



## Redefinition of the cicada tribe Hemidictyini Distant, 1905, status of the tribe Iruanini Boulard, 1993 rev. stat., and the establishment of Hovanini n. tribe and Sapantangini n. tribe (Hemiptera: Cicadidae)

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### ABSTRACT

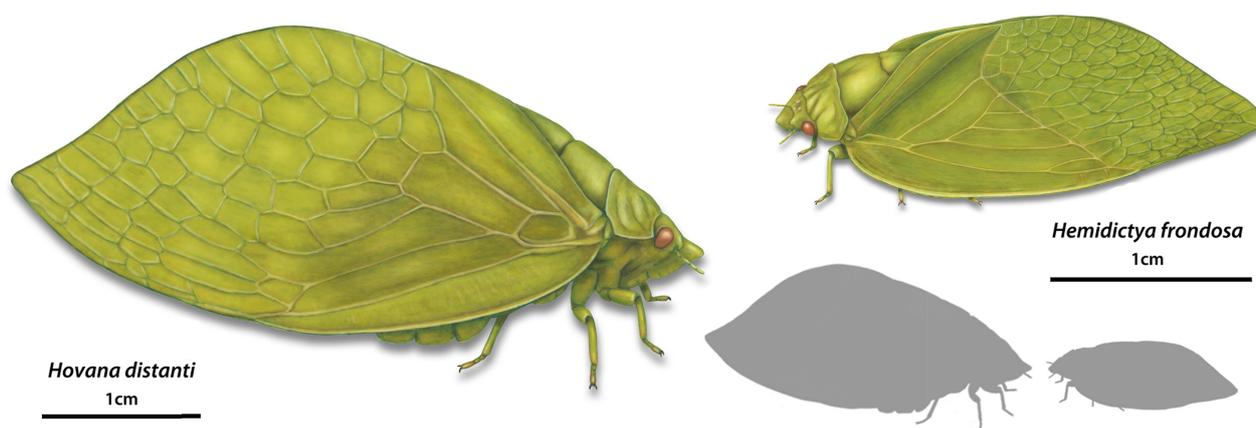
A recent paper by Ruschel & Campos (2019) on “leaf-winged” cicadas proposed a significant reorganization of the cicada tribe Hemidictyini Distant, 1905g, including synonymization of the monogeneric tribe Lacetasini Moulds & Marshall, 2018 following the results of a cladistic parsimony analysis of morphological characters. In this study, we reconsider and revise the morphological analysis of Ruschel & Campos and obtain new genetic data for *Hemidictya*. We find that their study suffers from a limited taxon sample, inappropriate outgroup selection, and misinterpretation of genitalic characters (uncus vs. claspers). We show that Hemidictyini *sensu* Ruschel & Campos includes members of multiple tribes and subfamilies, and we conclude that some of the taxonomic transfers by Ruschel & Campos are not supported. The two most similar and leaf-like cicadas, *Hemidictya* Burmeister, 1835 (South America) and *Hovana* Distant, 1905g (Madagascar), are probably not closely related but rather an excellent example of convergent evolution. Lacetasini is not a junior synonym of the Hemidictyini but a distinct part of the Tettigomyiinae Distant, 1905g as originally classified. We return or transfer the genera *Lacetas* Karsch, 1890, *Iruana* Distant, 1905g, *Bafutalna* Boulard, 1993, and *Murphyalna* Boulard, 2012 to the Lacetasini. With the transfer of all genera of Iruanina Boulard, 1993 and Bafutalnina Boulard, 1993 to Lacetasini and with *Lacetas* transferred to the Iruanina, Lacetasini **n. syn.** becomes a subjective junior synonym of Iruanini **rev. stat.** in the Tettigomyiinae. We assign *Hovana* to Hovanini **n. tribe** in the Tettigomyiinae and *Sapantanga* Distant, 1905g to Sapantangini **n. tribe** in the Tibicininae Distant, 1905b. We propose that Hemidictyini *sensu novo* contains only the genus *Hemidictya* and we assign the tribe to Tibicininae with a revised diagnosis.

### INTRODUCTION

Ruschel & Campos (2019) published a cladistic parsimony analysis of the phylogenetic relationships of 39 species in 23 genera of cicadas (Cicadidae Latreille, 1802), with an emphasis on “leaf-winged species” (taxa with “phyllomorphic” wings (Boulard 1985; 1997)) then placed in the tribes Chlorocystini Distant, 1905f, Hemidictyini Distant, 1905g, Lacetasini Moulds & Marshall, 2018, and Prasiini Matsumura, 1917 (Fig. 1). Their analysis used subsets of morphological characters applied by Boer (1995) in an analysis of the Chlorocystini and Moulds (2005) in a family-wide cladistic study, together with new characters described by Ruschel & Campos, including many traits characterizing leaf-winged phenotypes. Following their phylogenetic results, Ruschel & Campos (2019) revised and reorganized the cicada tribe Hemidictyini, which had previously included only *Hemidictya* Burmeister, 1835 and *Hovana* Distant, 1905g, to include *Sapantanga* Distant, 1905g and four African taxa, including synonymizing the recently erected tribe Lacetasini. They then tentatively moved Hemidictyini from subfamily Cicadettinae Buckton,

1890 to the subfamily Tettigomyiinae Distant, 1905g, which had recently been introduced by Marshall *et al.* (2018) to accommodate African genera in a molecular analysis of the Cicadoidea Latreille, 1802.

In this paper, we draw attention to problems with the Ruschel & Campos (2019) study, especially misidentified genitalic characters, inappropriate choice of outgroup taxa, and a small taxon sample limited to two of the four then-existing Cicadidae subfamilies. We present the results of revised cladistic analyses and new molecular and combined-data analyses based on preliminary genetic data. We show that while Ruschel & Campos have correctly identified a subfamily level relationship between *Sapantanga* and *Hemidictya*, as well as a relationship between *Lacetas* Karsch, 1890 and three African genera previously placed in Prasiini, other taxonomic conclusions of the study are not supported and contradict more comprehensive studies of both morphology (e.g., Moulds 2005) and genes (e.g., Marshall *et al.* 2018; Simon *et al.* 2019; this study).



**FIGURE 1.** Coloured drawings of specimens of *Hovana distanti* (Brancsik, 1893) and *Hemidictya frondosa* Burmeister, 1835, two examples of “leaf-winged” cicadas, with silhouette profiles for additional scale. Drawing by Virge Kask.

## METHODS

### *Material examined*

Ruschel & Campos (2019) provided detailed images and drawings that permit us, in many cases, to clarify the taxonomic positions of the various taxa they considered, based on the characters used previously to distinguish the higher taxonomy of cicadas, some of which were not applied in their analysis. In addition to the information and photographs provided by Ruschel & Campos, we personally examined and photographed the holotype of *Sapantanga nutans* (Walker, 1850) held at the Natural History Museum, London (NHM) and three male specimens of *Hemidictya frondosa* Burmeister, 1835 – one in the Moulds collection from Guanay, Bolivia, one in the Simon lab collection from Bolivia (collector Fred Skillman, 2014), and another at the (NHM) mislabeled as *Hovana distanti* (Brancsik, 1893) with no location data. The sole known specimen of *Sapantanga* is of uncertain origin. We also examined and photographed a specimen of *Hovana distanti* from the Muséum national d’Histoire naturelle (MNHN) (label data “Madagascar N. Ouest\Ambanja\Vallée de l’Ifasy\XII.65 Monsarrat”). Lastly, we obtained additional photographs of the pygofer and operculum of the type specimen of *Hovana distanti* from the Hungarian Natural History Museum, Budapest.

The pygofer of the *Hemidictya* male from the Moulds collection was removed after relaxation of the specimen to avoid damage during excision. The extracted pygofer was placed in 10% KOH at room temperature for six hours, washed, and transferred to 50% ethanol for a few minutes before placement in 75% ethanol for permanent storage. Some excess muscle tissue was removed prior to examination. The pygofer of the *Hovana distanti* specimen from the MNHN was removed and suspended in dilute solvent overnight before dissection. For this specimen, photography was performed using a Leica M205C stereomicroscope and the “Focus Stacking” process of the Photoshop CS6 software.

Terminology and abbreviations for morphological features used in this paper follow Moulds (2005).

### **Clarification of genitalic morphology of *Sapantanga* and *Hemidictya***

Additional morphological examination of *Hemidictya* and *Sapantanga* was necessary in order to confirm our suspicion, based on Figs. 14 (*Hemidictya*) and 22 (*Sapantanga*) in Ruschel & Campos (2019), that the genitalic structure scored as claspers for those taxa in that study is, instead, a posteriorly directed uncus. The uncus and claspers are carried by segment 10 and are important features in distinguishing tribe- and subfamily-level groups in Cicadidae. Their misidentification can mislead taxonomic assignments.

As currently defined (see Moulds 2005, p. 404), the uncus in cicadas is a single process originating adjacent to the median portion of the anal tube (for examples see Figs. 14, 15, 22, 23 in Moulds (2005); Fig. 10 in Marshall *et al.* (2018); Fig. 7 in Simon *et al.* (2019)). In some species the uncus is apically divided into two arms, the lateral processes, which sometimes deeply divide it, but these processes rarely completely divide the uncus and the lateral processes arise from a common base. The theca (main shaft of the aedeagus) always sits directly below the uncus (or below the stem when the uncus is divided) and, in the absence of claspers, the uncus supports the theca from above by a membrane or ventral protuberances, the theca not ordinarily passing upwards between the base of the lateral processes regardless of how large the lateral processes may be.

In contrast, claspers are paired structures, each derived as an independent structure with its base positioned laterally and arising below the uncus (if one is present) distally (for examples see Figs. 16, 17, 19, 20 in Moulds (2005); some in Figs 11, 12 in Marshall *et al.* (2018)). Claspers are considered as the anterior or basal lobes of segment 10 (Boulard 1990; Duffels and Turner 2002). Claspers never originate from a common stem. They restrain the theca by having it pass between them and usually encircle it. Claspers are sometimes weakly fused distally. Further consideration of these concepts appears in the Discussion.

### **Morphological cladistic analyses**

The taxon sample of Ruschel & Campos (2019) included 37 species then listed in Cicadettinae and two species (*Lacetas annulicornis* Karsch, 1890 and *L. longicollis* Schumacher, 1912) from Tettigomyiinae (see Marshall *et al.* 2018). Despite the presence of genera from two subfamilies in their dataset, Ruschel & Campos selected *Carineta* Amyot & Audinet-Serville, 1843, a cicadettine genus, to root their cladistic tree. As explained further in the Discussion, we suspect that this outgroup choice deleteriously affected their results. To test this hypothesis, we added the outgroup *Tibicina haematodes* (Scopoli, 1763), type species of the subfamily Tibicininae, to the Ruschel & Campos data matrix and constructed a cladistic parsimony tree in TNT v. 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016) under implied weighting, following as closely as possible the procedure given by Ruschel & Campos (2019). Selection of *T. haematodes* was supported by previous morphological (Moulds 2005) and genetic (Marshall *et al.* 2018) studies of the Cicadidae, which showed that the subfamily Tibicininae forms the sister-clade to all other Cicadidae subfamilies then described. Replication of the implied weighting analysis was facilitated by the TNT script *implied\_w.run* obtained online at <http://phylo.wikidot.com/tntwiki> (here deposited as Supplementary Material under the filename *implied.run*). To confirm that we replicated the Ruschel & Campos (2019) method, we first re-ran their dataset and found that we were able to recover exactly the topology (see Results) and character-state reconstructions (not shown) reported in their study.

