A new family of froghoppers from the American tropics (Hemiptera: Cercopoidea: Epipygidae)

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ABSTRACT: Froghoppers (Cercopoidea) are divided into three families: spittlebugs or Cercopidae, which are efficient spittle-producers; Clastopteridae (including subfamily Machaerotinae, new status), inefficient spittle-producers and tube-dwellers; and the new-world tropical Epipygidae, a new family known only from small numbers of adult specimens. Epipygidae are probably single-brooded, with short-lived adults that appear to rely mainly on stored body fat as an energy source. Unlike the related spittlebugs they probably lay exposed eggs and have free-living nymphs. The new genera Epipyga (type-species Eicissus tenuifasciatus Jacobi) and Erugissa (type-species Erugissa pachitea sp.nov.) are described and Epipyga cribrata (Lethierry), a new combination from Aphrophora, plus Eicissus decipiens Fowler and twenty-seven undescribed species are included in the family.

Froghoppers, called superfamily Cercopoidea by scientists, are tiny insects that sometimes superficially resemble small toads (Figure 1). They belong to the “true bugs,” the Hemiptera. Froghoppers are jumping insects related to the leafhopper family called Cicadellidae, but have hind legs armed on the outside edge with stout, immobile spines (Figure 2) like those of planthoppers, the Fulgoroidea. The prominently swollen face that houses the sucking pump in Cercopoidea (Figures 2-4) immediately distinguishes them from the flat-faced Fulgoroidea.

Froghoppers include the insects known as “spittlebugs” because their juvenile forms (nymphs) have an unique biology, living an essentially aquatic existence submerged in frothy masses of plant sap (Figure 5). Some other froghopper nymphs live in sap-filled tubes (Figures 6-10). These tubes have been said to be “calcareous” with “not less than 75% calcium carbonate” (Ratte 1884) although modern studies show that they are mainly made of mucofibrils (Marshall 1965), which are thick, gelatinous compounds that dry to a rocklike hardness. Mucofibrils are produced by excretory ducts of the lower intestine called Malpighian tubules.

Froghoppers have been little studied. At present there are about 3000 species described, but only European, North American and New Zealand faunas have been studied sufficiently to recognize biological species. Taxonomic works have often relied upon mainly superficial appearance, with the result that scientists have described or illustrated only 10% of the species in sufficient detail for reliable recognition. Tropical species are particularly poorly known. In four Pacific island arcs, for example, 67 species out of a total of 127 species were found to be undescribed (Hamilton 1980a-b, 1981a-
b), representing more than 50% of the fauna. In Papua New Guinea at least 80% of the fauna at one site is undescribed (Novotny, personal communication). This suggests that thousands of species remain to be found. Some of these undescribed species, together with three little-known species that were described more than a century ago, represent a new family of froghoppers from Central and South America. This family has a unique biology and represents a basal lineage in the evolution of froghoppers. This study presents biological and evolutionary information on which this assessment is based, and formally names the new family as Epipygidae (“high tail family”).

Specimens of Epipygidae are rare in museum collections. The Canadian National Collection in Ottawa, with over 100 specimens, has the largest holdings. The remainder of the 182 specimens examined in this study are from eight other collections (see Acknowledgements); many other collections have no specimens at all. Nine species are known from only single individuals. This suggests that a much larger number of species will be found in future studies than the 31 species known so far.

**BIOLOGY OF EPIPYGIDAE**

*No spittle:* Although living Epipygidae have never been studied, much about them may be inferred from their structure and accumulated collection data. For example, although nymphs of Epipygidae are unknown, it is doubtful that they produce spittle. Spittle masses are easily found, and those reported from the new world tropics contained nymphs of all the other known major groups. Yet, even though they may not produce spittle, Epipygidae are certainly froghoppers because they have all the characteristic morphological features of the superfamily, such as a projecting flange (meron) on each of the middle leg bases.

