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Taxonomic review, morphometry, and phylogenetic analysis of *Mahanarva* (*Ipiranga*) Fennah, 1968 (Hemiptera: Auchenorrhyncha: Cercopidae)

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Abstract

Mahanarva (*Ipiranga*) Fennah, 1968, currently comprises nine described species. The subgenus is characterized by an inflated postclypeus with a convex profile, longer than wide tegmina, and male genitalia with a short, laterally compressed aedeagus with a pair of slender dorsal processes. In this study, a phylogenetic hypothesis based on morphological data is presented to test the monophyly of *Mahanarva* (*Ipiranga*) and infer the relationship between its species. We present the redescriptions of its species and the description of two new species, *Mahanarva* (*Ipiranga*) *obliqua* **sp. nov.** and *Mahanarva* (*Ipiranga*) *nefasta* **sp. nov.**, along with a dichotomous key for identification. Moreover we synonymized *M.* (*I.*) *vittata* and *M.* (*I.*) *fortunata* based on morphological characters and a principal component analysis. The PCA results suggested no differences on the morphospace between these species; however, cluster analysis resulted in three groups. These groups don't show a geographic pattern structure or stable genitalic morphological differences. For phylogenetic analyses, a data matrix with 30 taxa and 56 characters was constructed. Based on the results of phylogenetic analyses, *Mahanarva* (*Ipiranga*) is recovered as paraphyletic and grouped with *Mahanarva* (*Mahanarva*) + *Kanaima*.

Keywords

Linear morphometry, morphological characters, Neotropical, new synonym, new taxa, spittlebugs, systematics

1. Introduction

The cercopids belonging to *Mahanarva* Distant, 1909 comprise over 45 species distributed in the Neotropical region (Paladini and Cavichioli 2014). Through their constant sap feeding, some *Mahanarva* species are known for causing severe crop damage, significantly reducing quality and productivity in cultivars such as sugarcane and pastures (Carvalho and Webb 2005; Valério 2009; Congio et al. 2020). Some of the diagnostic features of

the genus are: robust and subtriangular head; inflated and slightly compressed postclypeus forming an obtuse angle; the rostrum reaching the mesocoxa; and slightly robust legs (Distant 1909). Fennah (1968) synonymized *Luederwaldtia* Schmidt, 1922, *Funkhouseria* Lallemand, 1938, and *Delassor* Fennah, 1948 with *Mahanarva*. In the same study, Fennah proposed the division of *Mahanarva* into two subgenera: *Mahanarva* (sensu stricto) and *Mahanarva* (*Ipiranga*), mainly due to the difference in proportion between the length and width of the tegmina. Both subgenera belong to the tribe Tomaspidini. The type species of the subgenus *Ipiranga*, originally designated by Fennah (1968), is *Monecphora rubicunda* Walker, 1851. According to Fennah (1968), the main diagnostic characters of the subgenus are: a) inflated postclypeus, slightly convex in profile; b) the rostrum not reaching the mesocoxa; c) longer than wide tegmina; d) long subgenital plates; e) and short and tubular aedeagus, laterally compressed with a pair of processes. In that work, Fennah placed *Mahanarva* (*Ipiranga*) *aguirrei* (Berg, 1879) and *Mahanarva* (*Ipiranga*) *moreirae* (Lallemand, 1924) within the subgenus, along with the type species.

Currently, the subgenus comprises nine species: *M.* (*I.*) *rubicunda* (Walker, 1851), *M.* (*I.*) *vittata* (Walker, 1851), *M.* (*I.*) *indentata* (Walker, 1858), *M.* (*I.*) *integra* (Walker, 1858), *M.* (*I.*) *aguirrei*, *M.* (*I.*) *rubripennis* (Schmidt, 1922), *M.* (*I.*) *fortunata* (Lallemand, 1924), *M.* (*I.*) *bahiaensis* Carvalho & Webb, 2004, and *M.* (*I.*) *takiyae* Paladini and Cavichioli, 2014. The taxonomic history of *M.* (*I.*) *vittata* and *M.* (*I.*) *fortunata* indicates that the distinction between these species has been controversial. Fennah (1979), in addition to his 1968 review, synonymized *Monecphora vittata* with *Monecphora fortunata* and included this species in the genus *Kanaima* Distant, 1909. Carvalho and Webb (2005) revalidated the status of *Kanaima fortunata* (Lallemand, 1924). Paladini and Carvalho (2008) transferred both species to *M.* (*Ipiranga*).

Species descriptions are generally based on accurate observations of the organism morphology, and in many cases, the differences or similarities between them are clear enough to determine their identification (Mutanen and Pretorius 2007; Rasoarimalala et al. 2024). However, finding clear differences between entities is not always possible, and in such cases, morphometric analysis can help to make taxonomic decisions (Marcus 1990; Rasoarimalala et al. 2024). Linear morphometrics typically involves measurements such as length, width, and angles of structures (Rohlf and Marcus 1993), and has been used to distinguish many insect species within Hemiptera (Dietrich et al. 1991; Poswal et al. 1992), Diptera (Perre et al. 2014), Hymenoptera (Csősz and Fisher 2016; Rasoarimalala et al. 2024), and Lepidoptera (Prieto et al. 2009).

Recent phylogenetic studies using morphological data (Paladini et al. 2008; Paladini et al. 2015) and molecular data (Paladini et al. 2018) sampling all Neotropical genera of Cercopidae recovered *M.* (*Ipiranga*) as a monophyletic group and *M.* (*Mahanarva*) as paraphyletic. Based on the results from molecular data, the genera *Carpentiera* Lallemand, 1954, and *Kanaima* are nested within *Mahanarva* (*Mahanarva*). On the other hand, the morphology-based results recovered *Urubaxia tricolor* (Distant 1909) and *Mahanarva cruxminor* (Fowler 1896) as the sister group to *Mahanarva* (sensu lato). The taxon sampling in both published studies (Paladini et al. 2015; Paladini et al. 2018) is not equivalent to the current work, as the analysis were conducted at the tribe level, and not all *Mahanarva* species were included.

In this work, the species belonging to *Mahanarva* (*Ipiranga*) Fennah, 1968 are redescribed and illustrated, including the description of two new species and a dichotomous identification key. Besides, a phylogenetic analysis based on morphological data was performed to test the monophyly of the genus and to infer the relationship between its species. We also performed multivariate analyses, including three Cluster Analyses (CA) and Principal Component Analyses (PCA), in an attempt to discriminate between *M.* (*I.*) *fortunata* and *M.* (*I.*) *vittata*.

2. Material and Methods

2.1. Taxonomy

Specimens examined are deposited in the following institutions: Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCTP) and Coleção Pe. Jesus Santiago Moure, Departamento de Zoologia da Universidade Federal do Paraná (DZUP). We analyzed 739 specimens: 671 referring to *M.* (*Ipiranga*) and 68 to outgroups. The morphological study, including male and female genitalia, was carried out through the examination of specimens using a stereoscopic microscope. Preparation of genitalia structures follows the protocol proposed by Oman (1949). Measurements were given in millimeters and were taken using a Zeiss Stereo Discovery V8 stereomicroscope coupled to a Zeiss Stereo CL 1500 ECO camera. Seven measurements (total length, head width, head length, tegmina width, tegmina length, pronotum width and pronotum length) were taken and correspond to the average of ten specimens (five males and five females). Specimens and genitalia were photographed with Leica DMC2900 digital camara coupled to a Leica M205A stereomicroscope. Line drawings were made over photographs taken under light microscopy and double-checked by comparison with specimens.

2.2. Multivariate analyses

We examined 95 specimens from numerous localities in Brazil (see Table S1): *M.* (*I.*) *vittata* (63 males); four specimens of *M.* (*I.*) *fortunata* (4 males) and 28 females that cannot be identified because both species are externally identical and the females genitalia morphology is homogeneous. The specimens are deposited in DZUP and identified following Carvalho & Webb (2005) and Paladini et al. (2015) also with personal criteria according to the genitalia morphology. We evaluated a total of seven

measurements (see Table S1): head width, head length, tegmina width, tegmina length, total length, pronotum length, pronotum width. These measurements have been commonly used in other studies of Cercopidae taxonomy (Paladini and Carvalho 2008; Carvalho and Paladini 2017; Paladini and Cavichioli 2017; Schöbel et al. 2022).

Three Cluster Analyses (CA) and principal component analyses (PCA) were carried out. The first analysis was performed using male and female specimens in the same data matrix in order to evaluate differences between sexes according to morphological variables, the second analysis was performed using males, and the third analysis using females. Cluster analyses were performed using the same data matrix in order to classify morphology differences. All variables were transformed into log base 10. An Euclidean distance matrix was created and the Ward's linkage method was used to create the cluster analyses. The data was tested for normality, and statistical differences were evaluated between sexes and between suggested clusters with a multivariate Permutation Analysis of Variance (PERMANOVA).

2.3. Phylogenetic analyses

For phylogenetic analysis, a matrix based on morphological characters was constructed using Winclada v1.00.08 software (Nixon 2002) and the analysis were performed with TNT v1.5 (Goloboff and Catalano 2016). The characters construction was based on Sereno (2007). All species of *Mahanarva* (*Ipiranga*) were included in the analysis, except for *M.* (*I.*) *bahiaensis*, due to the lack of specimens in the referred collections. This species is known only by its holotype which is deposited in the Natural History Museum (London). The outgroup was composed of 22 species of the following genera: *Mahanarva* (*Mahanarva*), *Kanaima*, *Sphenorhina* Amyot & Serville, 1843, *Catrimania* Fennah, 1968, *Neosphenorhina* Distant, 1909, *Deois* Fennah, 1949, *Ferorhinella* Carvalho & Webb, 2004, and *Monecphora* Amyot & Serville, 1843. The topologies were rooted in *Neosphenorhina ocellata* (Walker, 1851). The characters used in this analysis were taken from Paladini et al. (2008) and 22 new characters were proposed based on descriptions, reviews, and our observations: seven of general morphology and 15 related to male genitalia. The characters were treated as unordered following Fitch's parsimony (Fitch 1971). Inapplicable and missing or unobservable character states were scored with "–" and "?", respectively; polymorphic characters are represented by "*". Tree search strategy was Exhaustive-search (Implicit enumeration) or Heuristic search (1000–10.000 replications) with TBR algorithm. Analyzes were performed attributing both equal weights and implied weights to the characters. In the implied weights scheme, Implied_w.run script with intervals of K1–K20 was used to determine the most stable concavities interval for the data matrix (Mirande 2009). Three metrics were used for comparing cladograms: SPR distance (Goloboff 2008), Farris' distortion coefficient (Farris 1989) and Robinson-Foulds index (Robinson and Foulds 1981), all calculated with TNT software. For each unambiguous character that was optimized in the most parsimonious tree, we indicated: number of steps, consistency index (CI) and retention index (RI) using Winclada software and character fit was provided using TNT software. Branch support was calculated using Bootstrap and Bremer (Felsenstein 1985, Bremer 1994). In Bootstrap, 1000 replicates were performed with the TBR algorithm, with absolute frequencies and collapsing groups below one. Relative Bremer support (Goloboff and Farris 2001) was calculated to implied weights using TBR algorithm, retaining suboptimal trees from one to nine extra steps and a relative fit difference varying from 0.9 to 0.1. The notation "group +" (Amorim 1982) was used in the results and in the discussion.

3. Results

3.1. Multivariate analysis

We found significative statistical differences between the male clusters and between the female clusters ($P < 0.05$). The "cluster" factor has three levels (Cluster 1, blue; Cluster 2, yellow; Cluster 3, grey), and the "Sex" factor has two levels (male and female). We choose to consider three clusters because most of the males of *M.* (*I.*) *fortunata* were grouped in one of the clusters (yellow).

The PCA for females (see Fig. S3A) plotting the first against the second principal component did not discriminate apparent groups, with eigenvalues of PC1 by 4.40 (accounting for 62.94% variability) and PC2 by 0.95 (accounting for 13.7% variability). The PCA for males and females (see Fig. S3B) also didn't discriminate groups, with eigenvalues of PC1 by 3.99 (accounting for 57% variability) and PC2 by 0.96 (accounting for 13.8% variability). A clear morphological distinction between females of both species is impossible due to a great similarity in color pattern and external morphology, for this reason in all statistical analysis females were treated as potential candidates of being *M.* (*I.*) *fortunata* or *M.* (*I.*) *vittata*. The PCA for males (Fig. 1) did not discriminate groups with eigenvalues of PC1 by 4.40 (accounting for 56.9% variability) and PC2 by 0.95 (accounting for 13.7% variability). None of the cluster analyses showed a geographic pattern structure (see Figs 2, S1 and S2).

Only four specimens have been primary identified as *M.* (*I.*) *fortunata* (Fig. 2, specimens 251, 569, 570, 571 indicated by red squares); however, with an accurate study of the male genitalia, we found that other specimens exhibit intermediate morphological variations from both species (Fig. 3 [65–A, 253–B, 558–B]). Although we found a statistical difference between the male clusters, these differences are not reflected in the male genitalia. For that reason, we have made the decision to propose a new synonymy for *M.* (*I.*) *fortunata* and *M.* (*I.*) *vittata*, asserting that the variation observed in the male genitalia represents an intra-specific variation without population structure.

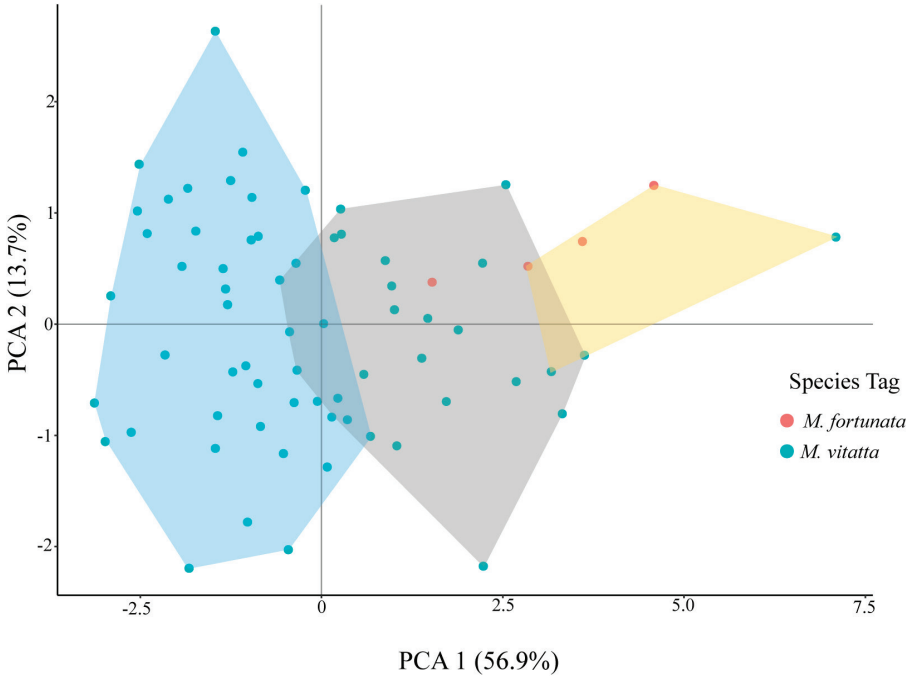

Figure 1. Plot of the PCA and Cluster analyses of males of *M.* (*I.*) *fortunata* **syn. nov.** and *M.* (*I.*) *vittata* based on linear morphometric characters.

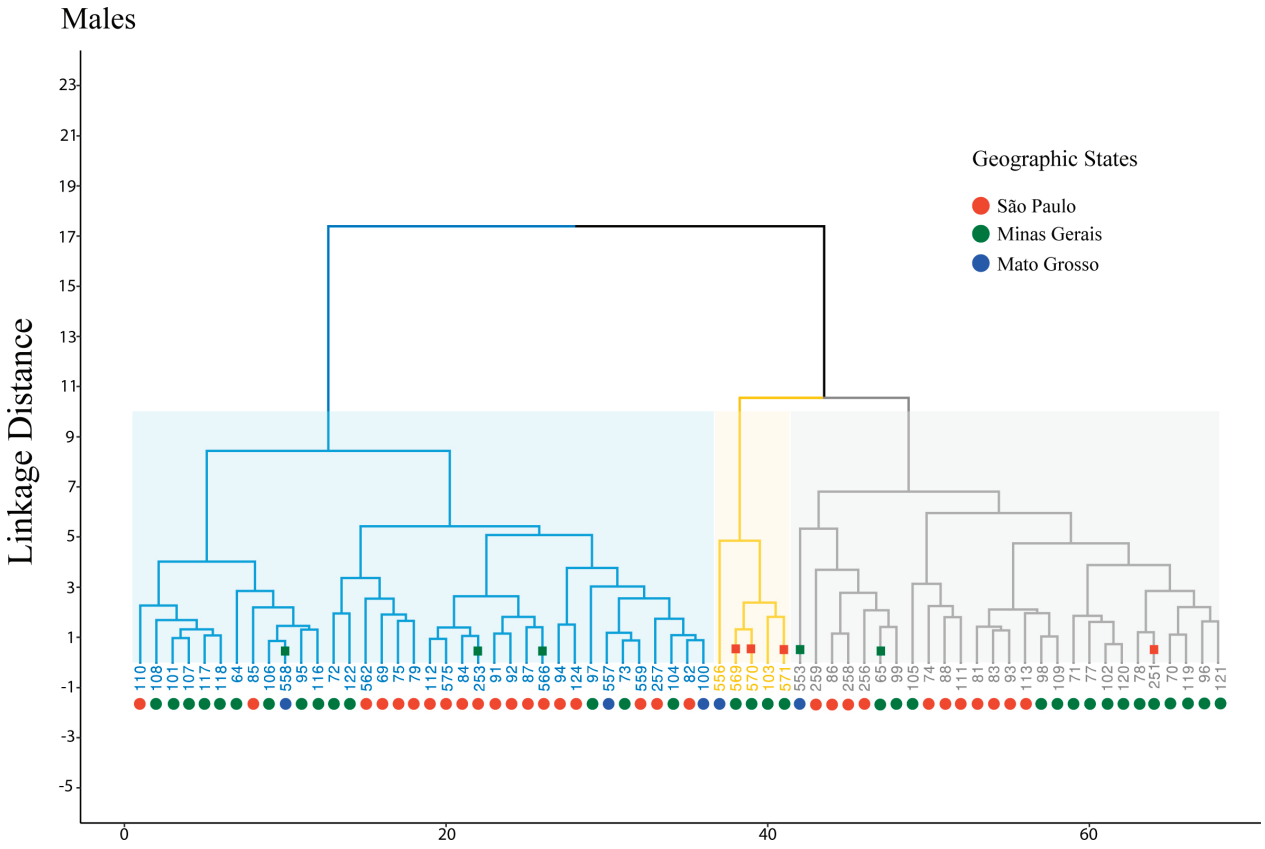

Figure 2. Cluster analyses of males of *M.* (*I.*) *fortunata* **syn. nov.** and *M.* (*I.*) *vittata* based on linear morphometry. Red squares above branches represent specimens identified as *M. fortunata* **syn. nov.** or with intermediate genitalic characters. Green squares above branches represent specimens with intermediate characters.