As part of both analyses above (with and without *Tibicina haematodes*), we also tested versions of the dataset with the character states for uncus and claspers corrected following our results above. Characters 48-51 for *Hemidictya* and *Sapantanga* were changed to states 0, 0, inapplicable, and inapplicable, respectively.

### **Molecular phylogenetic analysis with *Hemidictya***

Sanger-sequenced nucleotide data for *Hemidictya* were collected for four of the genes that were used to estimate the Marshall *et al.* (2018) tree: COI, COII, EF-1 $\alpha$ , and 18S (see Acknowledgments). These sequences have been deposited in GenBank with accession numbers MN381962-4 and MN382134. We added the *Hemidictya* genes to the Marshall *et al.* (2018) dataset along with recent data for *Derotettix* Berg, 1882 (which forms a new subfamily Derotettiginae Moulds described in Simon *et al.* 2019). We analysed the new data set with maximum-likelihood following the methodology detailed in Marshall *et al.* (2018). Bootstrap replicates were run on the CIPRES Science Gateway server (Miller *et al.* 2010).

Following reviewer requests for a combined analysis of the genetic and morphological data, we assembled a

data matrix for the 11 taxa possessing both data types. This sample included two genera from Hemidictyini *sensu* Ruschel & Campos (*Hemidictya* and *Lacetas*). Two MrBayes v3.2.2 (Ronquist *et al.* 2012) analyses were run for  $5 \times 10^6$  generations with the morphological matrix handled as “standard” data, with the DNA data partitioned and modeled as in the maximum-likelihood analysis. Default priors were used (e.g., *ngammacat=4*, *ratepr=variable*, *brlens=unconstrained:exponential[10]*). Model parameters were estimated separately (unlinked) for each partition, for two independent, simultaneous runs (*nruns=2*) in each analysis. Stationarity was assessed by confirming values of the average standard deviation of split frequencies below 0.01. Effective sample sizes were checked using Tracer v1.5 (Rambaut and Drummond 2007), and 25% of the samples from each run were excluded as burnin. The samples from the two runs were combined to produce the MrBayes 50% majority-rule consensus phylogram.

## RESULTS

### *Clarification of genitalic morphology of Sapantanga and Hemidictya*

Fig. 2A is our posterolateral photo of the *Sapantanga* genitalia showing that the structure identified as paired claspers by Ruschel & Campos (2019) originates medially on the 10<sup>th</sup> segment, which identifies it as an uncus (a dorsal angle was not possible because of the position of the anal styles). Unexpectedly, a ventral photo (Fig. 2B) shows that the structure is not substantially divided or split distally as appears in the Ruschel & Campos image (their Fig. 22B), which may have been distorted by the image stacking process, so the uncus does not possess the two lobes recognized as claspers by Ruschel & Campos. While the lateral sections of the uncus do appear divided by a thinner medial strip, the structure forms a single plate distally with only a tiny notch at the apex (#7 in Fig. 2B). If the apical section of the *Sapantanga* uncus does form two lobes, then they are tightly appressed or connected by dried secretions. The dark brown theca is visible and is apparently guided in *Sapantanga* by lateroventral swellings that create a channel, similar to the ventral support found in many other Cicadidae possessing an uncus. In the lateral view, a spine or blade can be seen just protruding from the tip of the theca. Additional photographs of the *Sapantanga* holotype are available for download from [www.insectsinergers.com/sapantanga.html](http://www.insectsinergers.com/sapantanga.html).

On examination of the three *Hemidictya frondosa* specimens (e.g., Fig. 2C, D), we found an uncus that originates medially as in *Sapantanga*, with the structure substantially divided apically as shown in the Ruschel & Campos drawing. The theca is supported ventrally in a manner similar to that of *Sapantanga*, although with only a channel and no prominent ventral lobes.

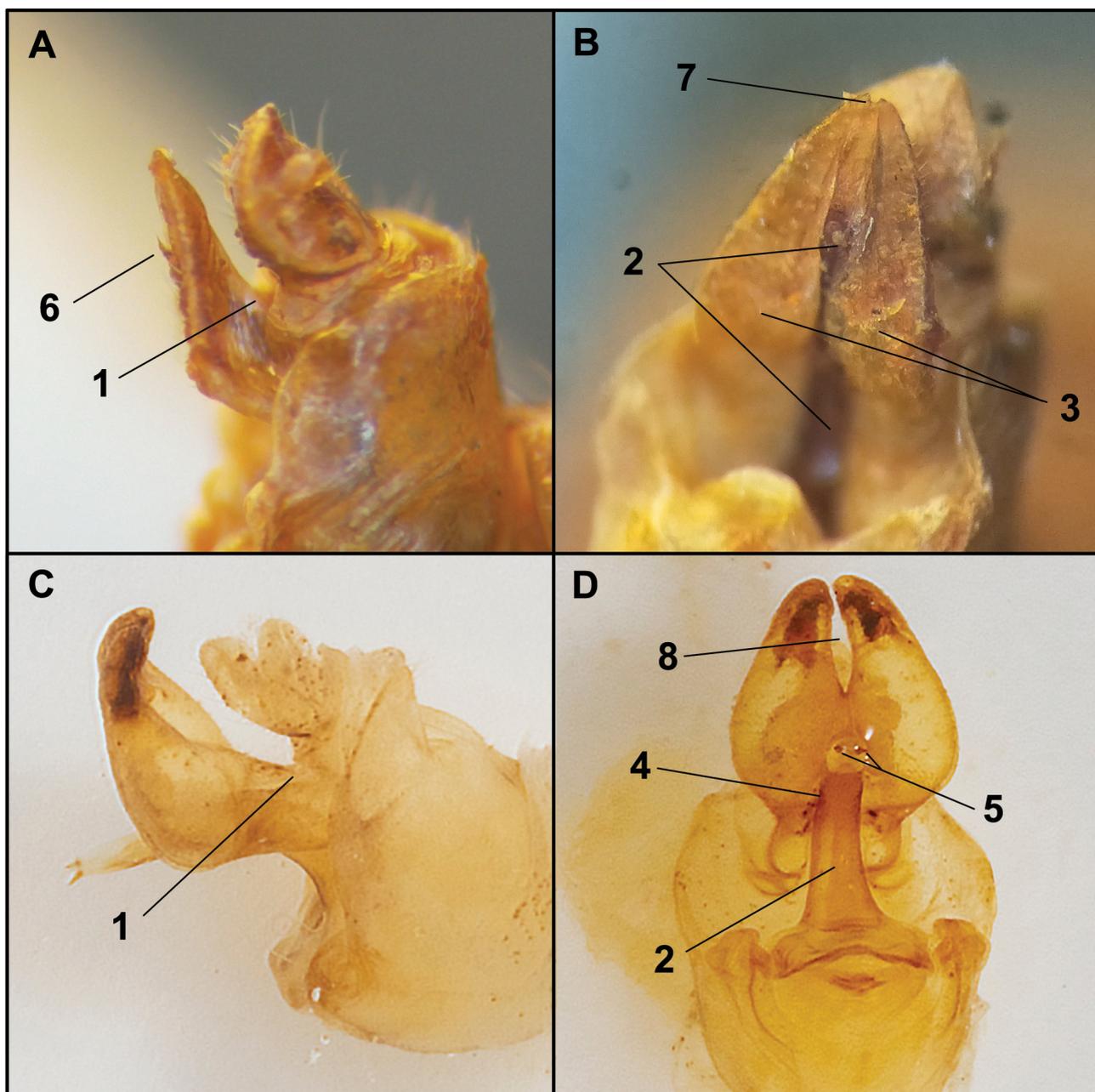
### *Morphological cladistic analyses*

Adding *Tibicina* to the Ruschel & Campos (2019) morphological data matrix and using that taxon as the root in a cladistic analysis considerably altered the structure of the tree (Fig. 3). Instead of Hemidictyini *sensu* Ruschel & Campos forming one monophyletic clade as in the replicated Ruschel & Campos analysis (Fig. 3A), the taxa now form two separate early diverging lineages, one with *Hemidictya*+*Hovana*+*Lacetas*+*Iruana* Distant, 1905g and the other with *Sapantanga* alone (Fig. 3B). Also, those genera that were previously shown to belong to Cicadettinae in the Marshall *et al.* (2018) genetic tree form part of a distal monophyletic clade in the revised morphological tree exclusive of *Lacetas*, in contrast to the Ruschel & Campos tree which has Tettigomyiinae nested within Cicadettinae. Changing the scoring of claspers and uncus did not affect the recovery of Hemidictyini *sensu* Ruschel & Campos as a group or change the relationships within that group in either analysis, although there were substantial changes to other aspects of the topology in the analysis without *Tibicina*. A file containing the data matrices and scripts for these analyses is included in the Supplementary Material.