**Collapsed sucking pump:** Other observations imply that Epipygidae have a highly distinctive life-cycle for a true bug. For example, the abdomen of the adult is typically filled with flocculent white masses of fat body, a situation unknown in other Hemiptera. Also peculiar to this family is their face (Figure 4) with laterally compressed, apparently collapsed, small facial plate called the frons, indicative of a small sucking pump, the cibarial chamber inside the frons. By contrast, spittlebugs have an enormous sucking pump (Figure 3) so they can feed copiously on the dilute fluids of major sap-carrying tubes in plants. From these facts it is deduced that adult Epipygidae, if they feed at all, do so only to replenish body fluids, their energy needs being supplied by fat reserves. A similar life style is found in silkworm moths, the family Saturniidae.

**Unknown food sources:** Canon Fowler (1897) implied knowledge of their biology when he named a genus as *Eicissus*, apparently meaning “on vines.” In fact, nobody really knows which plants these insects prefer. There is no evidence that Fowler, resident in England, knew anything about the lives of these insects. Perhaps he merely wanted to imply that they live in tropical areas.

**Scattered distribution:** Members of the Epipygidae occupy coastal rainforests or live in cloud forests up to 2,600 m above sea level. The known species are widely scattered among hills and mountains of South America and lowlands of Central America (Map 1). Closely related species may be widely disjunct (for
example, found on hills of coastal Brazil and also on the foothills of the Andes). Such distributions may be relict populations of once more extensive ranges. Alternatively, they may reflect only the incomplete knowledge of these insects.

**Seasonality:** Epipygidae are apparently absent from dry regions and areas with strong seasonality. Different species have been collected at different periods in the year in both summer and winter months, but few have been collected during the dry periods of late April until late June, and in October. Possibly full-grown nymphs complete their development to the adult stage in synchrony with local rainy periods, or possibly egg-laying occurs during seasonal growth of their hosts following such rainy periods. This implies either a long dormancy period as eggs, or a lengthy period of growth for nymphs, that would be adversely affected by severe periods of drought or cold. By contrast, most spittlebugs have nymphal growth periods ranging from one to three months (Hamilton 1982).

**Sporadic adults:** Most species of Epipygidae have only one brood per year, but possibly two in some species of *Eicissus*. From collection data it appears that adults are active for a maximum period of two months, but more frequently for a month or less. Seasonal differences at differing elevations may extend this period. By contrast, tropical spittlebugs can be found almost year-round. Spittlebug adult life can extend for 3-6 months, up to 10 months in the case of the overwintering *Philaronia canadensis* (Walley) (Hanna 1967; reported as *Philaenus abjectus*).

The only known collection of numerous Epipygid adults (27 males and 33 females of an undescribed species) was found by L. Masner on low vegetation along a road in Costa Rican coastal rainforest on 23 and 28 August 1986. Ten males and 14 females of another undescribed species came to a flight interception trap in Venezuela over a five-week period. There is nothing to indicate whether the latter species was collected over the entire period or just in a single night. The next longest series is 4 males and 2 females, of yet another undescribed species, taken on 17 June 1975 in Venezuela. Such data suggests that these insects occur only sporadically and are not long-lived as adults.

**Many eggs:** A single specimen of an undescribed species found in Costa Rica had 37 eggs in the abdomen. A specimen of another undescribed species in a different genus contained 32 eggs. These numbers are equal to, or in excess of, the *entire* lifetime egg production of most other spittlebugs studied to date, which usually range from fewer-than-10 to 35 eggs (Hamilton 1982). They are, indeed, high compared to egg numbers commonly found in the abdomens of related families, such as leafhoppers (typically fewer than 15). From this it may be inferred that juvenile mortality is high, or the egg-laying period is short, or both. High mortality might be associated simply with an extended nymphal growth period, but if the assumption about Epipygidae having little or no spittle is correct, mortality might be attributed to a lack of protective spittle. Nymphs of spittlebugs have low mortality due to the inability of most predators and parasites to find nymphs within a large spittle mass.