3.2. Phylogenetic characters

The phylogenetic matrix includes 56 characters (51 binaries and 5 multistate), with 30 taxa (see table S2). The number of steps, consistency index (CI) and retention index (RI) of each character were obtained from the implicit weight tree (K = 3.153) using Implied_w.run script (Fig. 4). Comments of each characters are presented when necessary and the illustration of some characters is presented in Figure 5.

Figure 3. *Mahanarva* (*I.*) *fortunata* **syn. nov.** and *M.* (*I.*) *vittata* male genitalia from the same specimens utilized in the PCA and Cluster analyses, see the unique number. **A** aedeagus, **B** paramere, **C** subgenital plate.

Head:

1 Tylus, median carina: **(0)** with (Fig. 5C); **(1)** without (Fig. 5B). L = 4, CI = 25, RI = 70, F = 0.49

2 Vertex, median carina: **(0)** with (Fig. 5C); **(1)** without (Fig. 5B). L = 4, CI = 25, RI = 70, F = 0.49

3 Ocelli, position relative to the imaginary line passes between the eyes: **(0)** in front of; **(1)** in the middle

(Fig. 5E); **(2)** back (Fig. 5D). L = 7, CI = 28, RI = 61, F = 0.61. New proposed character

4 Tylus, height relative to the head: **(0)** higher (Fig. 5A); **(1)** on the same level (Fig. 5B, C). L = 1, CI = 100, RI = 100, F = 0. New proposed character

5 Tylus, shape in dorsal view: **(0)** quadrangular (Fig. 5B, C); **(1)** rectangular (Fig. 5A). L = 7, CI = 14, RI = 53, F = 0.66. New proposed character

6 Antennae, shape of the basal body of flagellum**: (0)** conical (fig. 2b in Paladini et al. 2008); **(1)** subcylindrical (figs 1a, 3b in Paladini et al. 2008). L = 0, CI = Uninformative, RI = Uninformative, F = Uninformative

7 Antennae, length of arista relative to pedicel: **(0)** shorter; **(1)** longer. L = 1, CI = 100, RI = 100, F = 0

8 Postclypeus, shape in ventral view: **(0)** compressed (fig. 28a in Paladini et al. 2008); **(1)** inflated (fig. 27a in Paladini et al. 2008). L = 1, CI = 100, RI = 100, F = 0

9 Postclypeus, shape of profile: **(0)** angled (Fig. 5K); **(1)** convex (Fig. 5J). L = 2, CI = 50, RI = 88, F = 0.24

10 Postclypeus, depth of horizontal ridges: **(0)** weakly marked (Fig. 5F); **(1)** strongly marked (Fig. 5G). L = 3, CI = 33, RI = 83, F = 0.39

11 Postclypeus, longitudinal carina: **(0)** strongly marked (Fig. 5F); **(1)** slightly marked (Fig. 5G). L = 1, CI = Uninformative, RI = Uninformative, F = Uninformative. This character was modified from that proposed by Paladini et al. (2008).

12 Postclypeus, triangle formed in apex with tylus: **(0)** prominent (Fig. 5H, I); **(1)** absent. L = 5, CI = 20, RI = 33, F = 0.56. New proposed character

13 Rostrum, length relative to mesothoracic coxae: **(0)** reaching base of mesocoxae; **(1)** reaching middle of mesocoxae. L = 2, CI = 50, RI = 90, F = 0.24. This character was modified from that proposed by Paladini et al. (2008).

Thorax:

14 Pronotum, depth of concavities: **(0)** deep (Fig. 5D); **(1)** shallow (Fig. 5E). L = 4, CI = 25, RI = 66, F = 0.49. New proposed character

15 Pronotum, shape of anterior margin: **(0)** convex (Fig. 5D); **(1)** straight (Fig. 5E). L = 5, CI = 20, RI = 50, F = 0.56

16 Pronotum, shape of anterolateral margin: **(0)** straight (Fig. 5E); **(1)** convex (Fig. 5D). L = 6, CI = 16, RI = 50, F = 0.61

17 Pronotum, shape of the humeral angles: **(0)** acute (Fig. 5E); **(1)** rounded. L = 5, CI = 20, RI = 60, F = 0.56

18 Tegmina**,** pattern: **(0)** with bands (Figs 9A, 12A); **(1)** with spots (Fig. 6G); **(2)** with band and spots (Fig. 13A, B). L = 10, CI = 20, RI = 38, F = 0.72. New proposed character

19 Tegmina, ratio of length/width: **(0)** narrow; **(1)** wide. L = 6, CI = 16, RI = 54, F = 0,61. The proportion of the length and width (L/W) of the tegmina is classified as follows: narrow tegmina (L/W = >3,0) and wide tegmina (L/W = < 2,9) (Fennah 1968).

20 Tegmina, venation: **(0)** barely visible; **(1)** prominent. L = 4, CI = 25, RI = 62, F = 0.49. This character was modified from that proposed by Paladini et al. (2008).

21 Tegmina, vein A_2: **(0)** indistinct; **(1)** distinct. L = 3, CI = 33, RI = 85, F = 0.39. This character was modified from that proposed by Paladini et al. (2008).

22 Tegmina, condition of the apical plexus: **(0)** reduced; **(1)** developed. L = 4, CI = 25, RI = 57, F = 0.49

23 Posterior leg, spine on inner face of femur: **(0)** inconspicuous; **(1)** conspicuous (Fig. 5L). L = 7, CI = 14, RI = 57, F = 0.66

24 Posterior leg, size of basal spine of tibia relative to those of apical crown: **(0)** similar to apicals; **(1)** smaller than apicals (Fig. 5L). L = 3, CI = 33, RI = 84, F = 0.39

25 Posterior leg, thickness of tibia: **(0)** robust; **(1)** slender (Fig. 5L). L = 1, CI = 100, RI = 100, F = 0. New proposed character

26 Posterior leg, number of rows of spines on the basitarsus: **(0)** one row; **(1)** three rows; **(2)** two rows. L = 6, CI = 33, RI = 71, F = 0.56

27 Posterior leg, density of setae on the basitarsus: **(0)** sparse, not obscuring spines; **(1)** dense, obscuring spines. L = 2, CI = 50, RI = 90, F = 0.24

28 Posterior leg, subungueal process: **(0)** absent; **(1)** present (figs 23a, 24a in Paladini et al. 2008). L = 1, CI = 100, RI = 100, F = 0

Male abdomen:

29 Pygofer, shape of process on lateral margin, between anal tube and subgenital plates: **(0)** acuminate (Fig. 5N); **(1)** digitiform (Fig. 5M). L = 1, CI = 100, RI = 100, F = 0

30 Subgenital plate, basal process on dorsal margin: **(0)** present (Fig. 5M, N); **(1)** absent. L = 6, CI = 16, RI = 61, F = 0.61. New proposed character

31 Subgenital plate, shape of basal process on dorsal margin: **(0)** long and acuminate (Fig. 5N); **(1)** short and rounded (Fig. 5M). L = 1, CI = 100, RI = 100, F = 0. New proposed character

32 Subgenital plate, apical denticles on dorsal margin: **(0)** absent; **(1)** present. L = 2, CI = 50, RI = 50, F = 0.24. New proposed character

33 Subgenital plate, dorsal elevation: **(0)** absent (Fig. 13D); **(1)** present (Figs 7H, 9D). L = 3, CI = 33, RI = 75, F = 0.39

34 Paramere, number of spines: **(0)** one (Fig. 5P, Q); **(1)** two (Fig. 5R). L = 4, CI = 25, RI = 40, F = 0.49

35 Paramere, position of spine: **(0)** apical (Fig. 5T); **(1)** subapical (Fig. 5P, Q). L = 4, CI = 25, RI = 40, F = 0.49

36 Paramere, insertion of spine: **(0)** external face (Fig. 5P, Q); **(1)** inner face (Fig. 5T). L = 1, CI = 100, RI = 100, F = 0. New proposed character

37 Paramere, shape of spine in lateral view: **(0)** hook like (Fig. 5Q–S); **(1)** laminate; **(2)** quadrangular (Fig. 5P). L = 2, CI = 100, RI = 100, F = 0. New proposed character

38 Paramere, condition of dorsal process: **(0)** developed (Fig. 5Q, R); **(1)** reduced (Fig. 5O). L = 4, CI = 25, RI = 66, F = 0.49

39 Paramere, shape of dorsal process: **(0)** rounded; **(1)** acuminate. L = 2, CI = 50, RI = 50, F = 0.24. New proposed character

40 Paramere, shape of apex: **(0)** short and rounded (Fig. 5R); **(1)** long and digitiform (Fig. 5S). L = 1, CI = 100, RI = 100, F = 0. New proposed character

41 Aedeagus, dorsal process: **(0)** absent (Fig. 5U); **(1)** present (Fig. 8J, K). L = 4, CI = 25, RI = 57, F = 0.49

42 Aedeagus, number of dorsal processes: **(0)** one; **(1)** a pair (Fig. 8J, K). L = 0, CI = Uninformative, RI = Uninformative, F = Uninformative. New proposed character

43 Aedeagus, position of dorsal processes: **(0)** apical third; **(1)** middle third. L = 1, CI = 100, RI = 100, F = 0. New proposed character

44 Aedeagus, shape of dorsal processes: **(0)** elongated; **(1)** spiniform. L = 1, CI = 100, RI = 100, F = 0. New proposed character

45 Aedeagus, apical shape of dorsal processes: **(0)** straight (figs 9a, 10a in Paladini et al. 2008); **(1)** curved (fig. 11a in Paladini et al. 2008). L = 1, CI = 100, RI = 100, F = 0

46 Aedeagus, ventral process: **(0)** absent; **(1)** present (Fig. 5U). L = 2, CI = 50, RI = 50, F = 0.24. New proposed character

47 Aedeagus, number of ventral processes: **(0)** one (Fig. 5U); **(1)** two. L = 0, CI = Uninformative, RI =

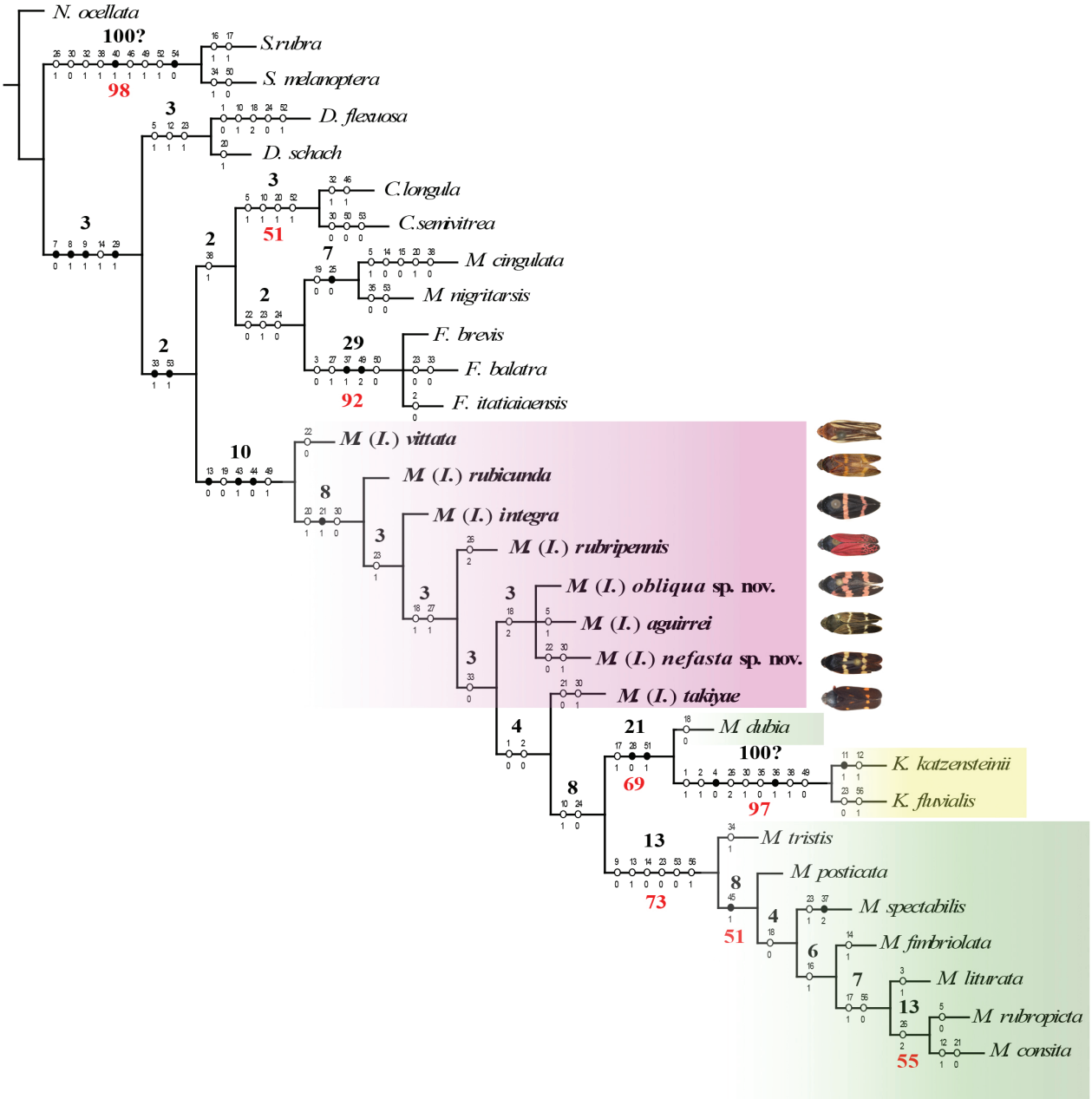

Figure 4. Topology resulting from implied weighting analysis of morphological data matrix using Implied_w.run script (k = 3.153). Bootstrap support is indicated below each branch (in red) and relative Bremer support is indicated above each branch (in black). White circles (○) indicate homoplastic transformations and black circles indicate (●) non-homoplastic transformations.

Uninformative, F = Uninformative. New proposed character

48 Aedeagus, apical shape of ventral processes: **(0)** acute (Fig. 5U); **(1)** rounded. L = 1, CI = Uninformative, RI = Uninformative, F = Uninformative. New proposed character

49 Aedeagus, shape of apex: **(0)** rounded; **(1)** truncate; **(2)** acuminate. L = 4, CI = 50, RI = 80, F = 0.39. This character was modified from that proposed by Paladini et al. (2008).

50 Aedeagus, apex: **(0)** bifid; **(1)** non bifid. L = 3, CI = 33, RI = 50, F = 0.39. New proposed character

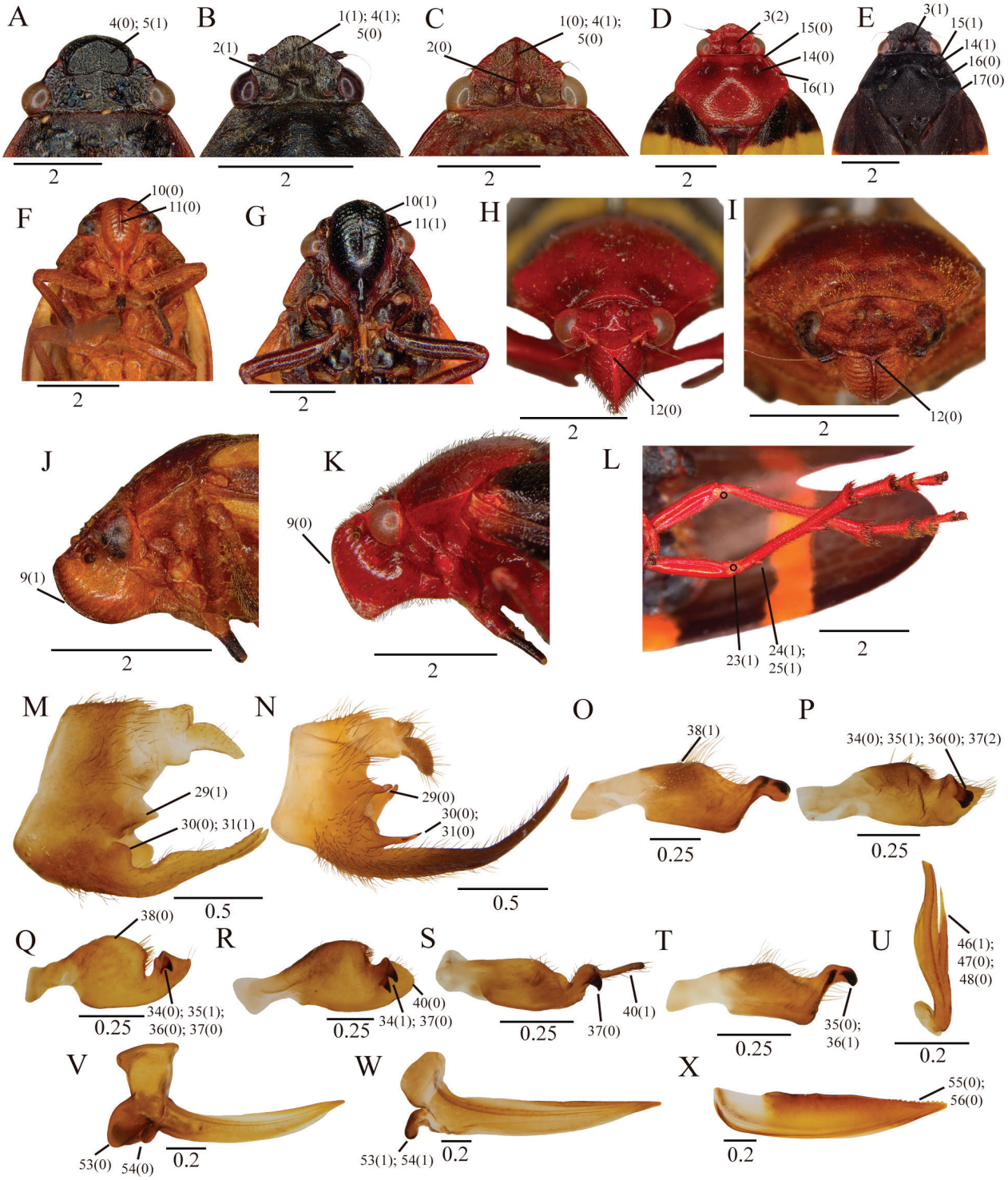

Figure 5. Illustration of characters. Head (dorsal view): **A** *K. katzensteinii*; **B** *M.* (*I.*) *rubripennis*; **C** *M.* (*M.*) *tristis*. Head and pronotum (dorsal view): **D** *S. rubra*; **E** *M.* (*I.*) *integra*. Head (ventral view): **F** *M.* (*I.*) *vittata*; **G** *K. katzensteinii*. Head (frontal view): **H** *S. rubra*; **I** *M.* (*I.*) *vittata*. Head (lateral view): **J** *M.* (*I.*) *vittata*; **K** *S. rubra*. Posterior legs: **L** *M.* (*I.*) *integra*. Male pygofer (lateral view): **M** *M.* (*I.*) *integra*; **N** *S. rubra*. Paramere (external lateral view): **O** *K. katzensteinii*; **P** *M.* (*M.*) *spectabilis*; **Q** *M.* (*I.*) *integra*; **R** *M.* (*M.*) *tristis*; **S** *S. rubra*. Paramere (inner lateral view): **T** *K. katzensteinii*. Aedeagus (lateral view): **U** *S. rubra*. First valvulae of ovipositor: **V** *S. rubra*; **W** *M.* (*I.*) *nefasta*. Second valvulae of ovipositor: **X** *M.* (*I.*) *rubripennis*. Scale bars in mm.