### *Molecular phylogenetic analysis*

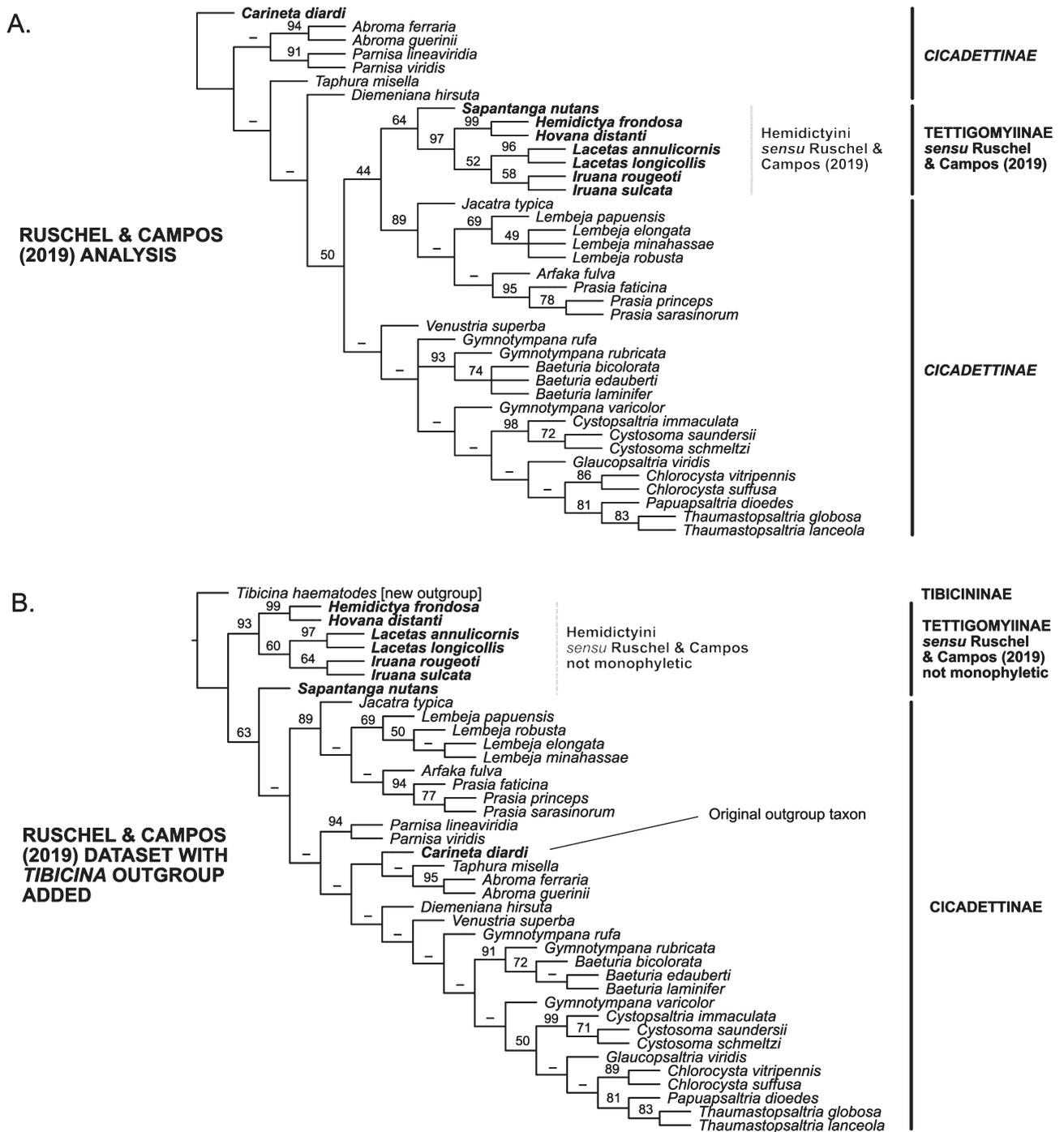
The genetic analysis places *Hemidictya* as a deep lineage within a clade containing all of the genera from subfamily Tibicininae (Fig. 4). The support for a monophyletic Tibicininae is only moderate (bootstrap percentage 67%) but it is somewhat improved from the previous genetic study, and there is strong support for the conclusion that *Hemidictya* does not belong to Tettigomyiinae, Cicadettinae, or Cicadinae Latreille, 1802 (bootstrap percentage 96%).

Two of the nodes separating *Lacetas* from *Hemidictya* are very strongly supported with 96% and 100% bootstrap values. The closest relatives of *Hemidictya* in the tree are *Selymbria* Stål, 1861 (Neotropics) and *Platypedia* Uhler, 1888 (N. America). Combining the morphological and DNA data into a single analysis for 11 taxa possessing both data types yielded a result that was concordant with the molecular tree (Fig. 5) aside from a minor difference within the Chlorocystini, with *Lacetas* still strongly supported as a distinct lineage not forming a monophyletic clade with *Hemidictya*.

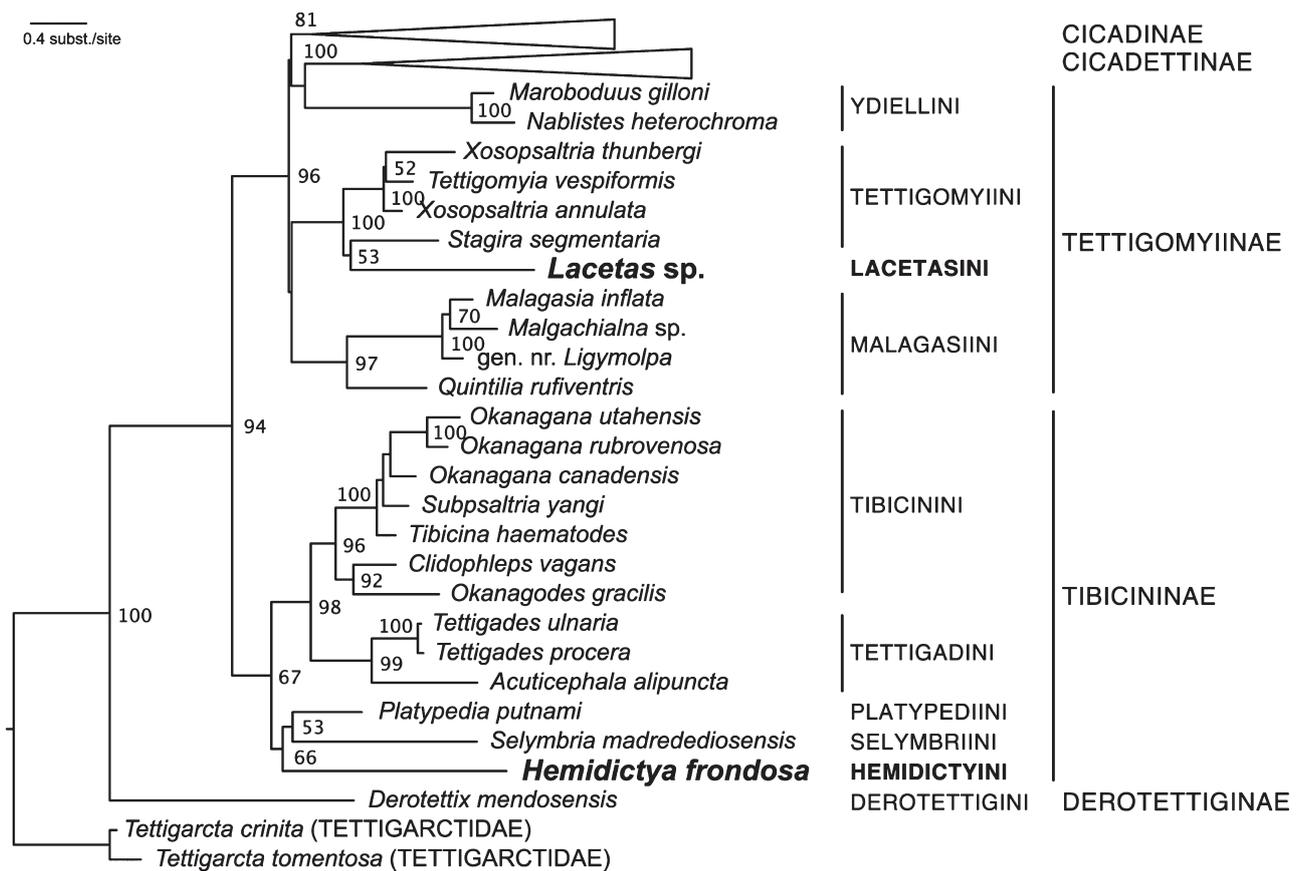


**FIGURE 2.** A and B. Posterolateral and ventral views of upper pygofer and uncus of *Sapantanga nutans* holotype (NHM). C and D. Views of the pygofer in *Hemidictya frondosa* (Moulds coll.). In both taxa, an uncus projects ventrally from an origin at a medial position (1) on the 10<sup>th</sup> abdominal segment and then turns posteriorly. The dark brown theca (2) is nested between ventral supporting lobes (3) in the *Sapantanga* specimen and within a shallow channel (4) in the *Hemidictya* specimen. Spines (5) and/or a blade-like process (6) are visible on the tip of the theca, which is only just visible just below the uncus in *Sapantanga*. The uncus is divided apically by only a slight notch (7) in *Sapantanga* but is deeply divided in *Hemidictya* (8).

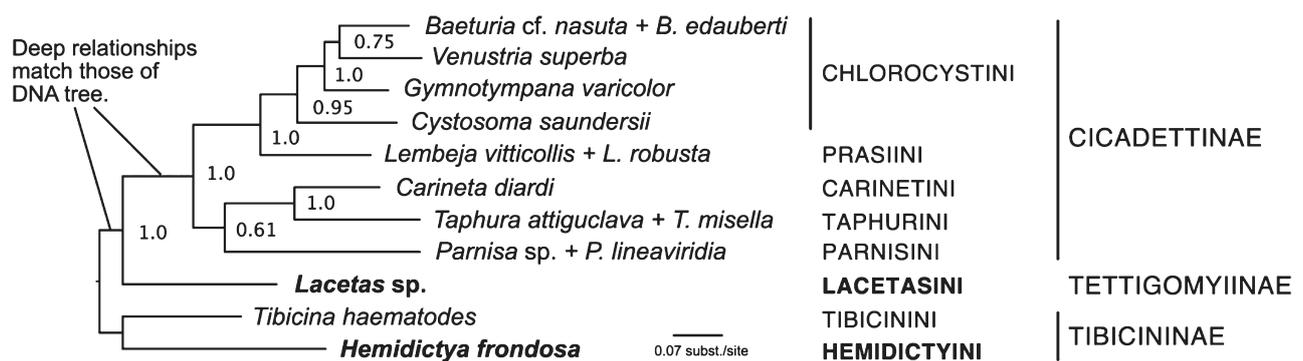
We have not been able to obtain tissue samples of *Hovana* or *Sapantanga*, so we have no genetic information for those genera. Analysis of genomic data (anchored phylogenomic, or AHE data) for approximately 150 genera of Cicadidae is ongoing in the C. Simon lab at the University of Connecticut; data vetting and analyses are currently in progress although preliminary examination of the data suggests confirmation of the results found here.



**FIGURE 3.** Effect of outgroup choice on cladistic reconstruction of Cicadidae relationships. A. Cladogram from analysis in TNT using the Ruschel & Campos (2019) dataset with implied weighting and with *Carineta diardi* (Cicadettinae) chosen as outgroup, as described in their study. B. The same Ruschel & Campos dataset with *Tibicina haematodes* (Tibicininae) included and used as the outgroup. Tibicininae has been identified as the earliest-diverging subfamily in earlier morphological (Moulds 2005) and molecular genetic (Marshall *et al.* 2018) analyses. In the latter tree, Hemidictyini *sensu* Ruschel & Campos is no longer monophyletic and contains early diverging genera rather than species that originated from within Cicadettinae as implied by the tree in A. Monophyly of the subfamily Cicadettinae has been recovered as in previous studies.