The eggs of Epipygidae are black, in contrast to the white eggs usual for related bugs. White eggs are inserted into crevices or slits in plant tissue where they are protected from desiccation and are not visible. If the eggs of Epipygidae are glued to an exposed surface they would need a thicker (and therefore darker) egg membrane that resists desiccation, and one that would not be so clearly visible against dark stems and foliage.
Froghoppers (Cercopoidea) are divided traditionally into the tube-dwelling Machaerotidae (“sword family,” named for the spine on the back of one genus) and the spittlebug family Cercopidae (“tumbling-bug family”). Sometimes spittlebugs are further divided to include two other families: Aphrophoridae (“froth-bearing family”) and Clastopteridae (“broken wing family”). Clastopteridae have peculiarly folded wing tips (Dohrn 1859) and Machaerotidae have tube-dwelling nymphs, so both these groups are distinctive or “apomorphic”. The same is not true of Aphrophoridae, which is based on superficial resemblance (Stål 1866). Revision of the Aphrophoridae was initiated in 1976 and has led to the present study. Analysis of many characters, such as the articulation of the front legs and the folding of the wings, show the Aphrophoridae to be a miscellaneous assembly of genera. Assigning these genera to “natural” groups (which scientists call “monophyletic”) splits off a number of taxa, some of which are here transferred to Clastopteridae and some to Epipygidae. A detailed phylogeny will be presented in a later paper, together with an analysis of numerous cases of character convergence. For now, it is sufficient to mention the salient characters of only a few groups that are important in defining basal evolutionary lineages of Cercopoidea.

Members of the superfamily Cercopoidea (froghoppers) are monophyletic because they have a protruding flange on the side of each middle coxal segment, which forms the leg base. Froghoppers in turn can be divided into three natural families: Cercopidae, Clastopteridae (including Machaerotinae new status), and Epipygidae. These have unique biological and morphological features (for technical terms used below, see Snodgrass 1935). Each is deduced to represent a monophyletic lineage based on the following synapomorphies or shared modifications or adaptations:

1. Members of the family Cercopidae (spittlebugs) have nymphs with valves on the abdomen to produce large bubbles in the “spittle” masses.
2. Members of the family Clastopteridae have deep antennal pits that hide the antennal bases. They apparently are inefficient foam producers, inhabiting small, sticky droplets composed of tiny bubbles, or (in the case of the Machaerotinae) enclosing the fluid in hardened tubes.
3. Members of the Epipygidae have numerous specializations; the most prominent one is their abundant fat body in the abdomen. They represent an early offshoot with free-living nymphs and non-feeding adults.

Key to families of Cercopoidea

1A. Eyes overlapping and concealing sides of pronotum, touching base of wings (Figure 12); nymphs probably free-living; eggs black. ........................................................... Epipygidae
1B. Eyes not reaching as far as wing bases (Figures 13-14); nymphs living in spittle mass or immersed in fluid enclosed in a tube; eggs white.

2A. Antennae set in circular pits that are deep (Figure 3), in dorsolateral aspect hiding basal two segments, or tightly embracing base of antennae (Figure 14); nymphs living in small spittle masses containing few bubbles, or in tubes. ........................................................... Clastopteridae
2B. Antennae set in shallow, open pits, or beneath prominent antennal ledges at margin of crown (Figure 1); nymphs living in large, frothy spittle masses .............. Cercopidae

REDEFINED FAMILY: CLASTOPTERIDAE

Clastopterinae and Machaerotinae have deep antennal pits that hide the antennal bases (similar to the antennal pits of the leafhopper tribe Xestocephalini). Also, females are more reliably identified than males (Doering 1928); this is unique in Hemiptera, being also characteristic of sawflies, the Hymenoptera-Symphyta. By contrast, true spittlebugs exhibit great structural differences in males but none at all (or very little) in females. The evidence is clear that all these taxa have shared modifications, called synapomorphies, and together form a monophyletic lineage. Since Clastopterinae and Machaerotinae are differentiated from each other only by a single hind wing vein they should be combined as subfamilies of a single family.

Figure 11. Facsimile of Stål (1858).
This redefined family should be called Clastopteridae Dohrn, 1859, which has precedence over “Machaerotida” Stål, 1866. Maa (1963: 6) incorrectly cites “Machaerotida Stål (1858: 233),” but does not give a reference to this publication. This citation must be incorrect. There is no reference to this name on p. 233, or elsewhere, in the only known publication by Stål with this page and date (Figure 11).