51 Aedeagus, size of the apex in lateral view: **(0)** not enlarged (fig. 11b in Paladini et al. 2008); **(1)** enlarged (figs 9b, 10b in Paladini et al. 2008). L = 1, CI = 100, RI = 100, F = 0

52 Aedeagus, denticles on the surface: **(0)** absent; **(1)** present. L = 3, CI = 33, RI = 50, F = 0.39. New proposed character

Female abdomen:

53 Ovipositor, condition of basal process of first valvulae: **(0)** developed (Fig. 5V); **(1)** reduced (Fig. 5W). L = 4, CI = 25, RI = 76, F = 0.49

54 Ovipositor, number of basal processes of first valvulae: **(0)** two (Fig. 5V); **(1)** one (Fig. 5W). L = 1, CI = 100, RI = 100, F = 0

55 Ovipositor, teeth on dorsal margin of second valvulae: **(0)** present (Fig. 5X); **(1)** absent. L = 4, CI = 25, RI = 50, F = 0.49

56 Ovipositor, position of teeth on dorsal margin of the second valvulae: **(0)** limited to third apical portion (Fig. 5X); **(1)** expanded beyond apical third. L = 5, CI = 20, RI = 50, F = 0.56

3.3. Phylogenetic analysis

For the analysis assigning equal weights to the characters, four most parsimonious trees with L = 170 were found. The strict consensus tree presented L = 183, CI = 32, and RI = 64 (see Fig. S4) with *Mahanarva* (*Ipiranga*) recovered as paraphyletic and grouped with *Mahanarva* (*Mahanarva*) + *Kanaima*. However, due to the low resolution presented (polytomy of the branches) we chose to discuss our results based on the implied weighting results.

In implied weighting analysis, proposed by Goloboff (1993), homoplastic characters receive lower weights and, therefore, have less influence on topology, resulting in trees with greater reliability. This approach has been used in phylogenies based on morphological data, providing trees with higher resolution and greater branch support (Goloboff 1995a, 1995b; Goloboff et al. 2008). Therefore, we chose to use this approach to support our discussion. In our analysis, the most stable concavity for the data matrix was given by the interval of K6–K11, with K values varying from 2.885 to 4.618 (see Tables S3, S4). All trees resulted by this range of K showed the same topology discussed and illustrated herein, with Total Fit = 16.802 (see Table S3), L = 172, CI = 34, and RI = 67 (Fig. 4). *Mahanarva* (*Ipiranga*) was recovered as paraphyletic and grouped with *Mahanarva* (*Mahanarva*) + *Kanaima* (low relative Bremer support: 10) sharing with these genera three synapomorphies (rostrum reaching base of mesocoxae (13_0), dorsal processes of aedeagus located on the middle third (43_1), and elongated shape of dorsal processes of aedeagus (44_0)), and two homoplasies: tegmina narrow (19_0) and apex of aedeagus truncate (49_1). The clade *M.* (*I.*) *obliqua* **sp. nov.** + *M.* (*I.*) *aguirrei* + *M.* (*I.*) *nefasta* **sp. nov.** (Low relative Bremer support: 3) is supported by one homoplasy: tegmina with band and spots (18_2). Just as in the results obtained through equal weighting, in the implied weighting analysis *Kanaima* was recovered nested within *Mahanarva* (*Mahanarva*), with *M.* (*M.*) *dubia* (Stancik & Cavichioli, 2003) closer related to *K. fluvialis* (Lallemand, 1924) + *K. katzensteinii* (Berg, 1879). *Mahanarva* (*Mahanarva*) + *Kanaima* is supported by two homoplasies: horizontal ridges on postclypeus strongly marked (10_1) and basal spine of tibia similar in size related to apical spines (24_0) although this relationship has low relative Bremer support (8).

3.4. Taxonomic review

3.4.1. *Mahanarva* Distant

Mahanarva Distant, 1909: 210. Metcalf 1961: 504; Fennah 1968: 185, 1979: 270 — Type species: *Mahanarva indicata* Distant (by original designation)

Luederwaldtia Schmidt, 1922: 262. Metcalf 1961: 539; Fennah 1968: 185 (syn.) — Type species: *Luederwaldtia rubripennis* Schmidt (by original designation)

Funkhouseria Lallemand, 1938: 146. Metcalf 1961: 132; Fennah 1968: 185 (syn.) — Type species: *Sphenorhina quadripunctata* Walker (by original designation)

Delassor Fennah, 1948: 611. Metcalf 1961: 166; Fennah 1968: 88 (syn.) — Type species: *Cercopis tristis* Fabricius (by original designation).

3.4.2. *Mahanarva* (*Ipiranga*) Fennah, 1968

Mahanarva (*Ipiranga*) Fennah, 1968: 186 — Type species: *Monecphora rubicunda* Walker (by original designation).

Redescription. Head subtriangular, vertex and tylus with slightly marked median carina, ocelli closer to each other than to eyes; antenna with pedicel sparsely setose, basal body of flagellum subcylindrical, with a single and short arista shorter than the pedicel length. Postclypeus inflated, with convex profile, longitudinal carina present, lateral grooves slightly marked; rostrum reaching the base of mesocoxae. Pronotum with poorly marked muscular insertions, anterior and anterolateral margin straight, humeral angles acute. Tegmina generally narrow with prominent venation (except in *M.* (*I.*) *vittata*), vein A2 distinct (except in *M.* (*I.*) *vittata*), apical reticulation developed (except in *M.* (*I.*) *vittata*); hindwings with Cu1 thickened at the base. Metathoracic femur with small apical spine, tibia with two lateral spines: basal one smaller than the ones located at the apical crown which has 10–14 spines arranged in two rows; basitarsus with two or three rows of spines; subungueal process present. — **MALE: Genitalia:** Pygofer with one finger-like/rounded process between anal tube and subgenital plate, subgenital plate with acute or rounded apex (*M.* (*I.*) *rubicunda, M.* (*I.*) *aguirrei* and *M.* (*I.*) *obliqua* **sp. nov**.); dorsal margin of paramere rounded or montain-shaped (some specimens of *M.* (*I.*) *vittata*), a subapical hook-like spine directed outwards; aedeagus subcylindrical, narrowing towards

apex, with a pair of dorsal processes shorter than half shaft length (except for some specimens of *M.* (*I.*) *vittata*, where the dorsal processes are almost the same size of half of shaft length) and inserted between medium and apical third. — **FEMALE: Genitalia:** First valvula of ovipositor with basal process undeveloped (except for *M.* (*I.*) *nefasta* **sp. nov.**). Second valvula with dorsal margin covered by teeth in apical third (*M.* (*I.*) *vittata* has inconspicuous teeth).

Remarks. Fennah (1968) emphasized that the subgenus distinguishes from *Mahanarva* primarily by the convex profile of the postclypeus, relatively narrow body shape, and the basal process of the first ovipositor valve being much less developed than in *Mahanarva*. Additionally, the rostrum reaches only the base of the mesocoxa in *Ipiranga* (Paladini and Cavichioli 2014).

Distribution. Brazil, Paraguay and Argentina.

3.4.3. Key to species of *Mahanarva* (*Ipiranga*)

1 Tegmina with transverse complete and/or incomplete bands (Fig. 6C, D) **2**
– Tegmina with other color pattern (Fig. 6B, E) **8**
2 Tegmina black generally with incomplete bands, forming four orange spot-like maculae (Fig. 6G) ..... ***M.* (*I.*) *takiyae***
– Tegmina with other color pattern **3**
3 Tegmina with two transverse yellowish bands (Fig. 6F); paramere with a sclerotized process located over spine ..... ***M.* (*I.*) *bahiaensis***
– Tegmina with transverse bands orangish or whitish (Figs 9A, 10A); paramere without a sclerotized process located over spine (Figs 7J, 9F) **4**
4 Subgenital plate with an excavation on the basal third (Figs 7H, 9D, 10D) **5**
– Subgenital plate without an excavation on basal third (Fig. 12D, 13D) **7**
5 General color brownish-black, transverse bands on tegmina narrow whitish and incomplete (Fig. 10A, B); paramere spine long and slender with an acute apex, apical portion of paramere subquadrangular (Fig. 10F) ..... ***M.* (*I.*) *aguirrei***
– General color brownish-black, transverse bands on tegmina orange, yellowish or whitish never incomplete (Figs 7A–F, 9A); paramere spine short, robust, apical portion of paramere not subquadrangular (Figs 7J, 9F) **6**
6 Tegmina with transverse bands orange, narrow and widely spaced (Fig. 7A–F); subgenital plate with a rounded apex (Fig. 7H); paramere with a finger-like apex (Fig. 7J) ..... ***M.* (*I.*) *rubicunda***
– Tegmina with transverse bands orange, wide and not widely spaced (Fig. 9A, B); subgenital plate with an acute apex (Fig. 9D); paramere without a finger-like apex (Fig. 9F) ..... ***M.* (*I.*) *integra***
7 Subgenital plate with a rounded apex (Fig. 12D); paramere apex subtriangular (Fig. 12F); female first valvulae of ovipositor with basal process undeveloped (Fig. 12K) ..... ***M.* (*I.*) *obliqua* sp. nov.**
– Subgenital plate with an acute apex (Fig. 13D); paramere apex rounded (Fig. 13F); female first valvulae of ovipositor with basal process developed (Fig. 13K) ..... ***M.* (*I.*) *nefasta* sp. nov.**
8 Tegmina with longitudinal brownish bands (Fig. 8A, B) ..... ***M.* (*I.*) *vittata***
– Tegmina red, with black, rounded spots on apical plexus of veins (Fig. 11A, B) ..... ***M.* (*I.*) *rubripennis***

3.4.4. *Mahanarva* (*Ipiranga*) *rubicunda* (Walker, 1851)

Figures 6A, 7A–P

Monecphora rubicunda Walker, 1851b: 678
Tomaspis rubicunda: Lallemand 1912a: 97
Delassor rubicundus: Fennah 1953: 350. Metcalf 1961: 168
Mahanarva (*Ipiranga*) *rubicunda*: Fennah 1968: 187; **comb. nov**.
Monecphora indentata Walker, 1858
Delassor rubicundus indentatus: Fennah 1953; Metcalf 1961;
Mahanarva (*Ipiranga*) *rubicunda indentatus*: Fennah 1968
Mahanarva (*Ipiranga*) *indentata* (Walker, 1858): Carvalho and Webb 2005 **stat. nov.**, **syn. nov.**

Measurements male/female. Head length: 1.14/1.314; head width: 2.21/2.42; pronotum length: 2.06/2.28; pronotum width: 3.39/3.75; tegmen length: 9.5/10.38; tegmen width: 2.875/3.1; total length: 11.575/12.68 (in mm).

Diagnosis. Tegmina brownish to black with two narrow transverse bands in orange shades, posterior band never fragmented into spots; paramere with a dorsal margin rounded and developed and with a finger-like apex.

Redescription. Head black, vertex subretangular with a slightly marked median carina, ocelli brownish, closer to each other than to eyes, separated by about one and a half diameter from each other; tylus quadrangular, black, basal third with slightly marked carina, becoming indistinct towards the apex (Fig. 7A–E); antenna brownish, pedicel sparsely setose; basal body of flagellum subcylindrical with a single and short arista shorter than the pedicel length. Postclypeus black, inflated, with convex profile, longitudinal carina present, lateral grooves slightly marked (Fig. 7F, G); rostrum with second segment reddish and third segment brownish, reaching the base of mesocoxae. Pronotum brownish, hexagonal, with muscular insertions slightly apparent, median carina slightly marked; anterior and anterolateral margin straight; pos-

terolateral with slight sinuosity and posterior margin medially grooved, humeral angles acute; scutellum black, with slight central concavity and slightly marked horizontal grooves. Tegmina (Fig. 7A–E) brownish, narrow, with two narrow transverse bands orange: one between basal and medium third and another between medium and apical third; veins M and Cu1 united at base, veins A1 and A2 distincts, apical reticulation developed, prominent venation. Hindwings hyaline, with brownish venation, Cu1 thickened at the base, hamuli with four spines. Legs reddish, metathoracic femur with a small apical spine; tibia with two lateral spines, basal one smaller than the ones located at apical crown, which has 12–13 spines arranged in two rows; basitarsus with three rows of spines covered by long setae; subungueal process present. — **MALE: Genitalia:** Pygofer (Fig. 7H) with one finger-like processes between anal tube and subgenital plate; subgenital plate (Fig. 7H, I) narrowing towards apex, which is rounded, dorsal margin with rounded elevation covered with small tooth-like spines; basal process of subgenital plate short and rounded followed by an excavation. Paramere (Fig. 7J) subretangular, with a finger-like apex, dorsal margin rounded and developed, and a subapical hook-like spine bearing small denticles in the inferior margin, directed outwards and forward. Aedeagus (Fig. 7K–M) subcylindrical, narrowing towards apex, with a pair of straight dorsal processes, shorter than half length of shaft and inserted medially. — **FEMALE:** Morphology similar to that of the male, but slightly larger in relation to total body length. First valvula of ovipositor long (Fig. 7N, O), with acute apex, basal process rounded and undeveloped, directed downwards; second valvula (Fig. 7P) long with rounded apex and dorsal margin covered by teeth in apical third; third valvula short and wide, covered apical and ventrally by long setae.

Remarks. *M.* (*I.*) *rubicunda* shows a high variation in the body color, ranging from black to light brown and the transverse bands on the tegmina can vary in shades of red, orange, yellow, and whitish (Fig. 7A–E). *M.* (*I.*) *rubicunda* and *M.* (*I.*) *indentata* are synonyms because there are small and not significant morphological varia-

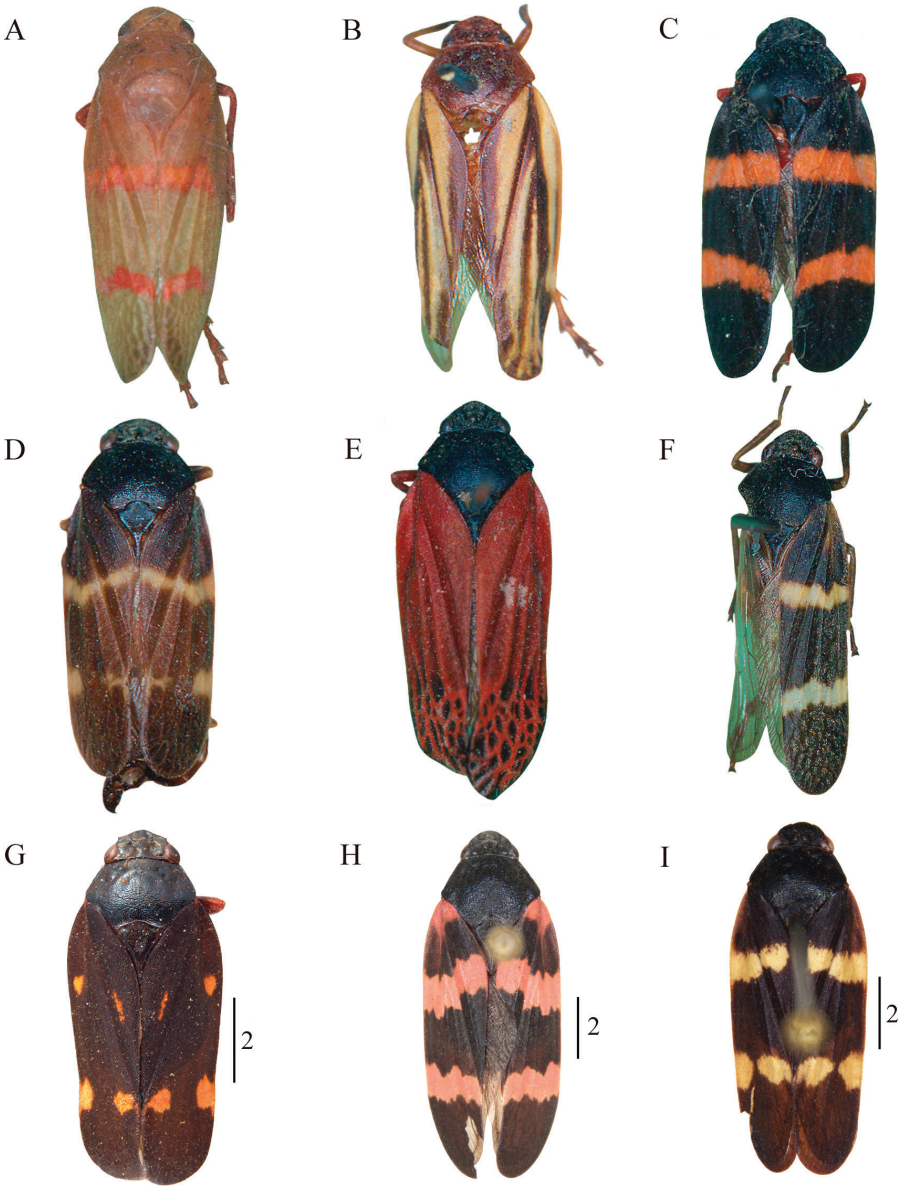

Figure 6. Holotypes of *M.* (*Ipiranga*) species. **A** *M.* (*I.*) *rubicunda*; **B** *M.* (*I.*) *vittata;* **C** *M.* (*I.*) *integra*; **D** *M.* (*I.*) *aguirrei*; **E** *M.* (*I.*) *rubripennis*; **F** *M.* (*I.*) *bahiaensis*; **G** *M.* (*I.*) *takiyae;* **H** *M.* (*I.*) *obliqua* **sp. nov.**; **I** *M.* (*I.*) *nefasta* **sp. nov.** Scale bars in mm.

tions between these species. Furthermore, Fennah (1953), while describing *Delassor*, mentions *M.* (*I.*) *indentata* as a subspecies of *Delassor rubicundus*, showing that the similarity between these two species was observed by the author. The wing pattern is also similar to that of *M.* (*I.*) *integra*; however, the bands are narrower and more widely spaced. Additionally, there are several differences in the male genitalia: the subgenital plate has a rounded apex, and the paramere has a digitiform-shaped apex in *M.* (*I.*) *rubicunda*, which is not observed in *M.* (*I.*) *integra*.