**FIGURE 4.** Molecular systematic position of *Hemidictya frondosa* as a deep lineage belonging to the subfamily Tibicininae and unrelated to *Lacetas* (Tettigomyiinae), as indicated by maximum-likelihood analysis of the Cicadidae genetic dataset from Marshall *et al.* (2018) with *Hemidictya* and *Derotettix mendosensis* added (the latter from Simon *et al.*, 2019). Current subfamilies and tribes are shown. Bootstrap supports from 200 pseudoreplicates are given for nodes with > 50% support. No supported differences from the 2018 tree were observed for the collapsed clades containing the remaining two subfamilies. *Selymbria madredediosensis* Sanborn, 2019 was identified as *S. stigmatica* in Marshall *et al.* (2018). Taxon authorships and specimen data for species not mentioned in the text here are found in Marshall *et al.* (2018).



**FIGURE 5.** Combined-data Bayesian analysis of genetic and morphological characters for 11 genera possessing data for both character types, with posterior probabilities shown for all nodes. The tree is rooted manually at the position observed in the DNA-only analysis. *Lacetas* and *Hemidictya* do not form an exclusive monophyletic as predicted by the classification of Hemidictyini *sensu* Ruschel & Campos (2019).

## DISCUSSION

### Outgroup Selection and Hemidictyini *sensu* Ruschel & Campos

Outgroup selection involves using knowledge separate from the study data to select one or more taxa which are believed to fall outside the ingroup, or the focal species in a phylogenetic study (Maddison *et al.* 1984). This allows the investigator to estimate character-state polarity and the position of attachment of the tree root. The taxon sample of Ruschel & Campos (2019) included species from two cicada subfamilies, Cicadettinae and Tettigomyiinae. Outgroup rooting of this dataset required the selection of a genus from a subfamily believed to diverge deeper in the Cicadidae tree, such as the Tibicininae, which recent genetic (Marshall *et al.* 2018) and morphological (Moulds, 2005) studies have found to be sister to the clade containing the remaining three Cicadidae subfamilies known at the time. (A more distantly related fifth subfamily, Derotettiginae Moulds in Simon *et al.* 2019, was recently established.) Another option would have been the genus *Tettigarcta* White, 1845 (Tettigarctidae Distant, 1905g), the sister-lineage to the family Cicadidae, although the distance to *Tettigarcta* is much greater. Instead, Ruschel & Campos selected *Carineta*, a genus that should not have been used to root the tree correctly given its well-supported position inside Cicadettinae (see Marshall *et al.* 2018).

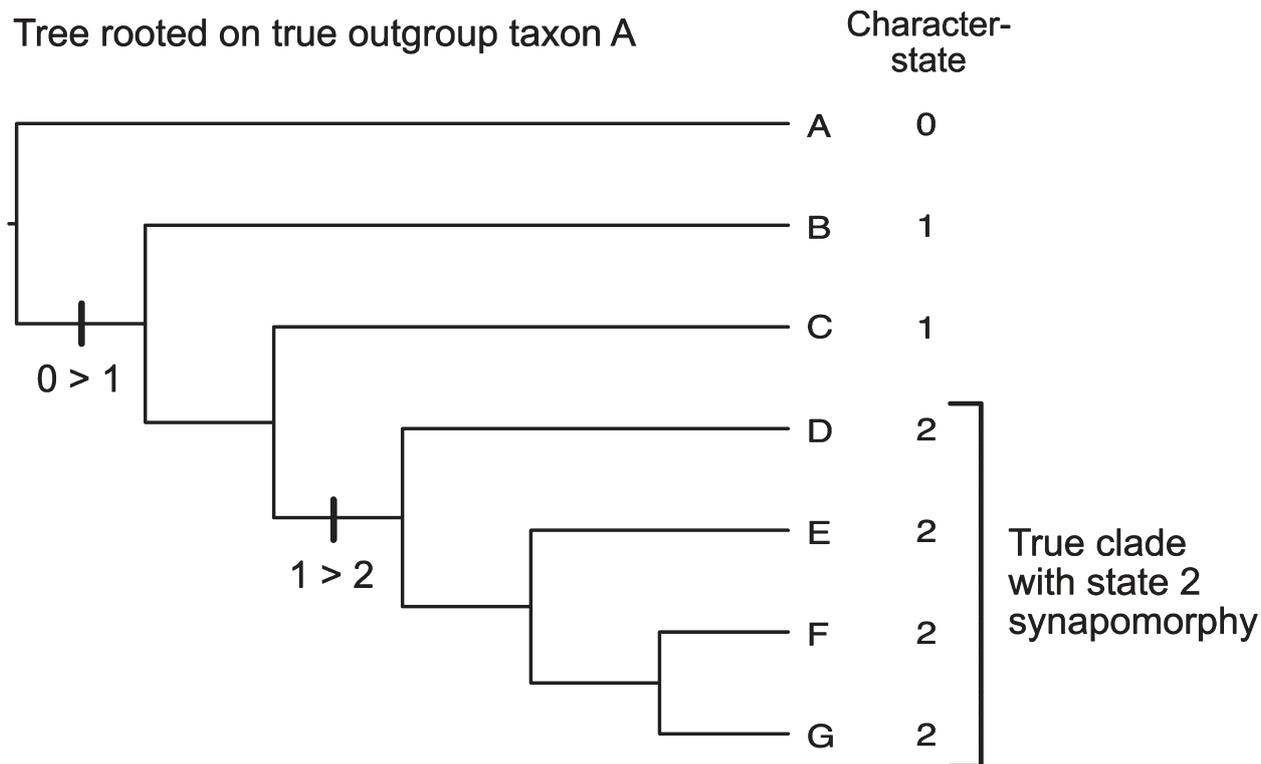
If a taxon that falls in a derived position within the ingroup is chosen to root a tree, the earliest-diverging taxa will form a more distally positioned, artifactual monophyletic clade. In essence, the tree will be turned inside-out (Fig. 6). We argue here that Hemidictyini *sensu* Ruschel & Campos is just such a false group of deeply divergent lineages caused by rooting of the tree on an ingroup taxon. With two different subfamilies sampled in the Ruschel & Campos dataset, the root position should be expected to fall somewhere outside them. Instead, they found *Lacetas* (Tettigomyiinae) nested well within a tree largely consisting of genera that are well-supported as members of Cicadettinae in the genetic analysis of Marshall *et al.* (2018) and the morphological cladistic analysis of Moulds (2005). The earlier genetic and morphological studies are based on a broader taxonomic sample than that of Ruschel & Campos (2019) (i.e., including Cicadettinae, Cicadinae and Tibicininae genera, albeit no Tettigomyiinae genera in the Moulds study). Our re-rooted cladistic analysis of the Ruschel & Campos (2019) dataset returns a phylogenetic result (Fig. 3B) that is more similar to relationships based on new genetic data (Fig. 4), with *Hemidictya* diverging early (rather than part of a more distal clade as in the Ruschel & Campos tree) and all Cicadettinae genera clustering into a monophyletic clade.

### Character States and Homology in Hemidictyini *sensu* Ruschel & Campos

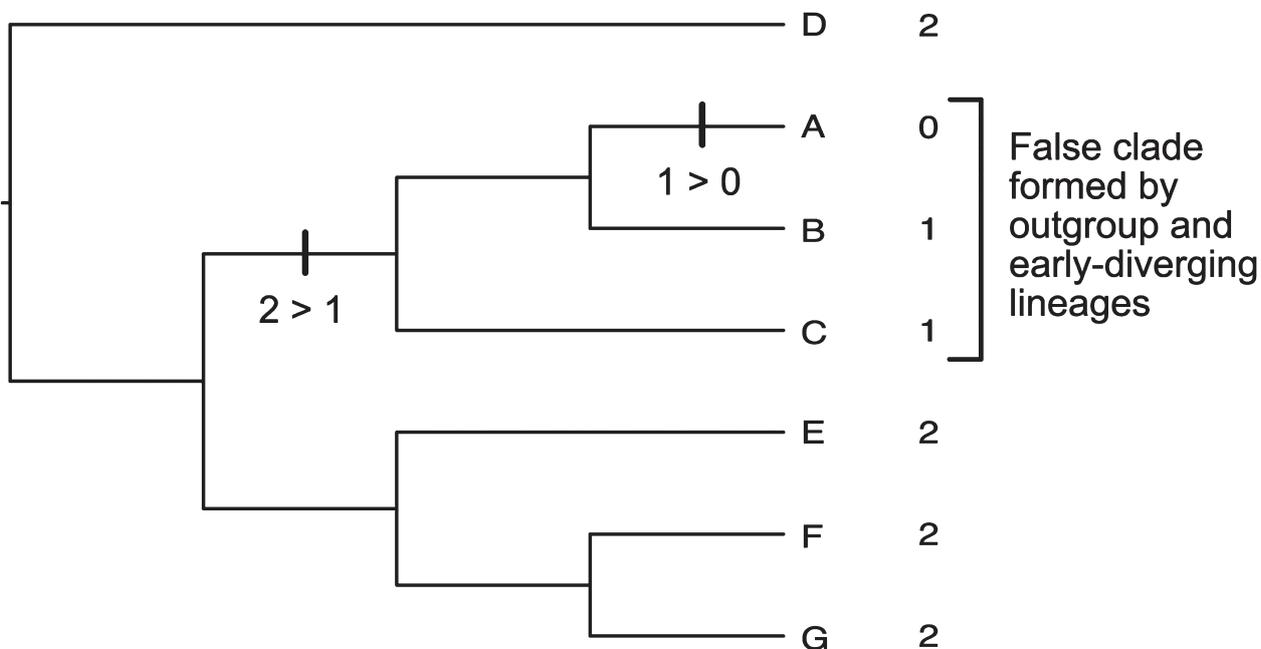
The uncus and claspers are important genitalic structures in Cicadidae classification, and their misidentification has created confusion regarding the classification of *Hemidictya*. After discussing the definitions of these structures (p. 1173), Ruschel & Campos (2019) say “We found the presence of uncus and claspers variable in Hemidictyini *sensu novo* ... we found claspers but no uncus in Chlorocystini, both uncus and claspers in Prasiini *sensu novo*, and either uncus or claspers in Hemidictyini *sensu novo*” (our emphasis). No other currently recognized Cicadidae tribes group uncus-only and claspers-only genera and, accordingly, we found that the apparent variability of Hemidictyini *sensu* Ruschel & Campos was caused by misidentification of the uncus as a pair of claspers in both *Hemidictya* and *Sapantanga*. We argue that the structure is an uncus in both genera because it originates from a single stem located medially on the 10<sup>th</sup> segment, rather than laterally with each lobe having a separate origin. Also, in both cases the aedeagus is guided along the ventral surface of the structure, as is typical for species possessing an uncus (see character 65, state 0, in Moulds 2005).

