Fig 6 with figs. 3C and 4C in Hamilton 2015). Details of morphology indicate that *Clastoptera* and *Iba* are closely related (Hamilton 2015); indeed, results of a molecular phylogenetic analysis (AB & JC, unpublished) of Cercopoidea grouped *Iba* and *Clastoptera* together as a monophyletic group with strong statistical support. Attempts to recover usable DNA from *P. erwini* failed, likely due to the age of the samples and preservation in relatively low concentration ethanol.

The geographical separation of *Iba* from *Clastoptera* and *Paraclastoptera* by 17,000 kilometers of ocean suggests that the latter two diverged in the New World after isolation from the line leading to *Iba*. In contrast, hind wing venation suggests that the lineages leading to *Iba* and *Clastoptera* diversified after their separation from the ancestors of *Paraclastoptera*. Clarification of the phylogenetic relationships of the three genera awaits detailed morphological comparisons and, ideally, recovery of usable genetic material from *Paraclastoptera*.



**FIGURE 19.** Distribution map. Known localities of *P. erwini* are indicated in black circles, with the holotype location starred in red. The localities in Ecuador and Brazil are about 1,800 km apart.

At a higher taxonomic level, Hamilton (2015) included Clastopterini within a redefined subfamily Clastopterinae, which also included the genera *Beesoniella*, *Grellaphia*, *Sepullia*, *Taphrotylus* and *Tremapterus* (i.e., the tribe Sepulliini). Hamilton grouped Clastopterinae together with the Machaerotidae (as Machaerotinae) in a redefined family Clastopteridae. That higher-level taxonomic rearrangement differed significantly from the results of DNA sequence-based, quantitative phylogenetic analyses (Cryan & Svenson 2010; Cryan & Urban 2012), in which



*Clastoptera* was a monophyletic lineage separate from a monophyletic Machaerotidae. When exemplars of *Iba* and Sepulliini were added to the analyses, *Iba* was placed as sister lineage to *Clastoptera* (thus recovering a monophyletic Clastopteridae *sensu stricto*) and Sepulliini grouped as a monophyletic sister lineage to Machaerotidae (AB & JC, unpublished).

The discovery of a new and wholly unsuspected clastopterid spittlebug in the canopy of the remote Amazon rain forest is a striking incidence of our incomplete understanding of the biodiversity of this vital habitat. The nine known *P. erwini* specimens come from the canopy at just three sites (Fig. 19). Two lie just 21 km apart in lowland forest at the margin of Ecuador's Yasuní National Park (Erwin *et al.* 2005), where Erwin estimates that there are 100,000 insect species per hectare, the highest unit area biodiversity in the world for any taxonomic group (cited in Bass *et al.* 2010). This unique and distinctive new spittlebug reinforces the importance of the Yasuní region as biodiversity hotspot.

The far removed third *P. erwini* site, in Brazil, about 1,800 km east of the Yasuní sites (Fig. 19), suggests that *P. erwini* might be distributed over a large area of Amazonia. All nine specimens were collected by insecticide fogging of canopy in terra firma (non-flooding) lowland forests. Nothing more is known of their ecology, but analysis of data on the tree species under which they were recovered may offer insight on their host relationships. The absence of other specimens in surveyed collections suggests either that *P. erwini* is intrinsically rare or that it occurs in infrequently sampled habitats.

Given its unique taxonomic position, more *P. erwini* specimens should be sought in Amazonia and adjacent regions. Recovery of additional specimens, suitable for DNA analysis, could greatly enhance understanding of the evolutionary history of this remarkable insect and related taxa.

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