Distribution. Brazil (Goiás [new record], Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná and Rio Grande do Sul [new record]).

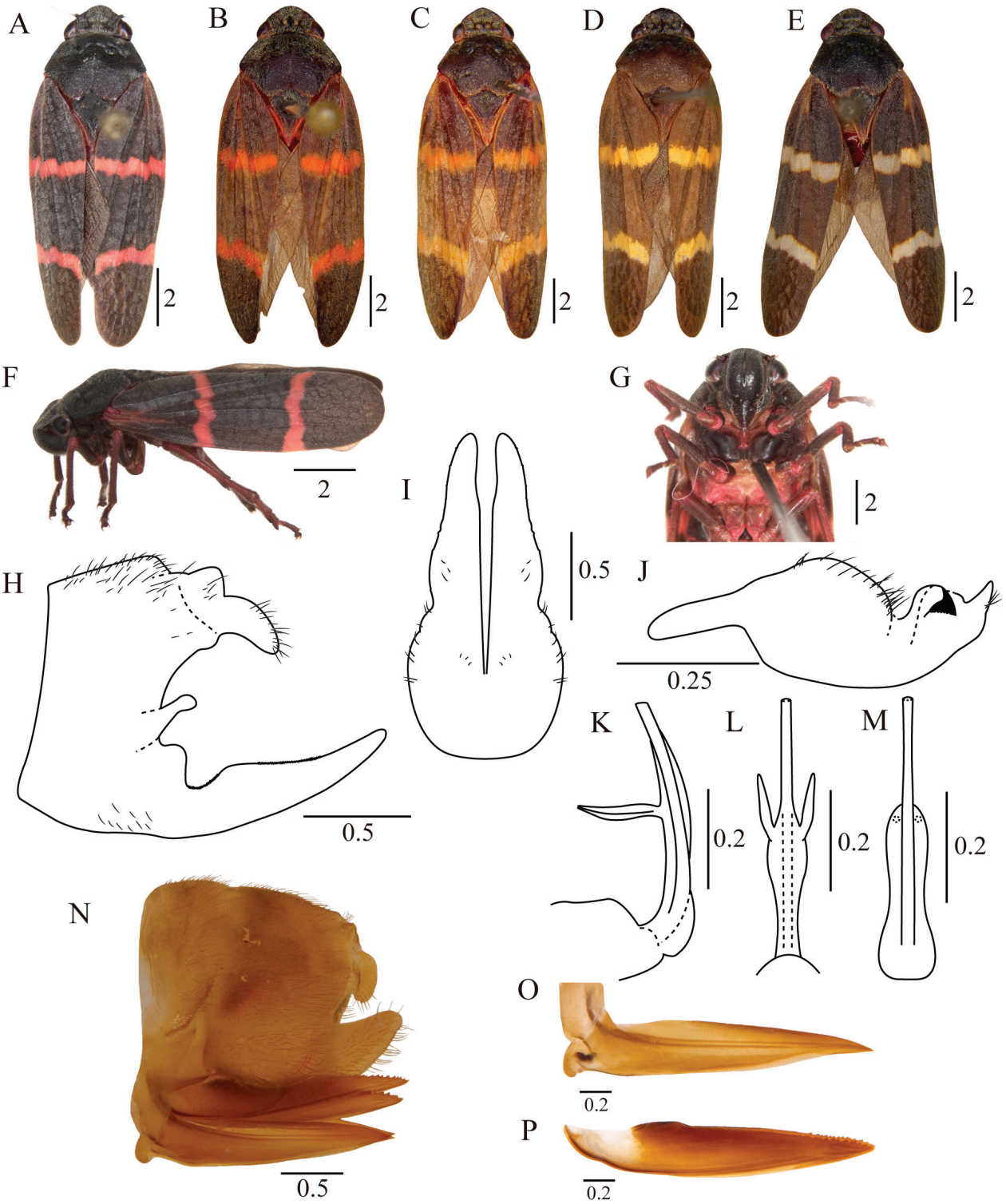

Figure 7. *Mahanarva* (*Ipiranga*) *rubicunda*. Habitus: **A–E** dorsal view; **F** lateral view; **G** ventral view. Male genitalia, pygofer: **H** lateral view; **I** ventral view. Paramere: **J** lateral view. Aedeagus: **K** lateral view; **L** dorsal view; **M** ventral view. Female genitalia, ovipositor: **N** lateral view. First valvulae: **O** lateral view. Second valvulae: **P** lateral view. Scale bars in mm.

Material examined. BRASIL, **Goiás:** Goiânia, vii.1976, D. Rodriguez leg., 1 ♂ (MCTP); **Minas Gerais:** Igarapé, 26.xii.1982, Koller, W.W. leg., 10 ♂, 12 ♀ (DZUP); idem: 31.xii.1981, Koller, W.W. leg., 2 ♂, 1 ♀ (DZUP); Marliéria, 19°45′43.7″S 42°37′52.3″W, 2–5.iii.2011, Pinto, A.P. & Silva, J.G. leg., 1 ♂ (MCTP); Oratórios, 20°25′5.3″S 42°47′27.8″W, 31.iii.2012, Silva, L. A. leg., 3 ♂, 3 ♀, 1 without genitalia (MCTP); Coronel Pacheco, 7.vi.2004, Anad, A. M. leg., 1 ♀, 1 without genitalia (MCTP); Astolfo Dutra, 28.vii.1974, G. S. Andrade col., 1 ♀ (MCTP), 5 ♀ (DZUP); **Espírito Santo:** Santa Teresa, 5.iv.1967, C.T. & C. Elias leg., 1 ♂ (MCTP); idem: 27.i.1966, C.T. & C. Elias leg., 1 ♂ (DZUP); Baixo Guandu, 23–30.ix.1970, C.& C.T.Elias leg., 1 ♂ (DZUP); **Rio de Janeiro:** Teresópolis, (no col. data), 1 ♀ (MCTP); (no location data), vii.1972, M. Alvarenga, 1 ♀ (DZUP); Silva Jardim, iii.1974, F. M. Oliveira leg., 1 ♂ (DZUP); **São Paulo:** Guanavora, xii.1972, M. Alvarenga leg., 1 ♂ (DZUP); **Paraná:** Adrianópolis, 09.i.2009, E. Domelles leg., 1 ♂, 2 ♀ (DZUP); Piraquara, Mananciais da Serra, 25°29′46″S 48°58′54″W, 18.xi.2009, R.R.Cavichioli & P.C. Grossi leg., 1 ♀ (DZUP); Curitiba, 25.iv.1976, E. Arias col., 1 ♂ (DZUP); Guaratuba, Est.dos Castelhanos, 25°48′45″S 48°54′56″W, ii.2007, E. Caron, J. A. Rafael & P. C. Grossi leg., 1 ♂ (DZUP); idem: 25°49′55″S 48°55′48″W, 25.xi.2009, (no col. data), 2 ♂ (DZUP); Morretes, 12.viii.1983, Cordoni, J. leg., 1 ♂ (DZUP); idem: 09.iv.1993, E.L.Tonetti col., 1 ♂ (DZUP); Caiobá, 15.x.1983, Mattana, leg., 1 ♀ (DZUP); **Rio Grande do Sul:** Candelária, 4.xi.1978, L.A.Grohe leg., 1 ♀ (MCTP); Torres, 11.x.1992, Rambo, P. R. col., 2 ♀ (MCTP).

3.4.5. *Mahanarva* (*Ipiranga*) *vittata* (Walker, 1851)

Figures 6B, 8A–P

Monecophora vittata Walker, 1851b: 681
Tomaspis vittata: Lallemand 1912a: 98; Metcalf 1961: 115
Mahanarva (*Ipiranga*) *vittata*: Paladini and Carvalho 2008: 325; **comb. nov.**
Monecphora fortunata Lallemand, 1924: 383. Metcalf 1961: 226
Kanaima vittata: Fennah 1979: 270; **syn. nov.**
Kanaima fortunata: Carvalho and Webb 2005: 66, status revalidated
Mahanarva (*Ipiranga*) *fortunata*: Paladini & Carvalho 2008: 325; **comb. nov.**
Mahanarva (*Ipiranga*) *fortunata* **syn. nov.**

Measurements male/female. Head length: 0.895/0.88; head width: 1.88/1.99; pronotum length: 1.63/1.56; pronotum width: 2.96/3.0; tegmen length: 8.14/8.4; tegmen width: 2.50/2.56; total length: 10.00/10.04 (in mm)

Diagnosis. Tegmina yellowish, with longitudinal brownish bands extending until the apical third; dorsal margin of subgenital plate straight or with rounded elevation.

Redescription. Head brownish to yellowish, vertex subretangular with a slightly marked median carina, ocelli closer to each other than to eyes, separated by about one diameter from each other; tylus quadrangular, median carina indistinct (Fig. 8A); antenna brownish, pedicel sparsely setose, basal body of flagellum subcylindrical with a single and short arista shorter than the pedicel length. Postclypeus yellowish, inflated, with convex profile, longitudinal brownish carina present, lateral grooves slightly marked (Fig. 8B, C); rostrum with second segment yellowish and third segment brownish, reaching the base of mesocoxae. Pronotum brownish, hexagonal, with muscular insertions slightly apparent, median carina indistinct; anterior and anterolateral margins straight; posterolateral with slight sinuosity and posterior margin medially grooved, humeral angles acute; scutellum brownish, with slight central concavity and slightly marked horizontal grooves. Tegmina (Fig. 8A, B) yellowish, narrow, with longitudinal brownish bands united near the base of tegmina and extending until its apical third, veins M and Cu1 united at base, veins A1 distinct and A2 indistinct, apical reticulation undeveloped, slightly visible venation. Hindwings hyaline, with brownish venation, Cu1 thickened at the base, hamuli with three to five spines. Legs yellowish, metathoracic femur with a small apical black spine; tibia with two lateral spines, basal one smaller than the ones located at apical crown, which has 12–13 spines arranged in two rows; basitarsus with two rows of spines covered by long setae; subungueal process present. — **MALE: Genitalia:** Pygofer (Fig. 8D, E) with one finger-like process between anal tube and subgenital plate; subgenital plate long with acute, spine-like apex (Fig. 8D–G), apical third slightly inclined towards dorsal margin (lateral view); dorsal margin of subgenital plate straight (Fig. 8D) or with a rounded elevation (Fig. 8E) covered with small tooth-like spines. Paramere (Fig. 8H, I) subrectangular with a subtriangular apex; dorsal margin rounded and slightly developed (Fig. 8H) or mountain-shaped (Fig. 8I), one subapical hook-like spine directed outwards and forward. Aedeagus (Fig. 8J–M) subcylindrical, narrowing towards apex, with a pair of straight dorsal processes, shorter than half length of shaft (Fig. 8K) or with almost the same length of half of the shaft (Fig. 8J), presenting intermediate morphs as showed in Figure 3, inserted between median and apical third of aedeagus. — **FEMALE:** Morphologically similar to male. First valvula of ovipositor long (Fig. 8N, O), with acute apex, basal process rounded and undeveloped, directed backwards; second valvula long (Fig. 8P) with rounded apex and dorsal margin covered by inconspicuous teeth in apical third; third valvula wide, with rounded apex, covered ventrally by long setae.

Remarks. This species presents a high variation in the male genitalia, as shown in Figure 3: the dorsal margin of the subgenital plate can range from straight to rounded; there are differences in the degree of elevation of the dorsal margin of paramere, and variability in the length of the dorsal processes of the aedeagus.

Distribution. Brazil (Pará, Mato Grosso, Goiás, Minas Gerais, Brasília [new record], São Paulo, Paraná).

Material examined. BRASIL, **Pará**: Gorotire Xingu, 31.x.1977, D.A. Posey leg., 1 ♀ (DZUP); **Mato Grosso:** Chapada dos Guimarães, 03–05.xii.1983, Exc. Dep. Zool-UFPR (Polonoroeste), 3 ♂, 1 ♀ (DZUP); idem: 06.xii.1983, Exc. Dep. Zool-UFPR (Polonoroeste), 1 ♂ (DZUP); idem: 01–03.xii.1983, Exc. Dep. Zool-UFPR (Polonoroeste), 1 ♀

(DZUP); idem: 03.ii.1961, J. & B. Bechyné, 1 ♀ (DZUP); **Goiás:** Jataí, xi.1963, M. Alvarenga leg., 1 ♀ (MCTP); Novo Mundo, 13°55′45.1″S 49°58′17.8″W, 282m, 26.xi.2010, Malaise, A.J.C. Aguiar leg. 1 ♂, 1 ♀ (DZUP); **Minas Gerais:** Alfenas, 30.xii.1982, Koller, W.W. leg., 28 ♂, 6 ♀ (DZUP); Uberaba, 04.i.1984, Koller, W.W. leg., 2 ♂, 1 ♀ (DZUP); Alpinópolis, ii.1961, Claudionor Elias, 1 ♂ (MCTP); Pirapora, xi.1975, M. Alvarenga leg., 1 ♂ (DZUP); Corinto, 15.xii.1979, C. Elias leg., 1 ♂ (DZUP); idem: 1–15.xi.1979, C. Elias leg., 1 ♂ (DZUP); **Brasília:** (no location data), 1000m, 15–30.v.1957, Barros-Albuquerque leg., 1 ♀ (DZUP); **São Paulo:** São Carlos,15.iii.1983, Pacheco, J. leg., 21 ♂, 3 ♀ (DZUP); Tabajara-Assis, 22°28′00.0″S 50°20′00.0″W, 9.iv.2011, Rosa, R. leg., 1 ♂ (MCTP); Araras, 18.xii.1981, V. Longo leg., 1 ♂ (MCTP); idem: 12.iv.1982, S. M. Nunes leg., 1 ♂ (MCTP); idem, 16.i.1981, J. Borges leg., 1 ♀ (MCTP); Batatais, 31.xii.1970, Pe. J. Moure leg., 3 ♂, 5 ♀, one without genitalia (DZUP); idem 24.xii.1970, Pe. Moure leg., 1 ♀ (DZUP); idem: 31.x.1969, Luiz C. Silva leg., 1 ♀ (DZUP); idem:

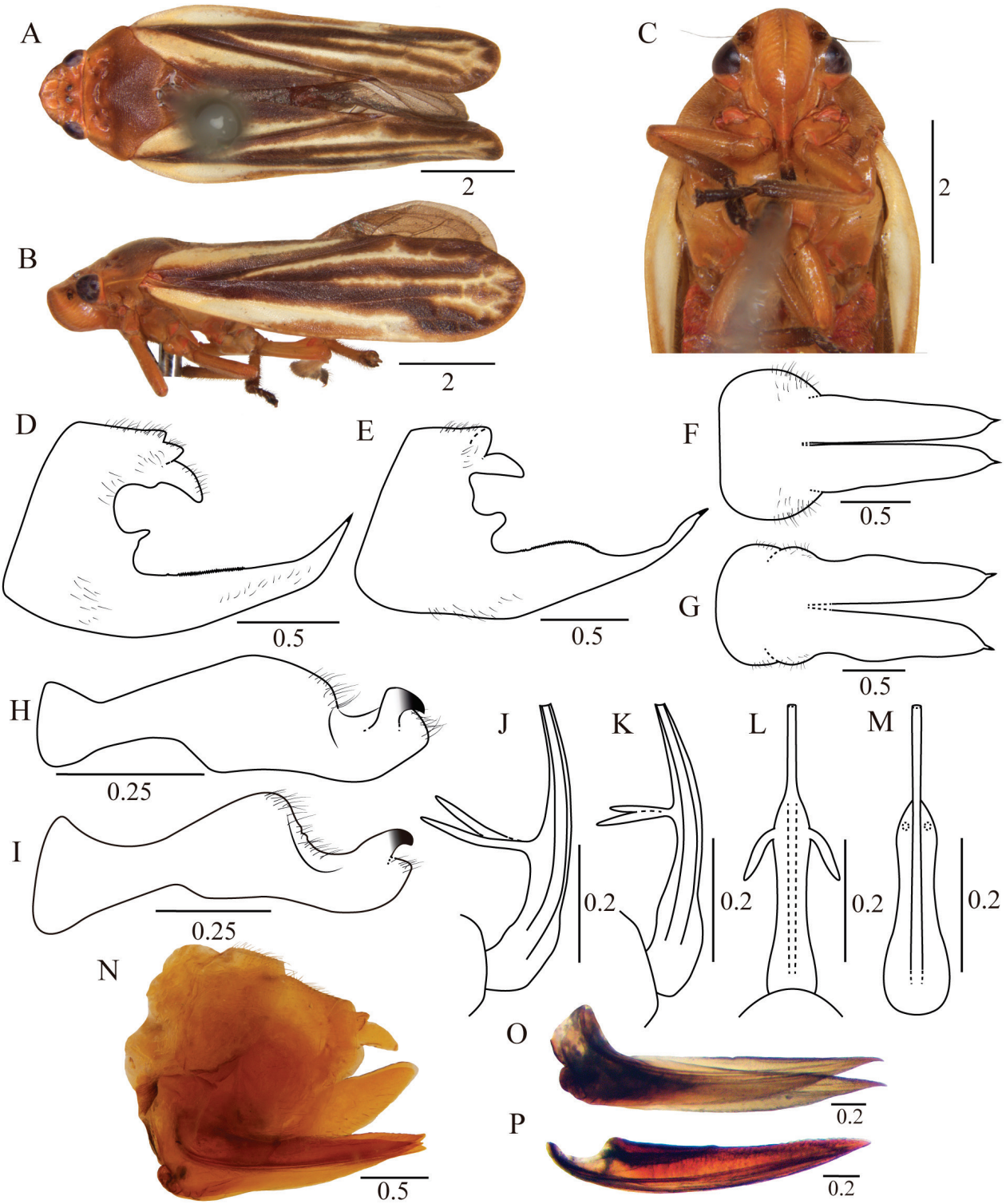

Figure 8. *Mahanarva* (*Ipiranga*) *vittata*. Habitus: **A** dorsal view; **B** lateral view; **C** ventral view. Male genitalia, pygofer: **D**–**E** lateral view; **F**–**G** ventral view. Paramere: **H**–**I** lateral view. Aedeagus: **J**–**K** lateral view; **L** dorsal view; **M** ventral view. Female genitalia, ovipositor: **N** lateral view. First valvulae: **O** lateral view. Second valvulae: **P** lateral view. Scale bars in mm.

02.i.1968, Pe. Moure leg., 1 ♀ (DZUP); Altinópolis, xii.1967, Pe. J. Moure leg., 1 ♂ (DZUP); **Paraná:** Bandeirantes, 30.i.2016, E.A. Taguti leg., 1 ♀ (DZUP).