It is important to recognize that ambiguity exists in the application of the definitions of the uncus and claspers for some taxa, and that further refinement is needed. For example, in some Cicadinae genera (e.g., *Champaka* Distant, 1905a (Duffels 1991); *Cicada* Linnaeus, 1758 (Boulard 1990; 2018); *Dundubia* Amyot & Audinet-Serville, 1843 (Beuk 1996); *Orientalpsaltria* Kato, 1944 (Duffels & Zaidi 1999)) two uncal arms or lobes originate close to the medial portion of the anal tube, commonly with a connecting median uncal section, and then diverge apically and curve downward (anteriorly) with the theca passing upward between them close to their point of divergence. In some species (e.g., *Dundubia nagarasingna* – Beuk 1996; *Orientalpsaltria montivaga* – Duffels & Zaidi 1999) a portion of each uncal arm angles sharply downward in a manner much resembling a Cicadettinae clasper. While

Tree rooted on true outgroup taxon A



Above tree incorrectly rooted on taxon D



**FIGURE 6.** Effect of incorrect outgroup choice on inferred relationships and character polarity. The top tree is rooted on the true outgroup species A (the most distantly related taxon). The mapped character supports a monophyletic clade sharing state 2. In the bottom tree, taxon D from the first tree is incorrectly used as the outgroup, causing the earliest diverging lineages A, B, and C to form a false clade. The implied direction of character evolution is reversed, with state 2 now ancestral.

these structures could be argued to meet the definition of claspers because of their semi-lateral origin and the mode of interaction with the theca, we suggest that in such cases the uncal arms and/or lobes can be identified by their ultimate origin from a position close to the posterior margin of the 10<sup>th</sup> segment, in contrast to Cicadettinae claspers that emerge from a more anterior position (i.e., from deeper within the pygofer). This concept will need testing by examination of more taxa. In *Hemidictya* the uncus is deeply divided apically as in these problematic Cicadinae cases, but the two arms have a common stem and curve caudally away from the theca and do not appear to interact with it. As discussed earlier in Methods and Results, the *Sapantanga* uncus does not possess separate lobes at all. We see no reason to doubt the identification of the uncus in either *Hemidictya* or *Sapantanga*.

*Hemidictya* and *Sapantanga* both possess an unusual “bent” uncus that sharply turns in a posterior direction after arising from the 10<sup>th</sup> segment. This feature is also commonly observed in *Platypedia* Uhler, 1888 (Simons 1954) and somewhat more subtly in *Selymbria* (Sanborn 2019). *Platypedia* and *Selymbria* are the closest known relatives of *Hemidictya* according to the genetic tree (Fig. 4), albeit with weak support. This pattern further suggests that the uncus has now been correctly identified in *Hemidictya* and *Sapantanga*.

The finding that *Hemidictya* and *Sapantanga* do not possess claspers eliminates the one proposed synapomorphy for Hemidictyini *sensu* Ruschel & Campos (2019), their character 51 “clasper apex orientation posterior or anterior”. This character had been scored as inapplicable for five of the seven taxa in the clade because structures identified as claspers were not present. It is now clear that the transition being mapped for character 51 is that between a more ordinary uncus (*Hovana*, *Lacetas*, *Iruana*) and a caudally bent one (*Sapantanga*, *Hemidictya*). This trait is therefore polymorphic across Hemidictyini *sensu* Ruschel & Campos.

Examination of the two synapomorphies found by Ruschel & Campos for the large clade excluding *Sapantanga* (i.e., *Hemidictya*, *Hovana*, *Iruana*, and *Lacetas*) raises additional questions. Character 1, eyes protruding (state 0) or not protruding (state 1) relative to lateral margins of the head in dorsal view, is described in terms of whether the largest linear dimension of the eyes lies perpendicular or oblique, respectively, to the longitudinal axis of the body. But in all of the illustrations shown in Fig. 2 of Ruschel & Campos (2019), the largest linear dimension of the eyes as measured from the photographs is oblique – for taxa scored both state 0 and state 1 – and in one case approaches being parallel. Measurement of this character is probably subject to considerable variation based on the interpretation of the observer. The remaining synapomorphy (character 18), the shape of the lateral margin of the pronotal collar as round versus truncate, is easier to replicate than character 1 but is not a clearly contrasting difference as shown in their illustrations. Independent investigators may not be able to replicate their application of the terms truncate and rounded since the taxa coded as truncate do not have sharply abbreviated margins.

## Reconsideration of Tribe Hemidictyini *sensu* Ruschel & Campos

As has been demonstrated by the above morphological and genetic analyses, important aspects of the proposed redefinition and reclassification of Hemidictyini by Ruschel & Campos (2019) are not supported by the evidence. In their cladistic tree (their Fig. 11), the clade forming the basis of the definition of their Hemidictyini is nested within the seven Cicadettinae tribes used. Their concept would imply that Hemidictyini is a member of the Cicadettinae, not the Tettigomyiinae as they suggest. Furthermore, by including almost exclusively representatives of the Cicadettinae in their analysis without taxa from most of the other subfamilies or an appropriate outgroup, Ruschel & Campos have restricted the potential taxonomic relationships that might have been revealed and produced a tree with incorrect character state polarities. By re-rooting their analysis on Tibicininae (Fig. 3B) and testing with genetic data, we have shown that the taxa currently classified in Hemidictyini *sensu* Ruschel & Campos now branch out away from all Cicadettinae and form multiple clades in at least two subfamilies.

The conclusion that Hemidictyini *sensu* Ruschel & Campos (2019) contains an assemblage of unrelated genera explains why the group lacks a set of shared features to distinguish them from all other cicada tribes. Ruschel & Campos listed 33 characters as having states that distinguish their tribe Hemidictyini; 19 of these character states (57.6%) are present in only some genera, while 14 character states (42.4%) are common to all genera (however, all of these are homoplasious). Included in the characters supporting Hemidictyini *sensu* Ruschel & Campos (2019) are taxonomically important structures such as a large, dominant uncus present (a character state of the Cicadinae, Tettigomyiinae, Tibicininae and Derotettiginae) and claspers present (a character state in the sense of the Cicadettinae). It has been shown through a more detailed morphological analysis (117 characters and 80 taxa of Moulds (2005)

vs. the 67 characters and 39 taxa of Ruschel & Campos (2019)), through phylogenetic analysis of mitochondrial genomes (Song *et al.* 2017; Łukasik *et al.* 2018), and phylogenetic analysis of multiple nuclear and mitochondrial genes (Marshall *et al.* 2018; Simon *et al.* 2019) that the genital structures can be used reliably to distinguish the subfamilies, with limited exceptions.

Final classification of many of the challenging genera considered here and by Ruschel & Campos (2019) will not be accomplished until more systematic morphological and molecular studies have been completed. In part due to the addition of many new genera since the Moulds (2005) classification, unique attributes are lacking for most subfamilies (Table 1). Discovery and description of new characters, and possibly new subfamilies, will likely be required as new taxa are added. For example, while all species of the genus *Dimissalna* possess claspers, as expected from their position in Cicadettinae following genetic analysis (Marshall *et al.*, 2015), they also exhibit a large, dominant uncus (Puissant & Sueur 2011) instead of the small, duck-billed or absent uncus as the subfamily is currently defined. A full morphological analysis of all relevant taxa using the Moulds (2005) character set plus new characters identified by Ruschel & Campos (2019) is beyond the preliminary and remedial scope of this study, and genetic material is not yet available for several taxa. However, our examination of the available data supports several changes that should be made to clarify cicada taxonomy in the interim, each of which is explained below: (1) Transfer of *Hemidictya* to subfamily Tibicininae; (2) Transfer of *Sapantanga* to Tibicininae with definition of a new tribe; (3) Transfer of *Iruana* and the other African genera to Lacetasini, which is left in Tettigomyiinae with a name change due to synonymy with Iruanina; (4) Transfer of *Hovana* into a new tribe in Tettigomyiinae; (5) Refinement of the definition of Hemidictyini.

### Subfamily Classification of Tribe Hemidictyini

With a mis-rooted tree creating a cluster of distantly related lineages, and the uncus incorrectly scored as claspers in both *Hemidictya* and *Sapantanga*, Ruschel & Campos (2019) faced a difficult problem in determining the subfamily placement for their Hemidictyini. After reviewing the conflicting character evidence, they placed the tribe in subfamily Tettigomyiinae pending the acquisition of further data, perhaps because the genetic evidence placed *Lacetas* in that group (Marshall *et al.* 2018).

Tettigomyiinae genera are defined in part by the presence of a non-retractable uncus (Marshall *et al.* 2018), and our discovery that *Hemidictya* possesses such an uncus rather than claspers at first appears to strengthen the case for the Ruschel & Campos classification. However, the posterior angling of this feature is different from that of the pre-Ruschel & Campos Tettigomyiinae as well as different from the uncus found in the four other African genera placed in Hemidictyini by Ruschel & Campos (2019). While *Malagasia* Distant, 1882 also possesses a caudally directed uncus, the structure does not emerge ventrally and then bend as in *Hemidictya* and *Sapantanga*. Species with an uncus that is sharply angled caudally as in *Hemidictya* (and *Sapantanga*) are otherwise common only in *Platypedia* (see Simons 1954) and *Selymbria* (Sanborn 2019), tibicinine genera that fall in the same region of the genetic tree as *Hemidictya*.

We argue that although *Hemidictya* cannot be unambiguously placed in any known subfamily according to current definitions, the current genetic and morphological evidence supports placement in Tibicininae better than in Tettigomyiinae (Tables 2 and 3). Important characters shared between *Hemidictya* and Tibicininae include the unfused forewing cubitus posterior (CuP) and anal 1 (1A) veins, the presence of a partially recurved rim on the margin of the timbal cavity, the presence of a ventrobasal pocket in the aedeagus (observed in *Platypedia* and *Selymbria*), and the sharply caudally bent, non-retractable uncus. *Hemidictya* does not, however, have the hind wing radius posterior (RP) and median (M) veins separate at their base as in other Tibicininae. Tibicininae have also been distinguished by the presence of lateral “leaf-like” lobes on the aedeagus, which are lacking in *Hemidictya*, but the addition of *Selymbria* by Marshall *et al.* (2018) rendered this character nondiagnostic and it has been omitted from Table 1. On the balance of the evidence, and in agreement with the genetic tree, we transfer the tribe Hemidictyini to subfamily Tibicininae.

The lack of uniformity in key wing vein characters across the genera now classified in Tibicininae, together with the deep lineages apparent in the genetic tree, suggests that a new subfamily may be needed for *Hemidictya* and possibly associated genera. But an attempt to define a new subfamily for *Hemidictya* and allies and redefine Tibicininae would be premature with genetic data pending and without the examination of all relevant genera in a more complete cladistic analysis.

**TABLE 1.** Characters for the five subfamilies of the family Cicadidae, modified from Marshall *et al.* (2018) and Simon *et al.* (2019). Characters especially useful for identifying one or two subfamilies are highlighted in gray.