One group of genera has morphology intermediate between that of Clastopterinae and Machaerotiinae. This is an unnamed segregate from the Aphrophorinae, which includes the African genera Abbalomba Distant, Nyanja Distant, Patriziana Lallemand, Pseudomachaerota Melichar, Sepullia Stål, and Tremapterus Spinola, plus the tropical Asian Beesoniella Lallemand and Grellaphia Schmidt. The subfamilial placement of this transitional group is not easily analysed and will be elucidated in another paper.

Nymphs of the genus Clastoptera Germar construct small, viscous, spittle masses that drip readily. Such spittle masses, unlike those of Cercopidae, can be penetrated by parasitoid wasps (Lintner 1889, Bennett and Hughes 1963) and fly maggots (Grimaldi and Nguyen 1999) that are presumably ectoparasitic. It seems likely that Clastopteridae cannot produce the large, protective bubbles that, in Cercopidae, are formed by opening and closing flaps (“valves”) of the terminal segments of the abdomen. The first instars of Machaerotiinae also produce small bubbles in a watery fluid like that of Clastoptera (Lomer, pers. comm.) and thus may be descended from a Clastoptera-like ancestor. It seems likely that the tube is constructed to rectify the deficiencies of the primitive spittle masses of Clastoptera. As a consequence of inefficient spittle production, most Clastopteridae are small compared to Cercopidae.

Nymphs of an African froghopper Patriziana somalicus Lallemand (and, presumably, those of related genera listed above) construct fragile, white tubes of dried spittle in which the nymphs live (Lallemand 1930). This life style probably represents a link between the “spittle-producing” subfamily Clastopterinae and the “tube-dwelling” subfamily Machaerotiinae.

**DESCRIPTION OF EPIPYGIDAE NEW FAMILY**
(Figures 4, 12, 15-21)

*Head* not flattened, crown not declivous, face receding; head with crown scarcely produced, very broad, at least 4 X as wide as long; ocelli separated by less than 2 diameters from each other, remote from inner margins of eyes, slightly closer to tylus than to posterior margin of head; eyes nearly globose, set far from frons giving a “stalked” appearance; antennal ledges foliaceous; tylus small (Figure 12); crown as long as eye, sulcate and declivous; frons narrow and collapsed, laterally compressed, medially carinate, transversely ribbed, not wider than combined width of lora; clypellus distinctly broader at midlength than at base (Figure 4), tip not extending as far as apices of fore coxae; lora large, each as wide as base of clypellus, extending to base of antenna; genal processes evenly tapered towards clypellus; and rostrum extending to or beyond hind
coxae. Thorax with proepimeron tapered before narrow, erect trochantin; pleural suture short, T-shaped; pronotum declivous, often steeply so, laterally overlapped and with sides concealed by eyes, so eyes reach wing bases (Figure 12); scutellum much shorter than commissure of tegmina; and pronotum pitted. Tegmen curved, elytriform or crumpled-looking; usually punctate to rugulose, with many reticulations (Figures 12, 15-16) or highly sculptured (Figures 17-18), with embossed ridge in position of “nodal line” extending from center of costal cell across M-Cu fork to middle of commissure, interrupted at claval suture; wing tip usually broad, nearly as wide as wing at midlength, with at least 4 apical cells on posterior edge and usually many on costal edge (Figures 15-16); 3 discal cells, inner discal cell wider than others, widest near midlength, closed apically by crossvein connected to stem of Cu (Figure 15); central cell open basally; tegminal appendix small, without crossveins; apical cells long (Figure 15), or divided by crossveins (Figure 16), or short, bounded basally by aligned crossveins (Figures 17-18). Hind wing armed with 3 minute marginal hooks on costal margin; with 3-4 apical cells (Cu may be unbranched), of which 3rd cell (m) is much the largest on all sides; with second and fourth apical cells usually less than half as long as third apical cell (4th cell long in Erugissa gen. nov.); and with appendix large, of even width around tip of wing as in Clastopteridae. Fore femora slightly longer than hind femora, or of similar length; hind tibiae each 1.8-2.0 X as long as femur, armed with 1 lateral spine on apical quarter and a double apical pecten of 10 black-tipped spines; and hind tarsi slender, basitarsal pecten of 5 black-tipped spines, that of second tarsomere with 4 such spines. Abdomen with segment IX (pygofer) of both sexes dorsally emarginate; anal tube flaplike caudal projection; styles elongate, bladelike, clearly visible in caudal aspect.