3.4.6. *Mahanarva* (*Ipiranga*) *integra* (Walker, 1858)

Figures 6C, 9A–L

Monecphora integra Walker, 1858a: 86

Delassor rubicundus integer [sic]: Fennah 1953c: 350; Metcalf 1961: 169

Mahanarva (*Ipiranga*) *integra*: Carvalho and Webb, 2005: 69; **stat. nov.**

Monecphora moreirae Lallemand, 1924: 381. Metcalf 1961: 228.

Mahanarva (*Ipiranga*) *moreirae*: Fennah 1968: 187; Carvalho and Webb 2005; **syn. nov.**

Measurements male/female. Head length: 1.05/1.155; head width: 1.99/2.2; pronotum length: 1.85/1.98; pronotum width: 2.99/3.36; tegmen length: 8.66/9.18; tegmen width: 2.96/3.14; total length: 10.46/11.12 (in mm).

Diagnosis. Tegmina black with two wide transverse orange bands, with margins approximately straight, posterior band never fragmented into spots; pygofer with one finger-like process between anal tube and subgenital plate, subgenital plate with an acute apex, basal process short and rounded.

Redescription. Head black, vertex subretangular with a slightly marked median carina, scarce pubescence, ocelli closer to each other than to eyes, separated by about one and a half diameter from each other; tylus quadrangular, black, basal third with slightly marked carina, becoming indistinct towards the apex (Fig. 9A); antenna brownish, pedicel sparsely setose; basal body of flagellum subcylindrical with a single and short arista shorter than the pedicel length. Postclypeus black, inflated, with convex profile, longitudinal carina present, lateral grooves slightly marked (Fig. 9B, C); rostrum with second segment reddish and third segment black, reaching the base of mesocoxae. Pronotum black, hexagonal, with muscular insertions slightly apparent, median carina slightly marked; anterior and anterolateral margins straight, posterolateral with slight sinuosity and posterior margin medially grooved, humeral angles acute scutellum black, with slight central concavity and slightly marked horizontal grooves. Tegmina (Fig. 9A, B) narrow, black, with two transverse wide bands orange: one between basal and medium third and another between medium and apical third; veins M and Cu1 united at base, veins A1 and A2 distincts, apical reticulation developed, prominent venation. Hindwings hyaline, with brownish venation, Cu1 thickened at the base, hamuli with three or four spines. Legs reddish, metathoracic femur with a small apical spine; tibia with two lateral spines, basal one smaller than the ones located at apical crown, which has 12–14 spines arranged in two rows; basitarsus with three rows of spines covered by long setae; subungueal process present. — **MALE: Genitalia:** Pygofer (Fig. 9D) with one finger-like process between anal tube and subgenital plate; subgenital plate narrowing towards apex, which is acute and spine-like directed outward (in ventral view) (Fig. 9E), dorsal margin with rounded elevation covered with small tooth-like spines; basal process of subgenital plate short and rounded followed by and excavation. Paramere (Fig. 9F) subretangular, dorsal margin rounded and developed, apex subtriangular and slightly acute with long setae; subapical hook-like spine bearing small denticles in the inferior margin, directed outwards and forward. Aedeagus (Fig. 9G–I) subcylindrical, narrowing towards apex, with a pair of straight dorsal processes, shorter than half length of shaft and inserted between median and apical third of aedeagus. — **FEMALE:** Morphology similar to that of the male, but slightly larger in relation to total body length. First valvula of ovipositor long (Fig. 9J, K), with acute apex, basal process rounded and undeveloped, directed downwards; second valvula (Fig. 9L) long with rounded apex and dorsal margin covered by teeth in apical third; third valvula short and wide, with rounded apex, covered ventrally by long setae.

Remarks. *M.* (*I.*) *integra* shares morphological similarities in the male genitalia with *M.* (*I.*) *rubicunda* and *M.* (*I.*) *rubripennis*. These include a rounded and short basal process on the subgenital plate followed by an excavation and a rounded elevated dorsal margin. *M.* (*I.*) *integra* exhibits variation in tegmina proportion with some specimens having wider tegmina comparing to others. While the color and pattern of transverse bands on the tegmina resembles those of *M.* (*I.*) *rubicunda*, the bands on *M.* (*I.*) *integra* are wider. Furthermore, *M.* (*I.*) *integra* has a predominantly black body color with reddish legs.

Distribution. Brazil (Rio de Janeiro, São Paulo [new record], Paraná, Santa Catarina and Rio Grande do Sul), Argentina (Misiones).

Material examined. BRASIL, **Rio de Janeiro:** Guaporé, 03.i.2008, P.C. Grossi leg., 3 ♀ (DZUP); **São Paulo:** Cássia dos Coqueiros, x.1954, M.P. Barretto col., 1 ♀ (MZSP); **Paraná:** Apucarana, 1975, H. Alvarenga, 1 ♀ (DZUP); Araucária, 02.xi.83, Palú, M.R. leg., 1 ♂ (DZUP); Vila Velha, 23.ii.65, C. Dipterologia, 1 ♀ (DZUP); Mariópolis, 06.xii.1983, Exc. Dep. Zool- UFPR, 1 ♂ (DZUP); Piraguara, Mananciais da Serra, 25°29′46″S 48°58′46″W, 02.i.2008, Grossi, P.C. leg., 4 ♀ (DZUP); idem: P.G. Grossi & Paladini leg., 1 ♂ (DZUP); idem: 17.xi.2009, Grossi, P.C. leg., 1 ♀ (DZUP); Campo Largo, BR 277 Km 115, 21.xi.2009, Dias, F.M.S & Serram leg., E.B.F, 1 ♂ (DZUP); Tijucas do Sul, Associação dos prof. UFPR Chácara, 25°50′14″S 49°02′57″W, A Paladini & R.R. Cavichioli leg., 1 ♂, 1 ♀, 1 without genitalia (DZUP); idem: Vossoroca, 17.i.2003, Excursão Fauna Local- DZOO, (no col. data), 3 ♀ (DZUP); São José dos Pinhais, 25°36′18″S 49°11′37″W, i-vii.2014, A.C. Domahovski leg., 18 ♂, 1 without genitalia (MCTP); idem: 880m, 12.x.2013, A.C. Domahovski leg., 1 ♂ (DZUP); Jaguariaíva, 28.xii.1966, F. Giacomel leg, 1 ♂ (MCTP); Foz do Iguaçu, 16.xii.1965, (no col. data), 1 ♂ (MCTP); Curitiba, 15–27.x.1983, E.C.Costa leg., 1 ♂ (DZUP); Fênix, 30.iii.1987, Dutra, R. leg., 1 ♂ (DZUP); Ponta Grossa, P.E. de Vila Velha, 25–26.xi.2011, Grosso, Santos & Melo leg., 1 ♂ (DZUP); **Santa**

Catarina: Nova Teutonia, 27°11′00.0″S 52°23′00.0″W, xi.1982, Fritz Plaumann leg., 1 ♂ (DZUP), 2 ♀ (DZUP); idem: ii.1981, Fritz Plaumann leg., 19 ♂ (DZUP), 1 ♀ (DZUP); idem: xi.1977, Fritz Plaumann leg., 2 ♂ (DZUP), 2 ♀(DZUP); Lages, 2.x.1983, col. R.L. CHI., 1 ♂ (DZUP); Joinville, 10.xi.1974, P. Moure col., 1 ♂ (DZUP); Ponte Alta, 12.ii.1973, A.M. Sakakibara, 2 ♀ (DZUP); Campo Alto, Sta. Cecília, 12.ii.73, Sakakibara e Mielke, leg., 1 ♀ (DZUP) e 1 without genitalia (DZUP); idem: 26.ii.1968, Moure & Mielke, 1 ♀ (DZUP); Rio Vermel-

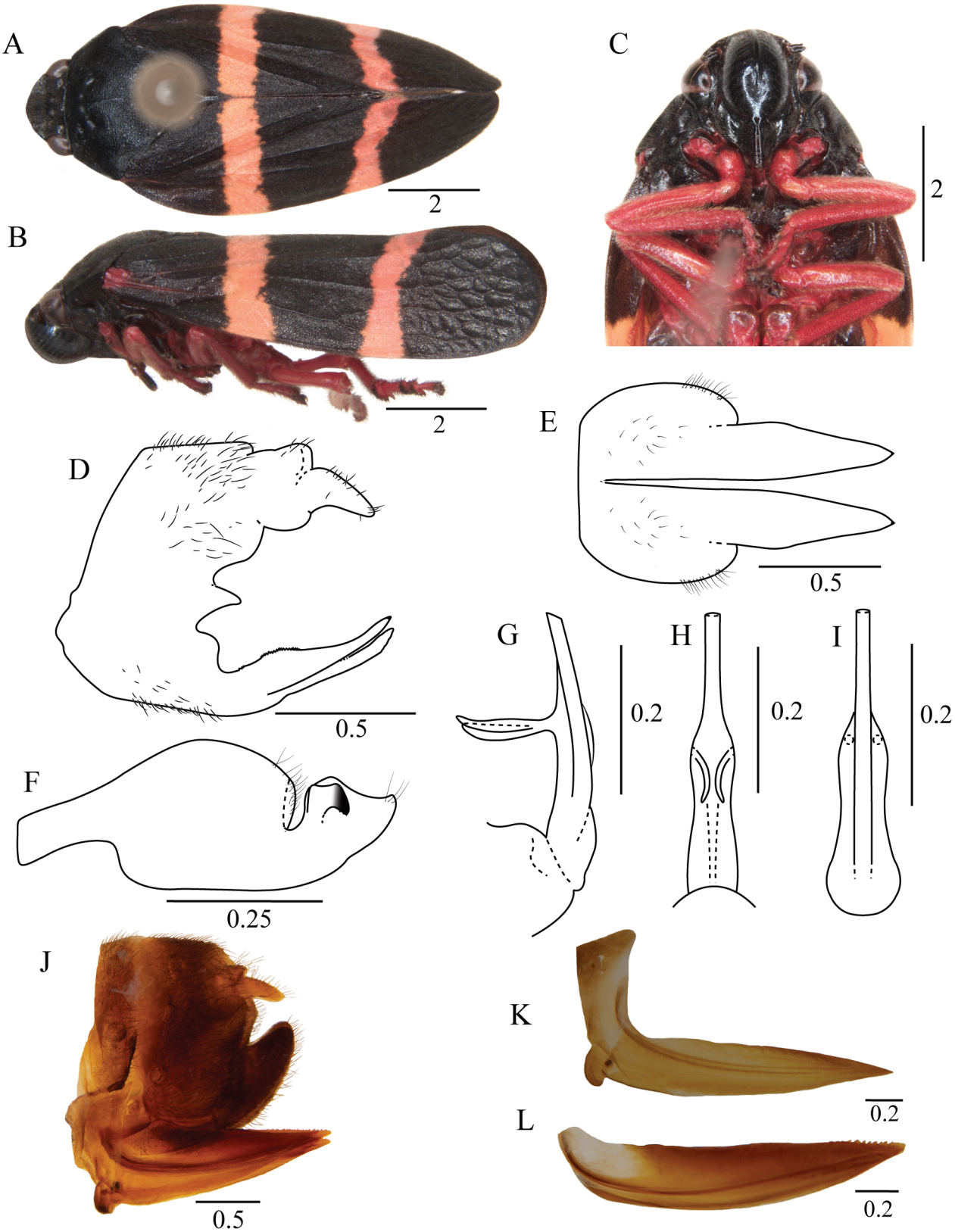

Figure 9. *Mahanarva* (*Ipiranga*) *integra*. Habitus: **A** dorsal view; **B** lateral view; **C** ventral view. Male genitalia, pygofer: **D** lateral view; **E** ventral view. Paramere: **F** lateral view. Aedeagus: **G** lateral view; **H** dorsal view; **I** ventral view. Female genitalia, ovipositor: **J** lateral view. First valvulae: **K** lateral view. Second valvulae: **L** lateral view. Scale bars in mm.

ho, ii.74, Abílio leg., 3 ♂ , 8 ♀ (DZUP); Rancho Queimado, 15–18. xi.1995, A. Bonaldo leg., 1 ♂ (MCTP); idem: 15–18.xi.1995, L. Moura leg., 2 ♂ (MCTP); Florianópolis, 27.iv.1980, Butignol C.A. leg., 2 ♂ (MCTP); Ponte Alta, 12.ii.1973, A.M. Sakakibara, 1 ♀ (MCTP); (no location data), 10.ii.1973, Lopez, P. leg., 1 ♀ (MCTP); Campos Novos, 7.i.1989, Mansur, C. & Périco, E., leg., 1 ♂ (MCTP); idem: 5.i.1989, Fernandes, J.A. & Penz, C.M. leg., 1 ♂, 1 ♀ (MCTP); idem: 6.i.1989, Mansur, C. & Pericie., leg., 1 ♂, 2 ♀, 1 without genitalia (MCTP); idem: 6.i.1989, Fernandes, J.A., leg., 1 ♀ (MCTP); idem: 6.i.1989, Penz, CM & Fernandes, J.A., leg., 1 ♀ (MCTP): idem: 04.i.1989, Equipe do Projeto E. col., 1 ♂ (MCTP); Campo Alegre, 15.ii.2008, Pinto, Â.P. col., 3 ♂, 5 ♀ (MCTP); idem: Rio do Turvo-SC301, 16.ii.2008, Pinto, Â.P. col., 1 ♀ (MCTP); Criciúma, Parque José Milaneze, 13.xii.2004, Martins, F. leg., 1 ♀ (MCTP); idem: 27.xii.2004, Martins, F. leg., 1 ♂ (MCTP); **Rio Grande do Sul:** São Francisco de Paula, Pró-Mata, 29°28′49″S 50°10′28″W, 14–17.xii.2009, A. Paladini leg., 2 ♂, 4 ♀ (DZUP); idem: 14–17.xii.2009, A Paladini & R.R. Cavichioli, 1 ♂ (DZUP); idem: 25.ii.1999, A. Köhler leg., 1 ♀ (MCTP); idem: 19–21.iii.1998, Carvalho, G.S. leg., 8 ♂, 2 ♀ (MCTP); idem: 26.iv.2003, (no col. data), 1 ♂, 1 ♀ (MCTP); idem: 19–20.xi.1998, Carvalho & Pulz, leg., 2 ♂, 4 ♀ (MCTP); idem: 15–16.v.2010, Carvalho, G.S. leg., 1 ♂, 1 ♀ (MCTP); idem: 15.iii.1996, Birgit Harter leg., 1 ♀ (MCTP); idem: 27.iv.2003, (no col. data), 1 ♀ (MCTP); idem: 23.iv.1999, Carvalho, G.S. leg., 1 ♀ (MCTP); idem: 2.v.1997, Carvalho, G.S. leg., 4 ♂, 1 ♀ (MCTP); idem: 11.iv.1997, Carvalho, G. S. leg., 2 ♀ (MCTP); idem: 20–21.x.2001, (no col. data), 1 ♀ (MCTP); idem: 24.iii.1998, Koehler, leg., 1 ♂ (MCTP); idem: 27.iv.2003, Lab. Ent. Sis. leg., 4 ♂ (MCTP); idem: 27-29.iii.2006, E.L.C.Silva & A.A.Lise leg., 1 ♀ (MCTP); Montenegro, 29°38′00.0″S 51°28′00.0″W, 12.xi.2009, A. Paladini leg., 3 ♂, 1 ♀ (DZUP); idem: 29.x.2009, A. Paladini leg., 1 ♂ (DZUP); idem: 19.x.2001, Ott, A.P. leg., 1 ♂, 2 ♀ (MCTP); idem: 30.v.2011, Citros- Pq.Gaúcho leg., 1 ♂ (MCTP); idem: 17.xi.2011, Citros- Pq.Gaúcho leg., 4 ♂, 4 ♀ (MCTP); idem: 29.xii.2011, Citros- Pq.Gaúcho, leg., 1 ♂, 3 ♀ (MCTP); idem: 12.i.2012, Citros- Pq.Gaúcho leg., 1 ♂,1 ♀ (MCTP); idem: 1.xii.2011, Citros- Pq.Gaúcho leg., 8 ♂, 3 ♀ (MCTP); idem: 15.xii.2011, Citros- Pq.Gaúcho leg., 2 ♂, 13 ♀ (MCTP); idem: 3.xi.2011, Citros- Pq.Gaúcho leg., 1 ♂ (MCTP); idem: 7.i.2011, Citros- Pq.Gaúcho leg., 1 ♀ (MCTP); idem: 8.x.2009, Gadelha,Y.E.A. col., 1 ♀ (MCTP); idem: 14.xii.2009, Gadelha,Y.E.A. col., 1 ♂, 6 ♀ (MCTP); idem: 12.xi.2009, Gadelha,Y.E.A. col., 1 ♂, 2 ♀ (MCTP); idem: 27.xi.2009, Gadelha,Y.E.A. col., 1 ♂, 4 ♀ (MCTP); idem: 27.xi.2009 Carvalho, G.S. leg., 3 ♂, 2 ♀ (MCTP); idem: 29.xii.2009, Gadelha,Y.E.A. col., 2 ♀ (MCTP); Passo Fundo, 28°13′40″S 52°24′19″W, 18.xi.2011, S. Lampert leg., 1 ♂ (DZUP); Bento Gonçalves, 28.iii.2007, Bertin, A. leg., 2 ♂ (MCTP); idem: 8.x.2008, Tognon, R. col., 1 ♂ (MCTP); idem: 20.xi.2008, Tognon, R. col., 1 ♂ (MCTP); Viamão, 25.xi.1994, Petersen, A. leg., 6 ♂, 11 ♀ (MCTP); idem: 7.xi.1995, Petersen, A., 2 ♂, 3 ♀ (MCTP); idem: 7.x.1994, Exc LSE leg., 1 ♂ (MCTP); idem: 2.xii.1994, Petersen, A. leg.,1 ♀ (MCTP); idem: 14.xi.1998, Prates, P. leg., 1 ♀ (MCTP); Guaíba, 24.x.1995, Petersen, A. leg., 1 ♀ (MCTP); Torres, 20.v.1995, (no col. data), 1 ♀ (MCTP); idem: Col. São Pedro, 8.xi.1997, Carvalho, G. leg., 4 ♂, 3 ♀ (MCTP); Salvador do Sul, ix–xii.1994, A. Specht, leg., 1 ♀ (MCTP); Ijuí, 4.xi.1978, A. Dressler leg., 1 ♂ (MCTP); Santa Maria, 8.xi.1978, J.Abreu, 1 ♂ (MCTP); idem: 26.x.1978, L. A. Grohe leg., 1 ♂ (MCTP); idem: 21.x.1978, L. C. Becker leg., 1 ♂ (MCTP); Pelotas, 6.iii.1979, Ortiz leg., 1 without genitalia (MCTP); Porto Alegre, i.1981, Carvalho, G. leg., 1 ♀ (MCTP); idem: 28.xii.1983, E. Corseuil leg., 1 ♀ (MCTP); idem: 2.iv.1963, C. Trés leg., 1 ♂ (MCTP); idem: 6.xii.1979, Butignol leg., 1 without genitalia (MCTP); Canela, 23.xii.1961, A. Lise leg., 1 ♂ (MCTP); Cotiporã, 28°59′00.0″S 51°38′00.0″W, 6–8.i.2011, Pinto, A. P, & Silva, J. G. leg., 2 ♂, 2 ♀; Barão de Cotegipe, 15.i.1967, F. Giacomel leg., 3 ♂ (DZUP), 1 ♀ (MCTP); idem: 21.i.1967, F. Giacomel leg., 1 ♂ (DZUP), 1 ♀(DZUP); Vila Maria, 26.ii.1998, Specht, A. col., 1 ♂ (MCTP); Capão da Canoa, 08.i.1983, Trois, C. leg., 1 ♂ (MCTP); Frederico Westphalen, vii.2009, Silva, E. R; Bussato, D. leg., 1 ♂, 1 ♀ (MCTP). ARGENTINA, **Misiones:** Cataratas del Iguazú, 24.xi.1980, Willink-Claps-Dominguez leg., 1 ♂ (MCTP); idem: 26.xi.1980, Willink-Claps leg, 1 ♀ (MCTP); idem: Bernardo de Irigoyen, 12.xi.1973, Escobar-Claps, 1 ♀ (MCTP); idem: xii.1961, L.N.Alem, A. Martinez leg., 1 ♂ (MZSP).