CHARACTER	Cicadinae	Cicadettinae	Tettigomyiinae	Tibicinae	Derotettiginae
<b>Forewing veins CuP and 1A</b>	Fused in part.	Fused in part.	Fused in part.	Unfused (fused in part in <i>Gibbocicada</i> , <i>Platypedia</i> & <i>Neoplatypedia</i> ).	Unfused.
<b>Fore wing vein CuA1 division (most common state)</b>	Such that proximal portion longest.	Such that proximal portion shortest.	Such that proximal portion shortest.	Such that proximal portion shortest or longest.	Such that proximal portion shortest.
<b>Hind wing 1st cubital cell width at distal end</b>	NOT much greater than 2nd cubital cell (twice or more)	Much greater than 2nd cubital cell (twice or more)	Much greater than 2nd cubital cell (twice or more)	NOT much greater than 2nd cubital cell (twice or more)	Much greater than 2nd cubital cell (twice or more)
<b>Hindwing veins RP and M</b>	Fused at base.	Fused at base.	Fused at their bases.	Unfused.	Unfused.
<b>Male timbal covers</b>	Present but lost in a few genera.	Lacking timbal covers.	Lacking timbal covers, or with a partial turned-back rim.	With a partial turned-back rim.	Lacking timbal covers.
<b>Pygofer distal shoulder</b>	Developed, often the most distal part of pygofer.	Undeveloped.	Developed, often the most distal part of pygofer.	Undeveloped.	Undeveloped.
<b>Pygofer upper lobe</b>	Usually absent, present in some Cryptotympanini	Present.	Absent.	Usually absent (present in Selymbriini).	Absent.
<b>Uncus shape</b>	Dominant, moderate length to long.	Absent or small and duck-bill shaped (large and bi-lobed in many <i>Taphura</i> , large in <i>Dimissalna</i> ).	Dominant, moderate length to long.	Dominant, moderate length to long.	Dominant, moderate length.
<b>Uncus strongly caudally bent?</b>	No.	No.	No.	Yes or No.	No.
<b>Uncus retractable?</b>	Yes.	Yes.	No.	No.	No.
<b>Claspers</b>	Absent, but present in some Dundubiini (if present, spined).	Present, usually large (small in Kaotini), not spined.	Absent.	Absent.	Absent.
<b>Ventrobasal pocket of aedeagus</b>	Absent.	Absent.	Absent.	Present.	Present.
<b>Basal plate of aedeagus</b>	Not deeply divided basally and attached to the theca by sinuation.	Not deeply divided basally and attached to the theca by sinuation.	Not deeply divided basally and attached to the theca by sinuation.	Not deeply divided basally and attached to the theca by sinuation.	Deeply divided basally and attached to the theca by sinuation.

**TABLE 2.** Character states for key taxa discussed in the text.

CHARACTER	<i>Hemidictya</i>	<i>Sapantanga</i>	<i>Lacetas</i>	<i>Hovana</i>
<b>Forewing veins CuP and 1A</b>	Unfused.	Partially fused.	Partially fused.	Partially fused.
<b>Fore wing vein CuA1 division (most common state)</b>	N/A	Such that proximal portion shortest.	Such that proximal portion shortest.	N/A
<b>Hind wing 1st cubital cell width at distal end</b>	NOT much greater than 2nd cubital cell (twice or more).	NOT much greater than 2nd cubital cell (twice or more).	Much greater than 2nd cubital cell (twice or more).	NOT much greater than 2nd cubital cell (twice or more).
<b>Hindwing veins RP and M</b>	Fused at base.	Unfused (just).	Fused at base.	Fused at base.
<b>Male timbal covers</b>	Absent, but cavity with partly formed turned back rim.	Absent, but cavity with partly formed turned back rim.	Absent, but cavity with partly formed turned back rim.	Absent, but cavity with partly formed turned back rim.
<b>Pygofer distal shoulder</b>	Undeveloped.	Undeveloped.	Developed but nearly fused as one due to apical narrowing of pygofer.	Undeveloped.
<b>Pygofer upper lobe</b>	Absent.	Absent.	Absent.	Well-developed.
<b>Uncus shape</b>	Dominant, moderate to long length.	Dominant, moderate to long length.	Dominant, moderate to long length.	Dominant, moderate to long length.
<b>Uncus strongly caudally bent?</b>	Yes.	Yes.	No.	No.
<b>Uncus retractable?</b>	No.	No.	No.	No.
<b>Claspers</b>	Absent.	Absent.	Absent.	Absent.
<b>Ventrobasal pocket of aedeagus</b>	Present.	Unknown.	Absent.	Absent.
<b>Basal plate of aedeagus</b>	Undivided basally, attachment completely chitinous with no mobility.	Unknown.	Undivided basally, attachment completely chitinous with no mobility.	Undivided basally, attachment completely chitinous with no mobility.

### The Classification of *Sapantanga*

No genetic data are available for *Sapantanga*, but our tabulation of character states suggests that *Sapantanga* best matches the character profile for Tibicininae (Tables 2 and 3). The ventrobasal pocket unfortunately cannot be determined from examination of the holotype (the only known specimen), but otherwise no clear character conflicts were found. *Sapantanga* notably possesses the caudally bent uncus, the unfused hindwing veins RP and M, and the partially developed turned back rim on the margin of the timbal cavity. This assignment remains to be tested with genetic data.

Shared features of the pygofer, especially the caudally bent uncus, initially suggest that *Sapantanga* might be placed in the same tribe as *Hemidictya*. However, the bent uncus is not restricted to these two genera. Both our morphological analyses and the Ruschel & Campos (2019) tree suggest that *Sapantanga* possesses a highly divergent combination of character states (15 characters are listed as exceptions for *Sapantanga* in the diagnosis of the Ruschel & Campos (2019) Hemidictyini, more than 45%). We propose that a new tribe is necessary to accommodate *Sapantanga*. It is frustrating that locality information is missing from the only known specimen (NHM, early 19<sup>th</sup> century).

**TABLE 3.** Subfamily character matches, for key taxa discussed in the text. Taxa with an exact or potential match to a subfamily based on the states in Tables 1 and 2 are given a 1 for that character, otherwise zero. Values at the bottom are the summed scores along with the number of characters for which data are available. Gray highlights show subfamily assignments. Cd=Cicadinae, Ct=Cicadettinae, Tg=Tettigomyiinae, Ti=Tibicininae, De=Derotettiginae.

CHARACTER	<i>Hemidictya</i>					<i>Sapantanga</i>					<i>Lacetas</i>					<i>Hovana</i>				
	Cd	Ct	Tg	Ti	De	Cd	Ct	Tg	Ti	De	Cd	Ct	Tg	Ti	De	Cd	Ct	Tg	Ti	De
<b>Forewing veins CuP and 1A</b>	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
<b>FW vein CuA1 division (most common state)</b>	N/A	N/A	N/A	N/A	N/A	0	1	1	1	1	0	1	1	1	1	N/A	N/A	N/A	N/A	N/A
<b>Hind wing 1st cubital cell width at distal end</b>	1	0	0	1	0	1	0	0	1	0	0	1	1	0	1	1	0	0	1	0
<b>Hindwing veins RP and M</b>	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1	0	0
<b>Male timbal covers</b>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<b>Pygofer distal shoulder</b>	0	1	0	1	1	0	1	0	1	1	1	0	1	0	0	0	1	0	1	1
<b>Pygofer upper lobe</b>	1	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	1	0
<b>Uncus shape</b>	1	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	1	1	1
<b>Uncus strongly caudally bent?</b>	0	0	0	1	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1
<b>Uncus retractable?</b>	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1
<b>Claspers</b>	1	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	1	1	1
<b>Ventrobasal pocket of aedeagus</b>	0	0	0	1	1	?	?	?	?	?	1	1	1	0	0	1	1	1	0	0
<b>Basal plate of aedeagus</b>	1	1	1	1	0	?	?	?	?	?	1	1	1	1	0	1	1	1	1	0
	7/12	4/12	7/12	11/12	8/12	6/11	4/11	7/11	11/11	9/11	10/13	8/13	13/13	9/13	8/13	10/12	8/12	9/12	10/12	6/12

## Sapantangini Sanborn, Moulds & Marshall, n. tribe

Type genus *Sapantanga* Distant, 1905.

### Diagnosis

Head including eyes narrow, less than width across lateral pronotal angles; supra-antennal plates extending nearly to eye; eyes protruding laterally from head; lateral ocelli widely spaced, the distance between the lateral ocelli being greater than between each lateral to the median; postclypeus dorsal length at least as long as dorsal vertex; postclypeus apex rounded in lateral view, rounded in transverse cross section below head. Pronotum with shallow median groove; pronotal collar with paranota weakly developed; mid lateral tooth absent. Mesonotum and metanotum lacking auxiliary sound-producing structures; scutellum cruciform. Opercula small, not covering the tympanal cavity; meracanthus long and thin, finger-like, at base much narrower than base of operculum. Foreleg femoral primary spine prostrate. Forewing costal vein equal in width and contiguous to radius (R) + subcostal (Sc) vein; radius anterior vein 1 (RA1) diverging from Sc in subapical region; forewing CuP and 1A abutted (or perhaps partly fused); forewing veins M and CuA unfused and widely separated at basal cell; forewing cubitus anterior vein 1 (CuA1) divided by mediocubital crossvein (m-cu) such that proximal section shortest. Hind wing cubital cell 1 width at distal end not twice or more the width of cubital cell 2; hind wing RP and M veins unfused. Male abdominal tergites with sides convex in cross section; tergites 4–7 tapering; epipleurites reflexed to ventral surface. Timbals extended below level of wing bases; timbal covers absent, partially formed ridge on dorsal and ventral posterior timbal cavity. Pygofer dorsal beak absent; distal shoulder undeveloped; upper lobe absent; basal lobe moderately developed. Uncus large, minimally divided, not retractable within pygofer, bent almost at right angle near base, angled caudally; claspers absent. Aedeagus with theca simple; conjunctival claws and pseudoparameres unknown.

### Distinguishing features

Differs from all other tribes in having, in combination, the supra-antennal plates extending nearly to eye, forewing veins CuP and 1A abutted (perhaps partially fused), forewing veins M and CuA unfused and widely separated at basal cell, fore femora primary spine prostrate, the pygofer upper lobe absent, and a long non-retractable uncus that is significantly bent posteriorly near the base.