**Remarks.** The elongate, bladelike styles are distinctive, but subdivision of the genus may be warranted when the fauna is better known.

**Key to genera of Epipygidae**

1A. Apical cells of tegmen about twice as long as wide, sometimes obscured by reticulations (Figures 15-16). .......... Epipyga gen. nov.

1B. Apical cells of tegmen distinct, short, not longer than wide, clearly defined (Figures 12, 17-18).

2A. Tegminal membrane entirely glossy, without pits (Figures 17-18). .......... Erugissa new genus

2B. Tegminal membrane pitted, at least on basal half (Figure 12). .......... Eicissus Fowler

**Eicissus Fowler.**

Type-species by monotypy: *Eicissus decipiens* Fowler, 1897.

**Description.** Head wider than pronotum. Pronotum steeply declivous, anterior half at 45-60° slope; scutellum raised, disc depressed. Tegmen widest at or beyond midlength; membrane distinctly pitted; apical cells distinct, short, not longer than wide (Figure 12). Hind wing with Cu branched. Abdomen with male pygofer twice as high as long, or higher (Figure 19A), upper half narrow, curved cephalad; subgenital plates very short or spatulate, fused on midline. Aedeagus long and tubular, unarmed (Figure 19B), or with a single flaplike caudal projection; styles elongate, bladelike, clearly visible in caudal aspect.

**Included species.** *Eicissus decipiens* Fowler and eight undescribed species, all from Central America.

**Remarks.** The elongate, bladelike styles are distinctive, but subdivision of the genus may be warranted when the fauna is better known.

**Epipyga new genus**

Type-species: *Eicissus tenuifasciatus* Jacobi, 1921.

**Description.** Head wider than pronotum, or narrower; scutellum flat to raised, with disc depressed. Pronotum shallowly to steeply declivous, anterior half at 25-45° slope. Tegmen strongly arched on basal half, to widest beyond midlength; membrane distinctly pitted; apical cells of tegmen distinct, about twice as long as wide; reticulations usually weak or absent except along costa (Figure 15). Hind wing with Cu usually unbranched. Aedeagus with retractor processes (Figures 20A-B); styles short and pointed or hooked ventrad, not clearly visible.

**Included species.** *Aphrophoracribrata* Lethierry, 1889. *Eicissus tenuifasciatus* Jacobi, 1921, and eighteen undescribed species. One unassociated female (in the Canadian National Collection) with slender wing tips and densely reticulate venation (Figure 16) may be an atypical member of this genus, or of an undescribed genus.

**Remarks.** The short, concealed styles are distinctive, but subdivision of the genus may be warranted when the fauna is better known.
**Erugissa** new genus

Type-species: *Erugissa pachitea* new species.

**Description.** **Head** wider than pronotum. **Pronotum** steeply declivous, anterior half at 45° slope; scutellum raised, disc depressed. **Tegmen** widest at or beyond midlength; venation strongly carinate; membrane glossy, without pits; apex broadly rounded; apical cells short, bounded basally by aligned crossveins (Figures 17-18). **Hind wing** with Cu branched and 4° cell elongate. Male unknown.

**Included species.** *Erugissa pachitea* and a single female with longer wings (Figure 18) that may represent a second species in this genus or possibly a wing-dimorphic form. Both are from Amazonian lowlands of Peru.

**Remarks.** Their tegmina are the most strongly sculptured in the family, with strongly raised veins contrasting with shiny, membranous cells between them. Males are unknown.

**Erugissa pachitea** new species

**Description.** **Length:** female 6.1 mm. Blackish brown; face strongly contrasting pale yellow. **Tegmen** 1.5 X as long as wide, with 5 apical and 3 anteapical cells; stem of Cu straight (Figure 17).

**Holotype female.** PERU: Pachitea, Garlepp c., 1912-3 (A. Jacobi); in Staatliches Museum für Tierkunde, Dresden, Germany.

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