3.4.7. *Mahanarva* (*Ipiranga*) *aguirrei* (Berg, 1879)

Figures 6D, 10A–I

Tomaspis aguirrei Berg, 1879c: 216. Metcalf 1961: 85
Mahanarva (*Ipiranga*) *aguirrei*: Fennah 1968: 187

Measurements male. Head length:1.24; head width: 2.31; pronotum length: 2,13; pronotum width: 3.43; tegmen length: 9; tegmen width: 2.7; total length: 11.47 (in mm).

Diagnosis. Tegmina black or brownish with one thin transverse band whitish between basal and median third and an incomplete band between median and apical third; subgenital plate with excavation on the basal third, rounded apex, paramere apex subquadrangular, spine long and slender with an acute apex.

Redescription. Head black, vertex subretangular with a slightly marked median carina, ocelli closer to each other than to eyes, separated by about one diameter from each other; tylus subretangular, black, with a slightly marked carina on the basal third, becoming indistinct towards the apex (Fig. 10A); antenna black, pedicel sparsely setose; basal body of flagellum subcylindrical with a single and short arista shorter than the pedicel length. Postclypeus black, inflated, with convex profile, longitudinal carina present, lateral grooves slightly marked (Fig. 10B, C); rostrum with second segment centrally yellowish and laterally black and third segment black, reaching the base of mesocoxae. Pronotum black, hexagonal, with muscular insertions slightly apparent, median carina slightly marked; anterior and anterolateral margins straight; posterolateral with slight sinuosity and posterior margin medially grooved; scutellum black, with slight central concavity and slightly marked horizontal grooves. Tegmina (Fig. 10A, B) black or brownish, narrow, with one transverse band whitish between basal and median third and an incomplete band between median and apical third resembling two rounded spots; veins M and Cu1 united at base, veins A1 and A2 distincts, apical reticulation developed, prominent venation. Hindwings hyaline, with brownish venation, Cu1 thickened at the base, hamuli with three or four spines. Legs black or brownish, metathoracic femur with an apical spine; tibia with two lateral spines, basal one smaller than the ones located at

apical crown, which has 14 spines arranged in two rows; basitarsus with three rows of spines covered by long setae; subungueal process present. — **MALE: Genitalia:** Pygofer (Fig. 10D, E) with one finger-like process between anal tube and subgenital plate; subgenital plate long, with rounded apex; basal process short and rounded followed by an excavation, dorsal margin covered with small tooth-like spines. Paramere (Fig. 10F) subretangular, dorsal margin rounded and developed, apex subquadrangular, subapical hook-like spine slender bearing small denticles in the inferior margin, with an acute apex directed outwards and forward. Aedeagus (Fig. 10G–I) subcylindrical, narrowing towards apex with a pair of straight dorsal processes, shorter than half the length of the shaft and inserted between middle and apical third of aedeagus. — **FEMALE:** specimens unknown.

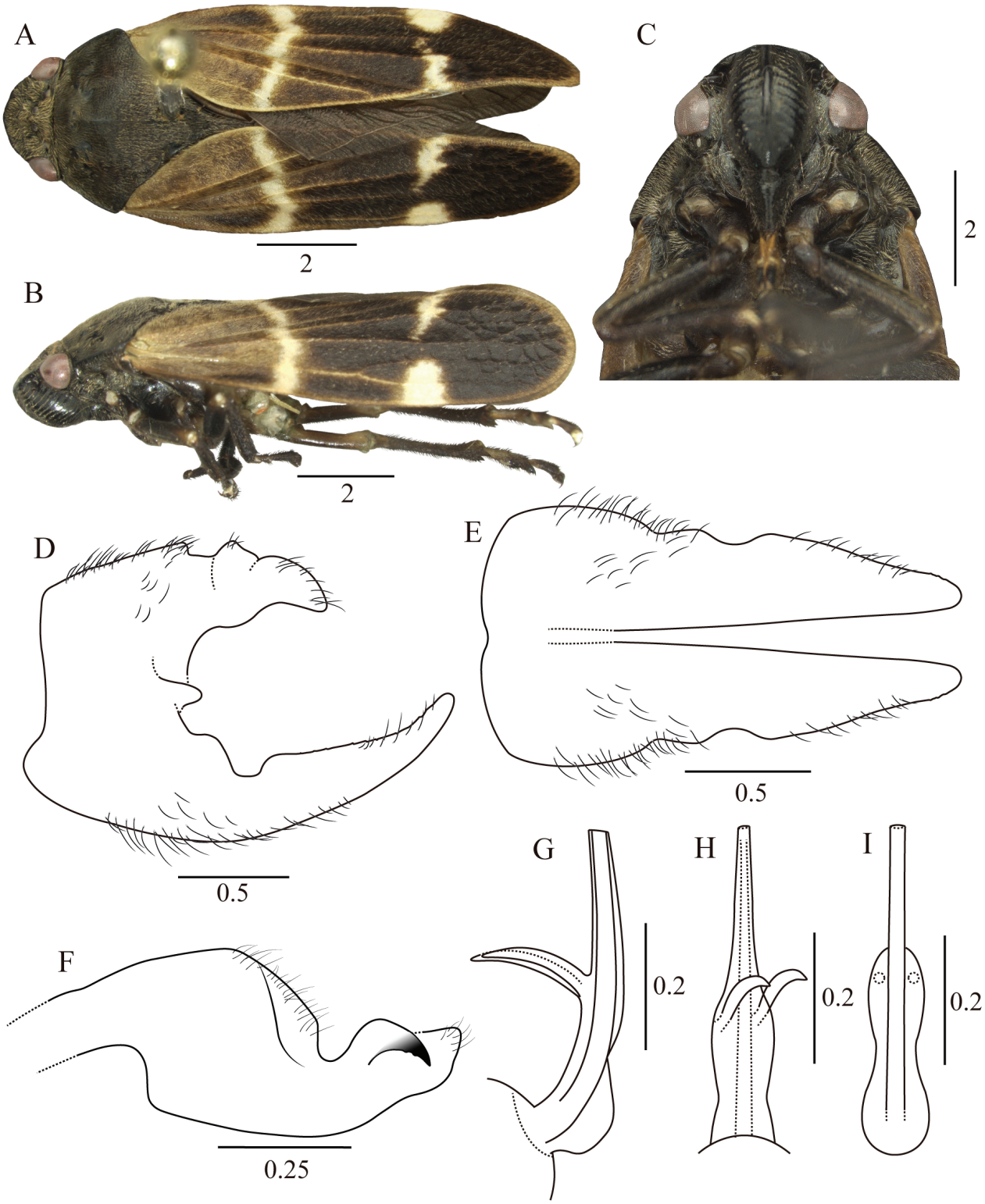

Figure 10. *Mahanarva* (*Ipiranga*) *aguirrei*. Habitus: **A** dorsal view; **B** lateral view; **C** ventral view. Male genitalia, pygofer: **D** lateral view; **E** ventral view. Paramere: **F** lateral view. Aedeagus: **G** lateral view; **H** dorsal view; **I** ventral view. Scale bars in mm.

Remarks. This species shows similarities to *M.* (*I.*) *nefasta* **sp. nov.** mainly due to the pattern and coloration of the tegmina, but presents some unique characters: a rounded subgenital plate apex, a subquadrangular paramere apex, and a slender, acute paramere spine. This species is registered for the first time in Brazil.

Distribution. Brazil ([new record] Paraná), Paraguay.

Material examined. BRASIL, **Paraná:** Umuarama, 5–10.x.1980, A. Yamamoto leg., 1 ♂ (MCTP); S. J. dos Pinhais, 25°36′18″S 49°11′37″W, 880m, 01–31.xii.2020, Malaise, A.C. Domahovski leg., 1 ♂ (DZUP); idem: 01–31.i.2020, A.C. Domahovski leg., 1 ♂ (DZUP). PARAGUAY, **Canindeyú**: Reserva Natural del Bosque Mbaracayu, Jejui-mi, Mal.3, 29.iii–09.iv.1996, A.C.F Costa leg., 1 ♂ (DZUP).

3.4.8. *Mahanarva* (*Ipiranga*) *rubripennis* (Schmidt, 1922)

Figures 6E, 11A–L

Luederwaldtia rubripennis Schmidt, 1922: 263. Metcalf 1961: 539
Mahanarva rubripennis: Fennah 1968: 186
Mahanarva (*Ipiranga*) *rubripennis*: Paladini and Cavichioli 2014: 483 **comb. nov.**

Measurements male/female. Head length: 0.90/1.02; head width: 1.82/1.98; pronotum length: 1.65/1.82; pronotum width: 2.76/3.04; tegmen length: 7.34/8.06; tegmen width: 2.26/2.56; total length: 8.79/10.11 (in mm).

Diagnosis. Tegmina red with black, rounded spots on apical plexus of veins; subgenital plate with an acute apex, basal process short and rounded followed by an excavation, paramere with a finger-like apex.

Redescription. Head black, vertex subretangular, with a slightly marked median carina in the apical third, ocelli closer to each other than to eyes, separated by about one and a half diameter from each other; tylus quadrangular, black, with its basal third with slightly marked carina, becoming indistinct towards the apex (Fig. 11A); antenna black, pedicel sparsely setose, basal body of flagellum subcylindrical with a single and short arista shorter than the pedicel length. Postclypeus black, inflated, with convex profile, longitudinal carina present, lateral grooves slightly marked (Fig. 11B, C); rostrum with second segment reddish and third segment black, reaching the base of mesocoxae. Pronotum black, hexagonal, with muscular insertions slightly apparent, median carina slightly marked; anterior and anterolateral margins straight; posterolateral with slight sinuosity and posterior margin medially grooved, humeral angles acute; scutellum black, with slight central concavity and slightly marked horizontal grooves. Tegmina (Figs 11A, B) narrow, red, with black, rounded spots on apical plexus of veins; veins M and Cu1 united at base, veins A1 and A2 distincts, apical reticulation developed, prominent venation. Hindwings hyaline, with brownish venation, Cu1 thickened at the base, hamuli with three spines. Legs brownish, metathoracic femur with a small apical spine; tibia with two lateral spines, basal one smaller than the ones located at apical crown, which has 10–12 spines arranged in two rows; basitarsus with three rows of spines covered by long setae; subungueal process present. — **MALE: Genitalia:** Pygofer (Fig. 11D) with one finger-like process between anal tube and subgenital plate; subgenital plate narrowing towards apex, which is acute and spine-like slightly directed outward (in ventral view) (Fig. 11E); dorsal margin with rounded elevation covered with small tooth-like spines; basal process of subgenital plate short and rounded followed by an excavation. Paramere (Fig. 11F) subretangular, dorsal margin rounded and developed; with an elongated and finger-like apex; subapical hook-like spine directed outwards and forward. Aedeagus (Fig. 11G–I) subcylindrical, narrowing towards apex, with a pair of straight dorsal processes, shorter than half length of shaft and inserted between median and apical thirds of aedeagus. — **FEMALE:** Morphology similar to that of the male, but slightly larger in relation to total body length. First valvula of ovipositor long (Fig. 11J, K), with acute apex, basal process rounded and undeveloped, directed downwards and backwards; second valvula long (Fig. 11L), with rounded apex and dorsal margin covered by teeth in apical third; third valvula short and wide, with rounded apex, covered ventrally by long setae.

Remarks. The male genitalia of *M.* (*I.*) *rubripennis* differs from *M.* (*I.*) *integra* due to the elongated paramere apex and the slightly longer subgenital plate. Additionally, the pattern and coloration of the tegmina are quite distinct between these species and can be used as a diagnostic character. *M.* (*I.*) *rubripennis* is the only species within the genus that exhibits red tegmina with a pattern of black maculae covering the apical reticulum, making it readily distinguishable from the other species.

Distribution. Brazil (Mato Grosso [new record], Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul).

Material examined. BRASIL, **Mato Grosso:** P.N. Chapada dos Guimarães, i.2013, Sweep M. Savaris & S.Lampert leg., 2 ♂ (DZUP); **Minas Gerais:** São Gonçalo do Rio Abaixo, 14.ii.2003, A.F.Kumagai col., 2 ♂ (DZUP); idem: 4.iv.2003, A.F.Kumagai col., 1 ♂ , 1 ♀ (DZUP); idem: 28.iii. 2003, A.F.Kumagai col., 1 ♀ (DZUP); **Espírito Santo:** Linhares, vii.1981, C. Elias leg. 1 ♂ (DZUP); Santa Teresa, 15.xi.1967, C.T. & C.Elias leg., 2 ♂ (MCTP, DZUP); idem: 12.v.1967, C.T. & C. Elias leg., 2 ♂ , 1 ♀ (DZUP); idem: 07.xii.1964, C. Elias leg., 1 ♂, 1 ♀ (DZUP); idem: 16–22.v.1967, C.& C.T.Elias leg., 2 ♂ (DZUP); idem: 21.ii.1966, C. Tadeu Elias leg. 2 ♀(DZUP); idem: 28.xi.1966, C.T. & C. Elias leg., 1 ♂ (DZUP); idem: 26.xi.1967, C.T. & C. Elias leg. 1 ♂ (DZUP); idem: 26.x.64, C. Elias leg., 1 ♂ (DZUP); **Rio de Janeiro:** Itatiaia, P.N. Itatiaia, 26.xii.1963, Alvarenga leg., 1 ♀ (MCTP); **São Paulo:** Santos, 10.i.93, Bittencourt, A. col., 1 ♀ (DZUP); São José do Barreiro (Serra Bocaina), iii.1973, F.M.Oliveira leg., 1 ♀ (DZUP); Salesópolis, Estação Biológica de Boracéia, 23°39′15.5″S 45°53′23″W, 23–29.xi.2008, A. Paladini, D.R Parizotto, P.C. Grossi, 19 ♂, 13 ♀ (DZUP); idem: 13.iv.2001, A.M.A. Lima leg., 5 ♂ ; 7 ♀ (DZUP); Cananéia, Pq.

Est. Ilha do Cardoso, 18–23.x.2011, Exp. Botu Cinza leg., 5 ♂, 2 ♀ (MCTP); idem: 25°04′00.0″S 47°55′00.0″W, 1 ♂, 1 ♀ (MCTP); Caraguatatuba, 09.xii.1983, Netto leg., 3 ♂ , 1 ♀ (DZUP); Cotia, 11.iii.73, J.R.Araújo leg., 1 ♂ , 1 ♀ (DZUP); Barueri, viii.1958, K. Lenco leg., 1 ♂ (DZUP); **Paraná:** Curitiba, 2.x.1983, Crepaldi S. leg., 1 ♂ (DZUP); idem, 9.iv.81, Juarez C. Oliveira leg., 1 ♂ (DZUP); idem: 10.xi.1985, Ferreira leg., 1 ♂ (DZUP); idem: 12–13.xi.83, Luís leg., 1 ♀ (DZUP); Piraquara, Mananciais da Serra, 25°29′46″S 48°58′54″W, 18.xi.09, R.R Cavichioli & P.G Grossi, 1 ♀ (DZUP); idem: Parque Estadual do Marumbi, 25°29′13″S 48°58′30″W, 24.i.2012, Grossi, Cavichioli & Silva leg., 2 ♂ (DZUP), 2 ♀(DZUP); idem: 22.xi.2005, R. Gonçalves leg., 1 ♀ (DZUP); Antonina, Reserva Rio Cachoeira, 25°18′58″S 48°41′46″W, 20–25.xi.2014, Altitude 50m, 1 ♂, 1 ♀ (DZUP); idem: 05–10.xi.2015, Entomologia UFPR, 1 ♀ (DZUP); idem: RPPN Gua-