Sapantangini **n. tribe** can be distinguished from the Chilecadinini Sanborn, 2014 by the forewing vein CuA1 being divided by m-cu such that the proximal section is shortest, the diverging veins RA1 and Sc in the subapical forewing, the base of meracanthus not about as wide as the base of operculum, the lack of a broadening on abdominal tergite 2 posterior to the timbal cavity, the pygofer basal lobe not reaching to the level of the uncus, and the slightly divided uncus bent posteriorly at an approximate right angle. Sapantangini **n. tribe** can be distinguished from the Platypediini Kato, 1932 by the presence of timbals and the lack of thickened and bowed forewing costa for sound production. Sapantangini **n. tribe** differs from the Selymbriini Moulds & Marshall (in Marshall *et al.* 2018) in the head that is narrower than the lateral pronotal collar angles, the turned-back rim on the timbal cavity being restricted to the dorsal and ventral margins of the timbal cavity, the lack of a well-developed dorsal beak, and the lack of an upper pygofer lobe. Sapantangini **n. tribe** differs from the Tettigadini Distant, 1905d in the head being not as wide as the mesonotum, the lack of dilated pronotal margins, the lack of a mesonotal stridulatory apparatus, the lack of a coiled aedeagus, and the presence of a caudally bent uncus. Sapantangini **n. tribe** differs from the Tibicinini Distant, 1905e in the lack of a broadening of abdominal tergite 2 posterior to the timbal cavity, lack of a cylindrical abdomen (e.g. semicircular dorsal cross-section with transverse ventral surface), and the presence of a caudally bent uncus, although *Sapantanga* does share some distinctive character states with various genera of the Tibicinini. Finally, Sapantangini **n. tribe** can be distinguished from Hemidictyini by the metanotum being exposed on the dorsal midline, the lack of multiple reticulations of the forewing and other leaf-mimicry attributes, the unfused CuP and 1A forewing veins, and the absence of a deep division of the uncus.

### The Classification of *Lacetas*, *Iruana* and Related African Genera

In the genetic tree (Fig. 4), *Lacetas* was well separated from *Hemidictya* and fell closer to *Tettigomyia* Amyot & Audinet-Serville, 1843, the type genus of subfamily Tettigomyiinae. This association is confirmed by our character

tabulation (Table 3), which shows no clear conflict with the characters of that subfamily, and we thereby remove *Lacetas* (and consequently also Lacetasini) from synonymy with Hemidictyini and place it in subfamily Tettigomyiinae as currently classified.

Ruschel & Campos (2019) found that the African genus *Iruana* grouped with *Lacetas* and *Hemidictya* in their tree and that the African genera *Bafutalna* Boulard, 1993 and *Murphyalna* Boulard, 2012 were closely allied based on morphology, so these genera were also moved to Hemidictyini in their list of included genera. The date priority of Hemidictyini led them to synonymize Lacetasini with Hemidictyini, an action that we have reversed above. *Hemidictya* possesses character states associated more with the Tibicininae as outlined above, while all of the African genera possess a non-retractable uncus, partially fused CuP and 1A in the forewing, and hind wing RP and M veins fused at the base, distinguishing them as members of the Tettigomyiinae (Marshall *et al.* 2018). These morphological characters support the close association of *Iruana*, *Bafutalna*, and *Murphyalna* with Lacetasini (Ruschel & Campos 2019, Figs. 11–12) and not with *Hemidictya*.

### **Iruanini Boulard, 1993 rev. stat.**

Iruanaria Boulard 1993: 92.

Lacetasini Moulds & Marshall (in Marshall *et al.*) 2018: 49. n. syn.

Recognising *Lacetas*, *Iruana*, *Bafutalna* and *Murphyalna* as a monophyletic group, that is the Lacetasini, raises an issue of nomenclatural priority. Marshall *et al.* (2018) erected the tribe Lacetasini; however Boulard (1993) erected the subtribes Iruanina Boulard, 1993 and Bafutalnina Boulard, 1993, family group names that now all become synonyms. Iruanina and Bafutalnina have date priority over Lacetasini (Articles 23.1 and 23.3, ICZN 1999). However, the names Iruanina and Bafutalnina were published simultaneously and require a decision on priority. The subtribes proposed by Boulard (1993) differ in their acoustic systems with the Iruanina having a complete sound system and the Bafutalnina lacking any mechanism to produce sound. Because *Lacetas* has a functioning timbal-based sound system like the Iruanina, we choose the name Iruanina as having priority, fixing it as the valid name under Article 24.2 (ICZN 1999). Thus, Lacetasini **n. syn.** becomes a subjective junior synonym of Iruanini **rev. stat.** (Article 61.3, ICZN 1999). The subtribe Iruanina is retained for the genera *Iruana* and *Lacetas* and Bafutalnina is retained for the genera *Bafutalna* and *Murphyalna*. This grouping also makes sense biogeographically as all the included genera are African.

### **The Classification of *Hovana***

*Hovana* (from the north-west of Madagascar) presents a more difficult problem, both because no genetic data are available and because it possesses a more unusual combination of characters (Tables 2 & 3). The reticulated forewing veins render one of the useful features inapplicable (forewing vein CuA1 division). The remaining characters support the classification of *Hovana* in Cicadinae, Tettigomyiinae, and Tibicininae about equally (Tables 2 & 3). However, there are issues with the known Tibicininae being absent from equatorial and southern Africa or Madagascar (Sanborn 2013; Marshall *et al.* 2018), and the lack of fused hindwing RP+M and lack of a ventrobasal pocket of the aedeagus suggest that *Hovana* does not belong in the Tibicininae. Similarly, a retractable uncus is an important genitalic structure found in Cicadinae that is lacking in *Hovana*. Although there are some contradictory structures in *Hovana* and other Tettigomyiinae, the long, non-retractable uncus and the turned-back rim of the timbal cavity suggest an affiliation with Tettigomyiinae. Furthermore, one tettigomyiine tribe (Iruanini **rev. stat.**) is noted to have “distal shoulders developed but fused as one due to apical narrowing of the pygofer” (Marshall *et al.*, 2018, p. 49), and we speculate that the broad dorsal beak of *Hovana* could represent a continuation of that trend. Because *Hovana* does not fall within any described Tettigomyiinae tribe, and appears incompatible with other tribes elsewhere, Hovanini **n. tribe** is proposed here with the type genus *Hovana* Distant, 1905g.

## ***Hovanini* Sanborn, Marshall & Moulds, n. tribe**

Type genus *Hovana* Distant 1905g: 279.

### ***Diagnosis***

Head including eyes narrow, much less than lateral angles of pronotal collar; supra-antennal plates extending to eye; lateral ocelli widely spaced, closer to eyes than to each other; postclypeus apex angular in lateral view. Pronotum with median groove, pronotal collar with paranota weakly developed; mid lateral tooth absent. Opercula small, not covering the tympanal cavity, with convex lateral margin, not S-shaped, not surrounding meracanthus. Meracanthus rudimentary. Foreleg primary spine prostrate. Forewing costal vein equal in width to R+Sc; CuP and 1A fused in part. Hind wing anal lobe narrow with anal vein 3 straight; hind wing cubital cell 1 width at distal end not twice or more the width of cubital cell 2; hind wing RP and M veins fused at base. Male abdominal tergites with sides convex in cross section, tergites 2–4 similar in size, tergites 4–7 reducing in width posteriorly; sternite I hidden; epipleurites deeply reflexed to ventral surface. Timbal covers absent, partially formed ridge on dorsal and ventral posterior timbal cavity. Pygofer distal shoulder undeveloped; upper lobe well-developed; basal lobes small; dorsal beak present. Uncus elongated, not retractable within pygofer, curving downward, with laterally expanding apex; claspers absent. Aedeagus lacking a ventrobasal pocket (Fig. 7).

### ***Distinguishing features***

*Hovanini n. tribe* differs from other tribes in having, in combination, a mesonotum with a triangular scutellum extending over the anterior abdominal tergites, opaque forewings, well-developed pygofer upper lobes, a dorsal beak, and a downward curving non-retractable uncus widening at its apex.

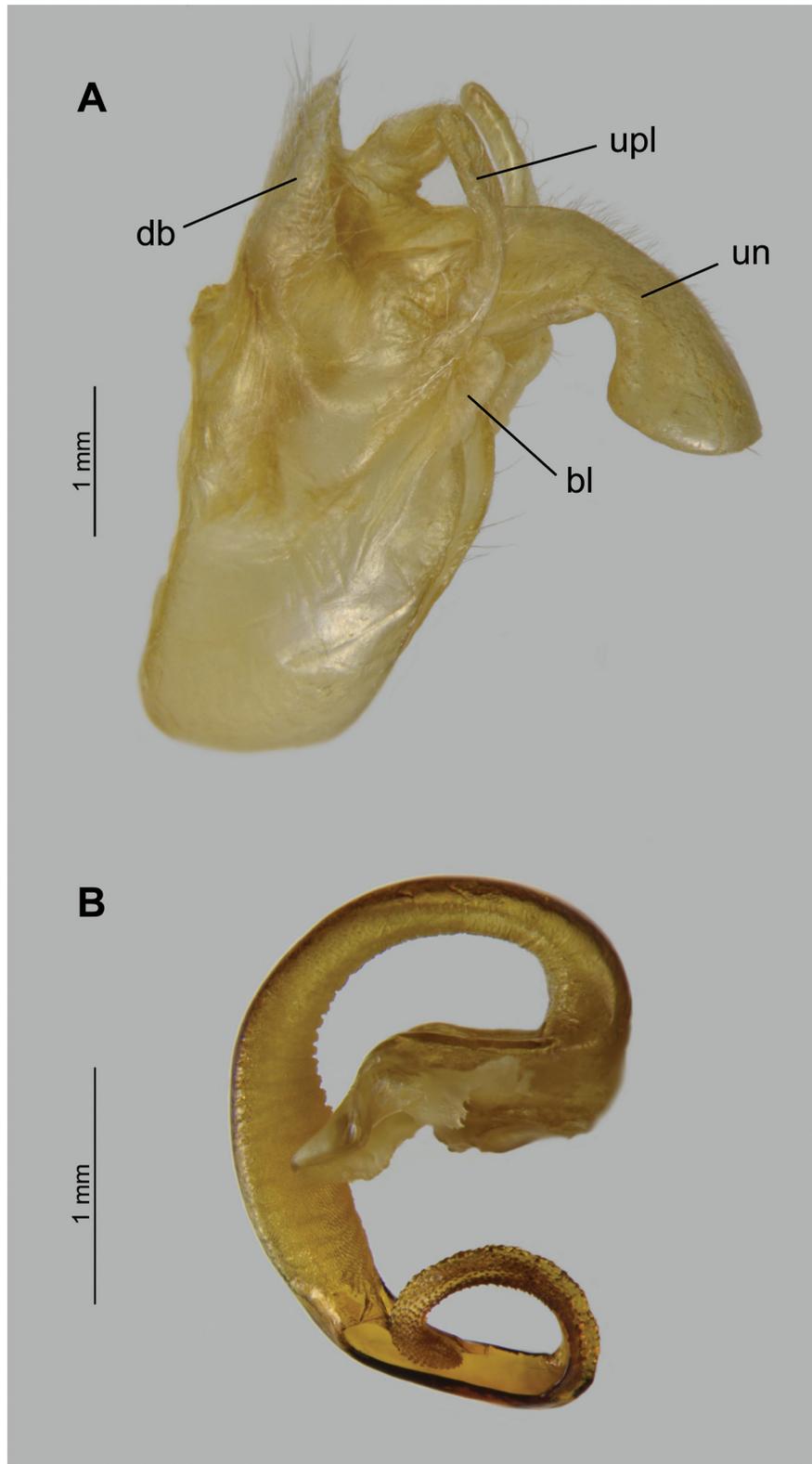
*Hovanini n. tribe* can be distinguished from the Lacetasini by the male operculum that fully encapsulates the meracanthus, the epipleurites reflexed to the ventral surface, the well-developed pygofer upper lobe, the presence of a dorsal beak, and an extended uncus widening at the apex. *Hovanini n. tribe* can be distinguished from the Malagasiini Moulds & Marshall, 2018 (in Marshall *et al.* 2018) by the comparatively wide pronotal collar, the widely separated costal and R+Sc veins in the forewings, the prostrate primary spine of the fore-femur, opercula that do not cover the tympanal cavity, the tapering posterior abdomen, the lack of any development in the pygofer distal shoulder, the presence of pygofer upper lobes, and an extended uncus widening at the apex. The *Hovanini n. tribe* differs from the Tettigomyiini in the forewings being significantly longer than the body, the lack of an inflated male abdomen, the deeply reflexed epipleurites, the lack of an extended distal shoulder to the pygofer, the well-developed pygofer upper lobes, the presence of a dorsal beak, and the extended uncus widening at the apex. Finally, the *Hovanini n. tribe* differs from the Ydiellini Boulard, 1973 in the presence of timbals, the lack of thickened forewing veins adjoining the apical and ulnar cells, the lack of large ulnar cells in the forewings, and the lack of a row of teeth on the hindwing costa.

### ***Comments***

Malagasiini appears to be the most closely related tribe based on the similarities in characters that distinguish both Malagasiini and *Hovanini n. tribe* from the other Tettigomyiinae tribes. Both tribes are found in Madagascar but differ in the diagnostic characters as outlined above.

The presence of the reticulated distal forewings in *Hovana* and *Hemidictya* alone does not warrant their classification in the same tribe. There are other cicada genera that possess reticulated, many-celled forewings that are not classified in the same tribes. For example, in the Cicadinae, *Talainga* Distant, 1890a and *Paratalainga* He, 1984 are in Gaeanini Distant, 1905c, whereas *Angamiana* Distant, 1890b and *Polyneura* Westwood, 1840 are in Polyneurini Amyot & Audinet-Serville, 1843. Note that the genitalia of these two pairs of genera are much more similar to each other than the genitalia of *Hovana* and *Hemidictya* are to each other. The differences in the forewing morphology of *Hovana* and *Hemidictya* are distinctive and suggest that these genera evolved the leaf-like appearance of their forewings through convergence rather than from a common ancestor. Boulard (2000) recognised this when he described the leaf-like appearance of the forewings of *Hemidictya*, *Hovana*, *Lacetas*, and *Cystosoma* Westwood, 1842

as parallel evolution from independent ancestors rather than being derived from a similar ancestor as proposed by Ruschel & Campos (2019). Leaf mimicry is common in insects being found in a number of diverse clades and dates back at least to the Permian (Garrouste *et al.* 2016). The structure of the genitalia alone suggests that *Hovana* should be classified in a different tribe and subfamily from *Hemidictya*, a view supported by the number of significant morphological differences outlined above.



**FIGURE 7.** Lateral view of pygofer (A) and dissected aedeagus (B) of *Hovana distante* (MNHN). (bl) basal lobe; (db) dorsal beak; (un) uncus; (upl) upper pygofer lobe.

## Redefinition of Hemidictyini

Because of the reassignment of all genera except *Hemidictya* to other tribes, the diagnosis of Hemidictyini proposed by Ruschel & Campos (2019) can be simplified.

### Tribe Hemidictyini *sensu novo*

Type genus *Hemidictya* Burmeister 1835: 178.

#### Diagnosis

Head including eyes narrow, much less than width across lateral pronotal angles; supra-antennal plates extending half the distance to eye; lateral ocelli widely spaced, the distance between the lateral ocelli being greater than between each lateral to the median; postclypeus dorsal length at least as long as dorsal vertex, postclypeus apex rounded in lateral view, rounded in transverse cross section below head. Pronotum with median groove; pronotal collar with paranota weakly developed; mid lateral tooth absent. Mesonotum and metanotum lacking auxiliary sound-producing structures; scutellum distally extended as a long triangular lobe. Opercula small, not covering the tympanal cavity and not completely surrounding meracanthus; meracanthus triangular or nearly so. Foreleg femoral primary spine prostrate. Forewing costal vein equal in width and widely separated from vein R+Sc; CuP and 1A unfused. Hind wing anal lobe narrow with anal vein 3 straight, cubital cell 1 width at distal end not twice or more the width of cubital cell 2; RP and M fused at base. Male abdominal tergites with sides convex in cross section; tergites 2 and 3 each wider than each of tergites 4–7; epipleurites obtusely reflexed to ventral surface. Timbals extended below level of wing bases; timbal covers absent, partially formed ridge on dorsal and ventral posterior timbal cavity. Pygofer dorsal beak absent; distal shoulder undeveloped; upper lobe absent; basal lobe moderately developed. Uncus large, deeply divided, not retractable within pygofer, bent almost at right angle at about 1/3rd its length from base; claspers absent. Aedeagus with theca simple; vesica retractable; conjunctival claws and pseudoparameres absent. Basal plate short, gently upturned apically, not deeply divided basally; rigidly attached to theca, ventral rib ill-defined and fused with surface of basal plate.

#### Distinguishing features

Differs from all other tribes in having, in combination, the metanotum being covered on the dorsal midline, the multiple reticulations of the forewing, forewing veins CuP and 1A unfused, the pygofer upper lobe absent, and a long non-retractable uncus that is significantly bent posteriorly at about 1/3rd its length from the base.

Hemidictyini can be distinguished from the Chilecicadini by the pronotum lacking parallel sides, the meracanthus not nearly as wide as the operculum, the lack of a broadening on abdominal tergite 2 posterior to the timbal cavity, male abdominal sternite VIII reaching beyond the base of the uncus, the pygofer basal lobe not reaching to the level of the uncus, and the divided uncus bent posteriorly at an approximate right angle. Hemidictyini can be distinguished from the Platypediini by the presence of timbals, the lack of thickened forewing veins for sound production, and the deeply divided, bent uncus. Hemidictyini differs from the Selymbriini in the head that is much narrower than the lateral pronotal collar angles, the straight hind wing anal vein 3, the lack of a complete turned-back rim on the timbal cavity, the lack of a well-developed dorsal beak, and the divided uncus that is bent at an approximate right angle. Hemidictyini differs from the Tettigadini in the head being not as wide as the mesonotum, the lack of dilated pronotal margins, the lack of a mesonotal stridulatory apparatus, and the lack of a coiled aedeagus. Hemidictyini differs from the Tibicinini in the lack of a broadening of abdominal tergite 2 posterior to the timbal cavity, lack of a cylindrical abdomen, the lack of mesonotal accessory sound producing apparatus, and the divided uncus bent at an approximate right angle. Finally, Hemidictyini can be distinguished from Sapantangini **n. tribe** by the supra-antennal plates extending only half the distance to the eye, the dorsally concealed metanotum, and the deeply divided uncus.

## Comments

In the tribal diagnosis we have refrained from including some characters used by Ruschel & Campos (2019) in defining their Hemidictyini, ones that we consider generic characters that show relationships *within* tribes rather than defining tribes. For example, the number of forewing apical cells, orientation of ulnar cell 3 and development of wing margins, are all characters whose states change readily within tribes, as shown in the cladograms of Moulds (2005) and Ruschel & Campos (2019). We believe that the distinctive forewings and the remarkable elongation of the scutellum in *Hemidictya* and *Hovana* are a consequence of generic divergence, similar to that found in the Chlorocystini, that includes both "leaf-wing" genera and more typical genera, as shown in the phylogenetic analyses of Boer (1995), Moulds (2005), Marshall *et al.* (2018) and Ruschel & Campos (2019).

## CONCLUSIONS

We have shown that tribe Hemidictyini as recently redefined by Ruschel & Campos (2019) includes genera from multiple tribes and subfamilies. Our phylogenetic analyses based on both morphological and molecular data suggest that the subjects of this study illustrate convergence in morphology rather than a common evolutionary history. The reorganization proposed here may solve certain problems described by Ruschel & Campos (2019) in the biogeography of their proposed groupings. Our reanalysis of the Ruschel & Campos data groups the species into geographically similar taxa, reducing the number of tribes found on multiple continents. We suggest that a thorough reanalysis of biogeography in light of our results is needed, including the addition of a significantly more diverse morphological data set and many more genera from additional cicada subfamilies and tribes.

Much work remains to be done to strengthen the classification of the taxa discussed here. Genetic evidence to further test the proposed assignments of *Sapantanga* and *Hovana* would be especially desirable. Furthermore, systematic morphological analysis of the Cicadidae as a whole, including investigation into the evolution of the development of the claspers in the Dundubiini Distant, 1905a, is needed to obtain more robust character sets for identifying tribe and subfamily level taxa (see also Marshall *et al.* 2018). Moulds' (2005) study lacked many genera from Africa and South America, where new deep lineages have been identified based on genetic data. The accumulation of newly discovered lineages such as *Derotettix* and *Hemidictya* near the base of the family may necessitate new subfamilies or redefinitions of existing ones. New family level morphological analyses should strive to apply all characters that have so far proven useful at tribe and subfamily level and test them further.

The revised classification that we propose for the taxa included in Hemidictyini *sensu* Ruschel & Campos, 2019 is summarized as follows.

Subfamily Tibicininae Distant, 1905b

Tribe Hemidictyini Distant, 1905g *sensu novo*

*Hemidictya* Burmeister, 1835

Tribe Sapantangini Sanborn, Moulds, and Marshall, **n. tribe**

*Sapantanga* Distant, 1905g

Subfamily Tettigomyiinae Distant, 1905g

Tribe Iruanini Boulard, 1993 **rev. stat.**

Lacetasini Moulds & Marshall, 2018 **n. syn.**

Subtribe Iruanina Boulard, 1993

*Iruana* Distant, 1905g

*Lacetas* Karsch, 1890

Subtribe Bafutalnina Boulard, 1993

*Bafutalna* Boulard, 1993

*Murphyalna* Boulard, 2012

Tribe Hovanini Sanborn, Marshall & Moulds, **n. tribe**

*Hovana* Distant, 1905g

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