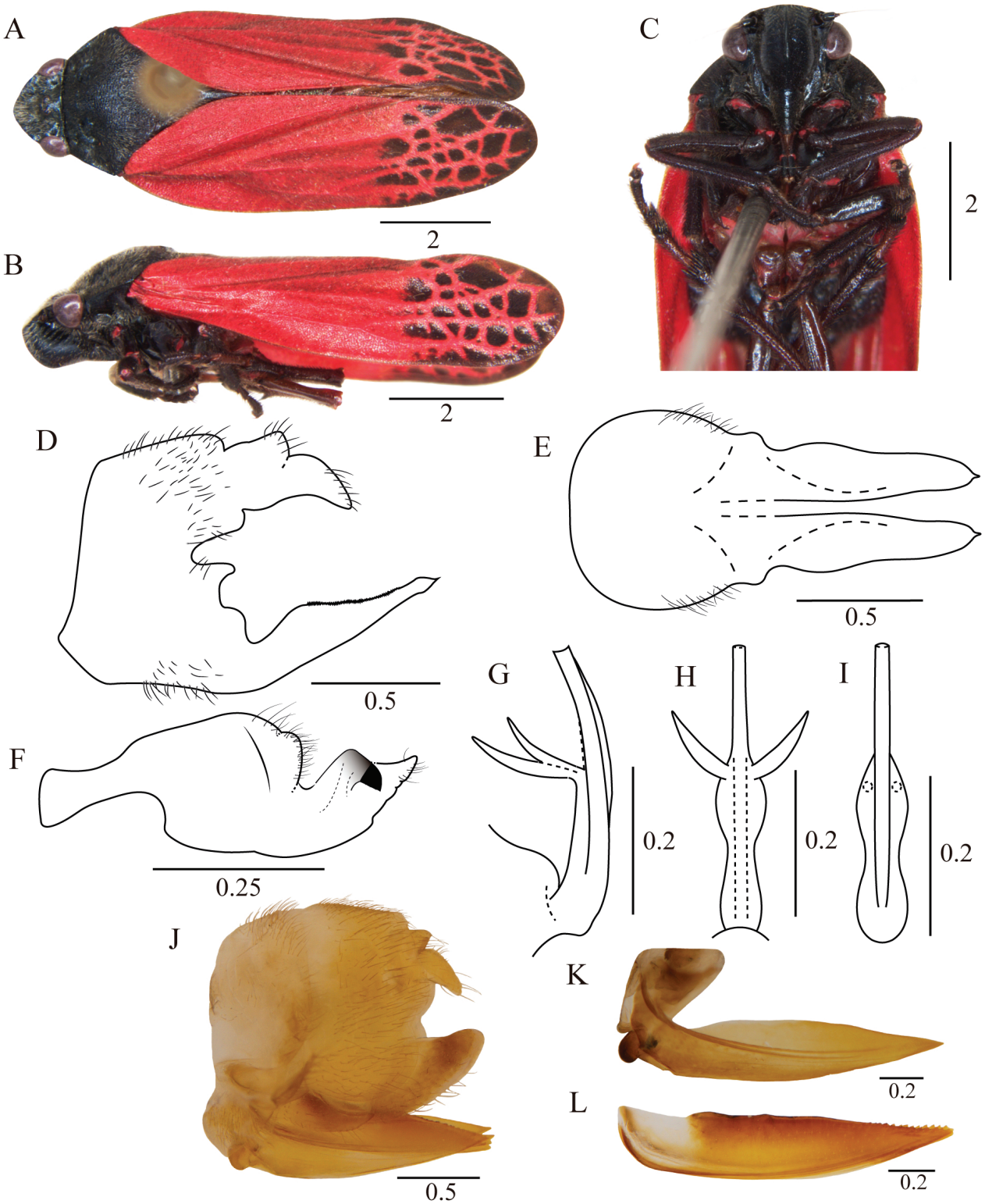

Figure 11. *Mahanarva* (*Ipiranga*) *rubripennis*. Habitus: **A** dorsal view; **B** lateral view; **C** ventral view. Male genitalia, pygofer: **D** lateral view; **E** ventral view. Paramere: **F** lateral view. Aedeagus: **G** lateral view; **H** dorsal view; **I** ventral view. Female genitalia, ovipositor: **J** lateral view. First valvulae: **K** lateral view. Second valvulae: **L** lateral view. Scale bars in mm.

ricica, 25°18′58″S 48°41′46″W, 23–27.x.2017, Sweep A.C. Domahovski leg., 2 ♂ (DZUP); idem: Rio dos Nunes, 15.vi.2001, A.C.F Da Costa, 1 ♀ (DZUP); idem: 16–20.v.2018, Luminosa, R. R. Cavichioli & A.P. Pinto leg. 1♂ (DZUP); idem, 23–27.i.2017, Luz solo, A.C. Domahovski leg., 1 ♀; idem: Reserva Sapitanduva, 20.x.1986, Lev. Ent. PROFAUPAU, Malaise, 1 ♀ (DZUP); Guaratuba, Estrada dos Castelhanos, 25°49′50″S 48°55′38″W, (no col. data), 1 ♂ (DZUP); idem: 25°50′00.0″S 48°56′00.0″W, 13.xii.2004, Carvalho, Mauro & Cavichioli, 1 ♂, 1 ♀ (DZUP); Pontal do Sul, 12.x.2004, Paladini, A leg., 4 ♂ (MCTP); idem: 11.x.2004, Paladini, A leg., 1 ♂, 1 ♀ (MCTP); São João de Petrópolis, 6–12.vi.1967, C. & C. T. Elias leg, 1 ♀ (MCTP); Paranaguá, Ilha do Mel, 7.x.1988, Zanella, F.C.V, leg., 1 ♀ (MCTP); Morretes, i.1982, A.M. Sakakibara leg., 3 ♂, 3 ♀ (DZUP); idem: i.1984, Sakakibara leg., 1 ♀ (DZUP); idem: 18.ii.1985, CIIF- luminosa, (no col. data), 1 ♂ (DZUP); idem: Viad. Caruru, 15.xii.1968, 700m, Pe. J.S. Moure leg., 1 ♀ (DZUP); Campo Largo, Est. Faxina km 4, 06.xii.2002, Excursão Fauna Local- DZOO, 2 ♂ (DZUP); Alexandra, 10.x.1970, Moure & Mielke, 2 ♀ (DZUP); São José dos Pinhais, Rep. Guaricana, 25°42′54″S 48°58′16″W, 12–14.xii.2017, Cavichioli & Domahovski, 1 ♀ (DZUP); Guaraqueçaba, 13.x.1983, Rupp J. leg., 1 ♀ (DZUP); idem: 14.x.1983, Rupp J. leg., 1 ♂ (DZUP); idem: 18.ix.1983, Crepaldi S. leg., 1 ♀ (DZUP); Serra Negra, 10.iii.1981, Isaias leg., 2 ♀ (DZUP); **Santa Catarina:** São Bento do Sul, Rio Vermelho, 9.iii.1974, 850m, Rank leg., 1 ♂ (MCTP), 1 ♀ (DZUP); **Rio Grande do Sul:** São Francisco de Paula, Pró-Mata, 19–21.iii.1998, Carvalho, G.S. leg, 1 ♀ (MCTP).

3.4.9. *Mahanarva* (*Ipiranga*) *bahiaensis* Carvalho & Webb, 2004

Figure 6F

Mahanarva (*Ipiranga*) *bahiaensis* Carvalho and Webb, 2004: 384

Diagnosis. Tegmina brownish with two transverse bands yellowish; subgenital plate elongated, paramere with a triangular subapical spine and acutely rounded apex.

Remarks. The male holotype was colected in Camacã, Bahia, Brazil and is currently deposited on British Museum of Natural History (BMNH). In this study, we examined three specimens from Bahia and the pattern of tegmina and male genitalia are very similar to *M.* (*I.*) *rubicunda* suggesting that *M.* (*I.*) *bahiaensis* can be a synonym of *M.* (*I.*) *rubicunda*. Since we didn't have access to the holotype in person and more sampling from Bahia, specifically in the type locality, we chose to not synonymize both species. The diagnosis provided here was based on original description made by Carvalho and Webb (2004).

Material examined. BRASIL, **Bahia:** Encruzilhada, xi.1972, Alvarenga & Seabra leg., 1 ♂, 2 ♀ (MCTP).

3.4.10. *Mahanarva* (*Ipiranga*) *takiyae* Paladini & Cavichioli, 2014

Figure 6G

Mahanarva (*Ipiranga*) *takiyae* Paladini and Cavichioli, 2014: 481

Diagnosis. Tegmina black with four orange maculae; subgenital plate elongated with a spine at apex, paramere with a subapical hook-like spine.

Remarks. This species was recently described by Paladini and Cavichioli (2014), presenting a complete and comprehensive description, as well as habitus illustrations and drawings of the male and female genitalia. The diagnosis presented here was based on the original description.

Material examined. BRASIL, **Brasília:** Distrito Federal, ii.1965 J.A.P. Dutra leg., paratypes 1 ♂, 1 ♀ (DZUP); idem: FLONA de Brasília, Gleba 1, 15°45′00.0″S 48°04′00.0″W, 1220m, 13.xi.2012, D. Luz, 1 ♀ (DZUP); idem: Fazenda Água Limpas, Mata de Galeria, 09–23.xi.2017, Malaise, J.R.P Luz leg., 3 ♂, 2 ♀ (DZUP); idem: Cerrado, 08–22.xii.2017, Malaise, J.R.P Luz leg., 4 ♂ (DZUP).

3.4.11. *Mahanarva* (*Ipiranga*) *obliqua* sp. nov.

https://zoobank.org/82A1779C-5CF7-4993-A0E7-0A8D-39A7CEFB

Figures 6H, 12A–L, 14A–D

Measurements male/female. Head length: 1.25/1.32; head width: 2.25/2.33; pronotum length: 2.31/2.45; pronotum width: 3.72/4.05; tegmen length: 10.3/10.9; tegmen width: 3.3/3.6; total length: 12.2/13.25 (in mm).

Diagnosis. Tegmina black with an orange spot near base and two wide, orange, transversal bands, zigzag-like; subgenital plates with a rounded apex, dorsal margin without elevation, paramere with subtriangular apex.

Description. Holotype. Head black, with a slight pubescence, vertex subretangular with a slightly marked median carina, ocelli closer to each other than to eyes, separated by about one and a half diameter from each other; tylus quadrangular, black, with its basal third with a slightly marked carina, becoming indistinct towards the apex (Fig. 12A); antenna black, pedicel sparsely setose; basal body of flagellum subcylindrical with a single and short arista shorter than the pedicel length. Postclypeus black, inflated, with convex profile, longitudinal carina strongly marked and lateral grooves slightly marked (Fig. 12B, C); rostrum reddish, barely reaching mesocoxae. Pronotum black, hexagonal, with muscular insertions slightly apparent, median carina slightly marked, anterior and anterolateral margins straight; posterolateral with slight sinuosity and posterior margin medially grooved, humeral angles acute; scutellum black, with slight central concavity and slightly marked horizontal grooves. Tegmina (Fig. 12A, B) black, narrow, with an orange spot near base and two wide, orange, transversal bands, zigzag-like, one located between basal and medium third and another between medium and apical third; vein R thickened at base, M and Cu1 united at base and A1 and A2 distincts, apical reticulation developed, prominent venation. Hindwings

hyaline, with brown venation, Cu1 thickened at the base, hamuli with three to four spines. Legs reddish, metathoracic femur with a small apical spine; tibia with two lateral spines, basal one smaller than the ones located at apical crown, which has 12–14 spines arranged in two rows; basitarsus with three irregular rows of spines covered by long and dense setae; subungueal process present. — **MALE: Genitalia:** Pygofer (Fig. 12D, E) with one subtriangular process between anal tube and subgenital plate; subgenital plate narrowing toward its extension with apex rounded with denticles on inner surface; basal process of dorsal margin short and rounded. Paramere (Fig. 12F)

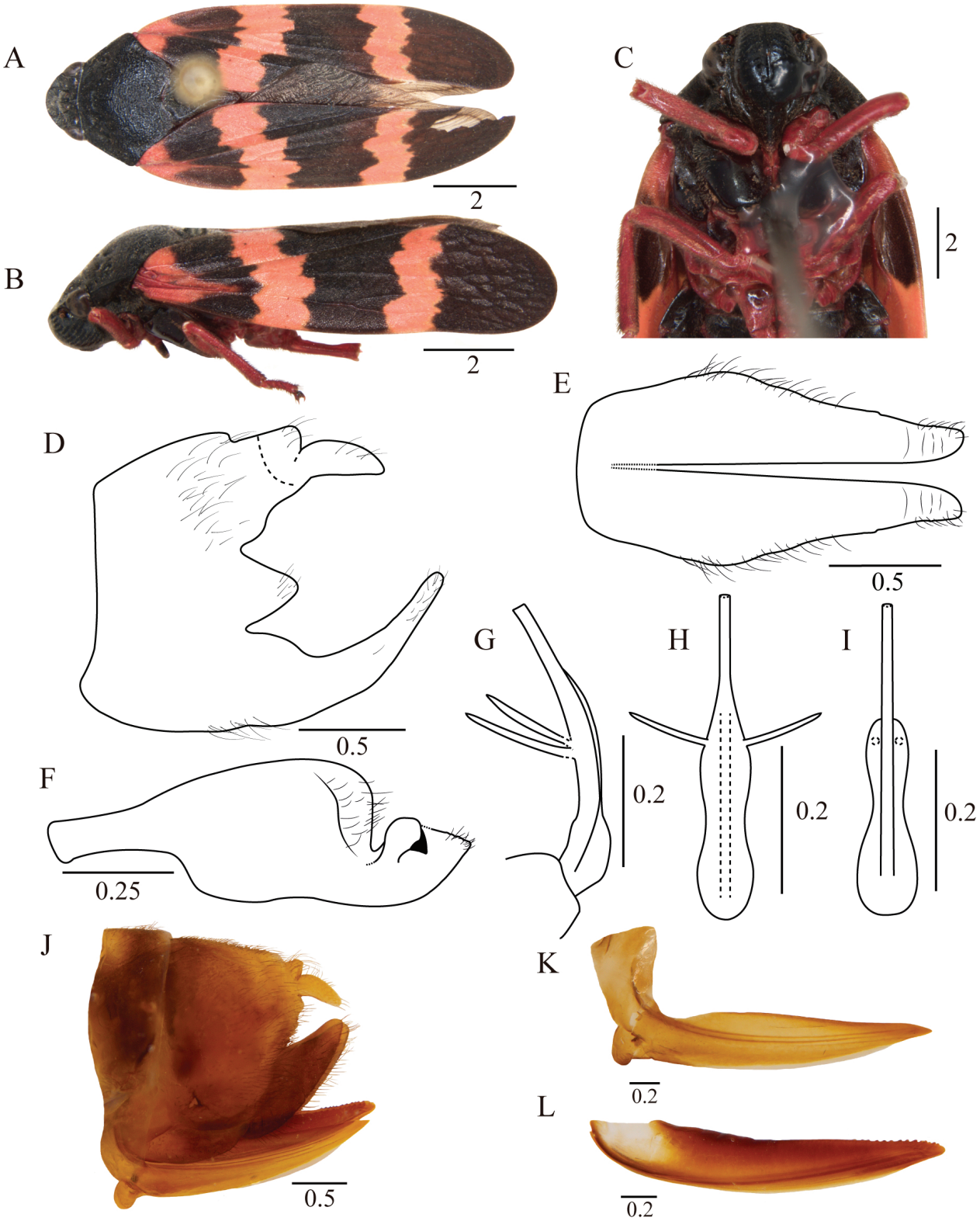

Figure 12. *Mahanarva* (*Ipiranga*) *obliqua* **sp. nov.** Habitus: **A** dorsal view; **B** lateral view; **C** ventral view. Male genitalia, pygofer: **D** lateral view; **E** ventral view. Paramere: **F** lateral view. Aedeagus: **G** lateral view; **H** dorsal view; **I** ventral view. Female genitalia, ovipositor: **J** lateral view. First valvulae: **K** lateral view. Second valvulae: **L** lateral view. Scale bars in mm.

subretangular, with a subtriangular apex, dorsal margin rounded and developed, subapical hook-like spine directed outwards and forward. Aedeagus (Fig. 12G–I) subcylindrical, narrowing towards apex, with a pair of straight dorsal processes, shorter than half length of shaft and inserted medially. — **FEMALE:** Morphology similar to that of the male, but slightly larger in relation to total body length. First valvula of ovipositor long (Fig. 12J, K), with slightly acute apex, basal process rounded and undeveloped, directed downwards; second valvula long (Fig. 12L), with rounded apex and dorsal margin covered by teeth in apical third; third valvula short and wide, with rounded apex, covered ventrally by long setae.

Remarks. This species was initially considered as a variation of *M.* (*I.*) *rubicunda*, however upon closer examination, it became evident that significant differences exist in the morphological characters such as the tegmina pattern and the male genitalia. In fact, *M.* (*I.*) *obliqua* **sp. nov.** presents several morphological similarities regarding other *Ipiranga* species: a rounded and developed dorsal margin of paramere, a subapical hook-like paramere spine, and a subcylindrical aedeagus with a pair of straight dorsal processes.

Etymology. In Latin, 'obliquum' means zigzag shape, thus this species name refers to the tegmina pattern with transversal bands.

Distribution. Brazil (Paraná and Santa Catarina).

Material examined. BRASIL, **Holotype** ♂**: Paraná:** Piraquara, riacho próximo à estrada, ativa, 25°31′01″S 49°00′32″W, 909 m a.s.l, 20.iii.2024, AP Pinto, L. Polizelli, & RC Varella leg. (DZUP); **Paratypes:** same data as holotype, 3 ♂, 2 ♀; idem: 07.xii.2023, AP Pinto, J Ehlert, MUM de Almeida & RC Varella leg., 7 ♂, 1 ♀ (DZUP); Curitiba, 28.vii.1983, L. L. Leite leg. 1 ♂, 1 ♀ (DZUP 449663); idem, 3.ix.1983, R. Amador leg., 2 ♀ (1 MCTP, 1 DZUP 449664); idem, Guajuvira, 8.vi.1980, A. Claret, leg., 1 ♂ (MCTP); idem, Quatro Barras, 22.ii.1969, Becker & Laroca, 1 ♀ (DZUP 449660); idem, Jaguariaíva, (no collect data), M. Linsing leg., 2 ♀ (DZUP 449667, DZUP 449668); **Santa Catarina:** Três Barras, 12.iii.1995, Jorge Cheren leg., 1 ♀ (MCTP); 1 ♀ no data (MCTP).

Adicional material examined. BRASIL, **Paraná:** Piraquara, riacho próximo à estrada, ativa, 25°31′01″S 49°00′32″W, 909 m a.s.l, 20.iii.2024, AP Pinto, L. Polizelli, & RC Varella leg. 6♂, 2 ♀ (DZUP).

3.4.11. *Mahanarva* (*Ipiranga*) *nefasta* sp. nov.

https://zoobank.org/8EA7F458-D443-459C-9ED0-6B7EEF-8273BC

Figures 6I, 13A–L

Measurements male/female. Head length: 0.84/0.97; head width: 1.87/2.02; pronotum length: 1.57/1.83; pronotum width: 2.75/3.01; tegmen length: 7.67/8.35; tegmen width: 2.33/2.4; total length: 9.1/10.22 (in mm).

Diagnosis. Tegmina brownish with one complete, yellowish transverse band between basal and median third, and an incomplete transverse band between median and apical third; subgenital plate not excavated at the basal portion and with an acute apex; paramere apex rounded.

Description. Head black, vertex subretangular with a slightly marked median carina in the apex, but indistinct on its base, ocelli closer to each other than to eyes, separated by about one diameter from each other; tylus quadrangular, black, with its basal third with slightly marked carina, becoming indistinct towards the apex (Fig. 13A); antenna brownish, pedicel sparsely setose; basal body of flagellum subcylindrical with a single and short arista shorter than the pedicel length. Postclypeus black, inflated, with convex profile, longitudinal carina present, lateral grooves slightly marked (Fig. 13B, C); rostrum with second segment yellowish and third segment brownish, reaching the base of mesocoxae. Pronotum black, hexagonal, with muscular insertions slightly apparent, median carina slightly marked; anterior and anterolateral margins straight; posterolateral with slight sinuosity and posterior margin medially grooved, humeral angles acute; scutellum black, with slight central concavity and slightly marked horizontal grooves. Tegmina (Fig. 13A, B) brownish, narrow, with one transverse complete band yellowish between basal and median third and an incomplete yellowish band resembling rounded spots, between median and apical third; veins M and Cu1 united at base, veins A1 and A2 distincts, apical reticulation undeveloped, prominent venation. Hindwings hyaline, with brownish venation, Cu1 thickened at the base, hamuli with three spines. Legs light brown, metathoracic femur with a small apical spine; tibia with two lateral spines, basal one smaller than the ones located at apical crown, which has 12–14 spines arranged in two rows; basitarsus with three rows of spines covered by long setae; subungueal process present. — **MALE: Genitalia:** Pygofer (Fig. 13D, E) with one finger-like processes between anal tube and subgenital plate; subgenital plate long, not excavated at the basal portion, covered with small tooth-like spines, and narrowing towards the apex, which is acute. Paramere (Fig. 13F) subretangular, dorsal margin rounded and developed, apex rounded; subapical hook-like spine directed outwards and forward. Aedeagus (Fig. 13G–I) subcylindrical, narrowing towards apex with a pair of straight dorsal processes, shorter than half the length of the shaft and inserted between middle and apical third of aedeagus. — **FEMALE:** Morphology similar to that of the male, but slightly larger in relation to total body length. First valvula of ovipositor long (Fig. 13J, K), with acute apex, basal process rounded and developed, directed downwards; second valvula (Fig. 13L) long with rounded apex and dorsal margin covered by teeth in apical third; third valvula short and wide, with rounded apex, covered ventrally by long setae.

Remarks. This species was being treated as *M.* (*I.*) *aguirrei* mainly by the pattern and coloration of the tegmina,

and the phylogenetic analysis presented here corroborates a close relationship between these species (Fig. 4). Despite this, they differ in several aspects in relation to male genitalia: while *M.* (*I.*) *aguirrei* presents a long subgenital plate with rounded apex and a rounded depression on its basal third, *M.* (*I.*) *nefasta* **sp. nov.** has an acute subgenital plate apex. Moreover, *M.* (*I.*) *aguirrei* has a subquadrangular paramere apex, which differs from the rounded paramere apex seen in *M.* (*I.*) *nefasta* **sp. nov.** In comparison to the other species within the subgenus, this species presents a more developed basal process of the ovipositor.

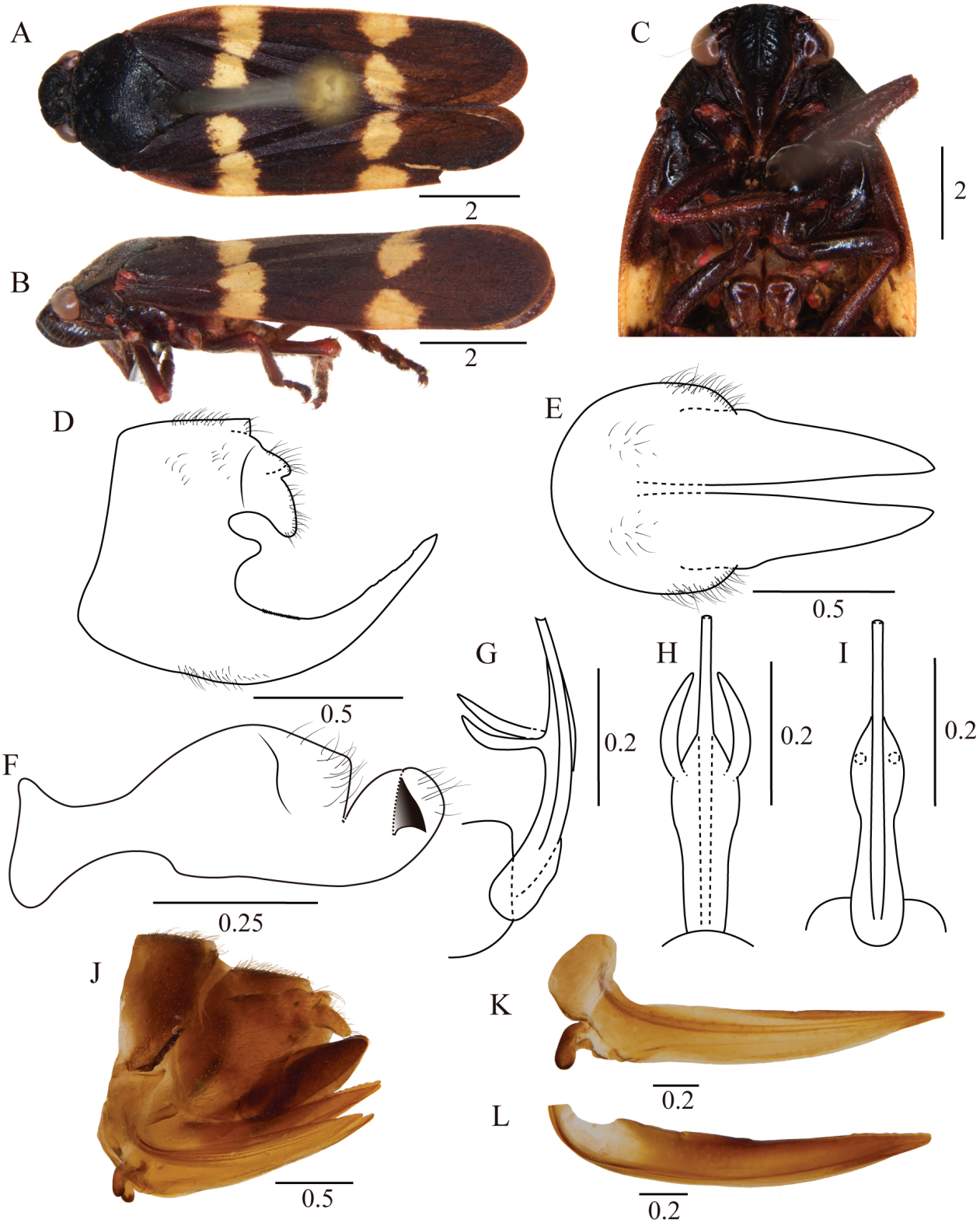

Figure 13. *Mahanarva* (*Ipiranga*) *nefasta* **sp. nov.** Habitus: **A** dorsal view; **B** lateral view; **C** ventral view. Male genitalia, pygofer: **D** lateral view; **E** ventral view. Paramere: **F** lateral view. Aedeagus: **G** lateral view; **H** dorsal view; **I** ventral view. Female genitalia, ovipositor: **J** lateral view. First valvulae: **K** lateral view. Second valvulae: **L** lateral view. Scale bars in mm.

Etymology. The new species name is due to the fact that it had long been mistaken for *M.* (*I.*) *aguirrei* in our morphological analyses.

Distribution. Brazil (Minas Gerais).

Material examined. BRASIL, **Holotype** ♂**: Minas Gerais:** Uberaba, 04.i.1984, Koller, W.W. leg. (MCTP); **Paratypes:** same data as holotype, 8 ♂, 6 ♀ (DZUP).
Adicional material examined. BRASIL, **Minas Gerais:** Uberaba, 04.i.1984, Koller, W.W. leg. 9 ♂, 3 ♀ (MCTP).

4. Discussion

4.1. Taxonomy and phylogenetic analysis

Several studies inferring the relationships within Cercopidae have been performed recently (Paladini et al. 2008; Paladini et al. 2010; Paladini et al. 2015; Paladini and Cavichioli 2015; Paladini et al. 2018), both at the tribal level as well as on genera and species level. Even

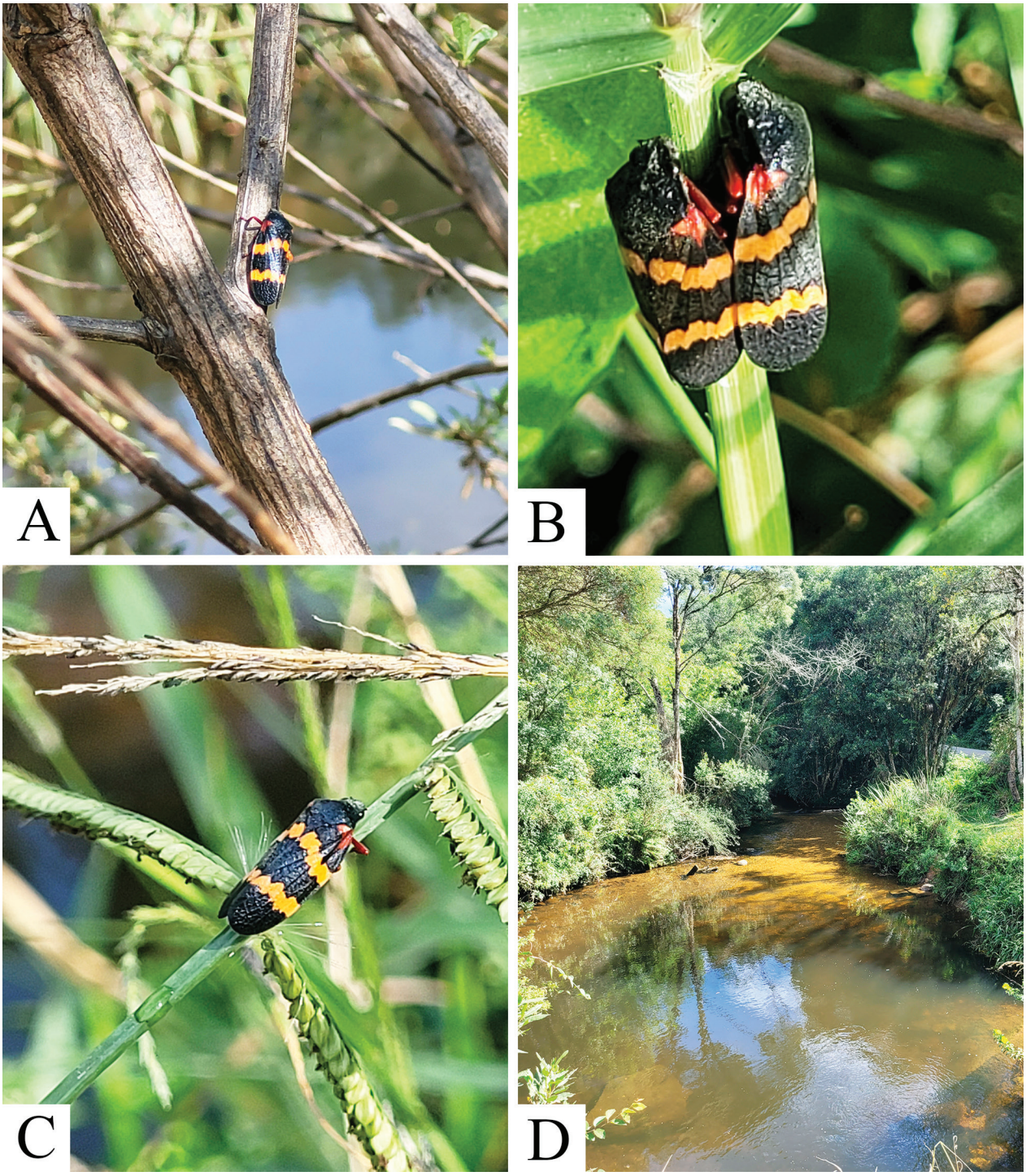

Figure 14. *Mahanarva* (*Ipiranga*) *obliqua* **sp. nov.** in its natural habitat. **A**–**C** *Mahanarva* (*Ipiranga*) *obliqua*: Brazil, Paraná, Piraquara (photo by Raul Czelujinski Varella); **D** Site where the species was collected (photo by Raul Czelujinski Varella).

though the number of phylogenetic studies is increasing, there are still many questions to be elucidated due to the great diversity and homogeneity of the group, especially within genera. In this study, *Mahanarva* (*Ipiranga*) was recovered as paraphyletic (Fig. 4), disagreeing with the results of previous studies that included a lower sampling of the subgenus (Paladini et al. 2008; Paladini et al. 2015; Paladini et al. 2018). While species of *Mahanarva* (*Ipiranga*) exhibit several morphological differences from *Mahanarva* (*Mahanarva*), the findings from our phylogenetic analyses suggest that these characteristics may not be sufficient for their clear separation on a phylogenetic basis.

Fennah (1968) distinguished between *M.* (*M.*) and *M.* (*I.*) primarily based on the proportion of the tegmina: the former typically has a length-to-width ratio of less than three (<3), whereas the latter tends to have a ratio greater than three (>3). Species of *Ipiranga* have a narrow tegmina, but in this analysis this character (19_0) supported the grouping of *M.* (*Ipiranga*) + *M.* (*Mahanarva*) + *Kanaima*, even though its homoplastic origin. In turn, the profile shape of the postclypeus, which is one of the taxonomic characters that morphologically distinguish both subgenera, supports *Mahanarva* (*Mahanarva*) *tristis* (Fabricius, 1803) + (postclypeus angled in profile- 9_0) and also is a homoplastic character.

In taxonomic studies, Cercopidae characteristics of genitalia are extensively utilized for identifying both genera and species. Often, the polymorphism in tegmina coloration, widely present in this family, or even the overall similarity within some distant related taxa can only be discerned through the extraction and analysis of the genitalia. This underscores the crucial role of genitalia analysis in achieving clear differentiation between genera and/or species (Fennah 1968; Schöbel and Carvalho 2021; Schöbel et al. 2022). Establishing phylogenetic characters that encompass all genitalia variations and constructing characters that adhere to the principles of homology present significant challenges. Sometimes characters that help on a taxonomic diagnosis are homoplastic or lack a clear phylogenetic signal. Fennah (1968) also grouped cercopid species according to male and female genitalia, highlighting that their characteristics are less susceptible to be influenced by parallel evolution. Similarly, two synapomorphic and one homoplastic male characters appear supporting *M.* (*Ipiranga*) + *M.* (*Mahanarva*) + *Kanaima* in the phylogenetic analysis presented here: dorsal processes of aedeagus located on the middle third (43_1), elongated shape of dorsal processes of aedeagus (44_0) and apex of aedeagus truncate (49_1), respectively.

Regarding the female genitalia, the first valvula of the ovipositor could exhibits variation in shape and in the presence or absence of the basal process (Fennah 1968). Only recently the ovipositor of *Mahanarva* species has been described and illustrated for a few species, and a study with Scanning Electron Microscopy shows differences in characters related to the three valvulae (Schöbel and Carvalho 2021). Fennah (1968) highlight that the basal process is significantly smaller in *M.* (*I.*) compared to *M.* (*M.*). Indeed, in our phylogenetic results, the first valvulae of the ovipositor with a developed basal process and the presence of teeth in dorsal margin of the second valvula extending beyond apical third are homoplastic characters supporting the paraphyletic *M.* (*M.*) *tristis* +.

Our phylogenetic results recovered *Mahanarva* (*Mahanarva*) as paraphyletic, with two species of *Kanaima* as sister group of *M.* (*M.*) *dubia*. Similar results was found by Paladini et al. (2015) using morphological data: *Mahanarva cruxminor* appears as sister group of *Urubaxia tricolor*. Furthermore, in a molecular-based analysis, *Carpentiera insignis* Lallemand, 1954, *Kanaima fluvialis*, and *Kanaima katzensteinii* were recovered nested within *Mahanarva* (*Mahanarva*) (Paladini et al. 2018).

The phylogenetic relationship between species of *Mahanarva* (*Mahanarva*) and *Kanaima* may be a consequence of the morphological similarity between both genera. Lallemand (1912), in his redescription of *Kanaima*, highlights the similarities with *Mahanarva*. In the original description of *Kanaima dubia*, Stancik and Cavichioli (2003) report their difficulty in including the species in either *Mahanarva* or *Kanaima* highlighting their reservations regarding its taxonomic status. Even with the morphological similarity between both genera, it is important to highlight that *Kanaima* species exhibit a preference for a specific host plant, being consistently found among the leaves of *Eryngium* spp. (Apiaceae). This preference reflects in the morphology of these species, as they present a more flattened postclypeus and a dorsoventrally flattened body.

Despite the morphological similarities and the results obtained from our phylogenetic analysis, in this study, we decided against modifying the taxonomic status of the subgenera and genus. The low branch support and the difficulty in gathering a greater number of characters highlights the need for future phylogenetic studies with molecular data including a higher taxonomic sampling.

4.2. Multivariate analysis

Male genitalia morphology has been an important diagnostic character in Cercopidae taxonomy (Paladini and Carvalho 2008; Paladini and Cavichioli 2014; Carvalho et al. 2016; Schöbel et al. 2022). However, the female morphology is quite homogeneous with low interspecific variation (Figs 7N–P, 8N–P, 9J–L, 11J–L, 12J–L, 13J–L). Some characteristics of the ovipositor valves can be used for genera diagnosis and intergeneric differentiation, however in *Mahanarva* (*Ipiranga*) we could not find the ovipositor valvulae as an useful character to discriminate between species.

M. (*I.*) *vittata* exhibits a wide range of intraspecific variation in male genitalia, leading Carvalho & Webb (2005) to revalidate its junior synonym: *M.* (*I.*) *fortunata*. *M.* (*I.*) *vittata* has an aedeagus with dorsal processes shorter than half the length of the shaft (Fig. 3 [103–A], yellow cluster), unlike *M.* (*I.*) *fortunata*, where the processes are longer (Fig. 3 [569–A, 570–A, 571–A], yellow cluster). However, some specimens have variable process lengths, such as specimen 65A from blue cluster,

in which the aedeagus resembles *M.* (*I.*) *fortunata* **syn. nov.** pattern, but the paramere and subgenital plate exhibit the *M.* (*I.*) *vittata* pattern. The paramere of *M.* (*I.*) *vittata* has the dorsal margin slightly elevated, whereas in *M.* (*I.*) *fortunata* **syn. nov.**, the elevation of the margin is more pronounced and mountain-shaped, as can be seen in Fig. 3 [569–B, 570–B, 571–B]. These specimens had been previously identified as *M.* (*I.*) *fortunata* **syn. nov.**, but some specimens grouped in the blue and grey cluster show an intermediate condition between both morphs, such as 253–B and 558–B. The same variation can be observed in the dorsal margin of the subgenital plate, which can be rounded (as in specimens 569–C, 570–C, 571–C) or straight, as in the rest of the specimens.

The principal component analysis (PCA) and cluster analysis are a multivariate statistical procedures commonly used to reveal patterns in measured correlated variables, however, in our results, the PCA suggested no difference on the morphospace between *M.* (*I.*) *vittata* and *M.* (*I.*) *fortunata* **syn. nov.** and the clusters obtained don't show a geographic or a morphological pattern, reinforcing the taxonomic synonym of these two species. Intraespecific variation in the genitalia pattern can be common in Auchenorrhyncha (Hamilton 1982; Domahovski and Cavichioli 2023).

5. Conclusion

Our study presents several pioneering aspects related to research with *Mahanarva* (*Ipiranga*): we performed the first phylogenetic analysis of the subgenus, the redescription of its species, the description of two new species, illustrations of their habits and genitalia, and a key for species identification. The results obtained from the phylogenetic analyses support the paraphyly of *Mahanarva* (*Ipiranga*) and the close relation with *Mahanarva* (*Mahanarva*) + *Kanaima*.

For future research, we highlight the need for a taxonomic and phylogenetic revision of *Mahanarva* (*Mahanarva*) to elucidate the relation between its species and with *Kanaima*. Finally, we emphasize the importance of taxonomic studies, especially in Cercopidae, to increasingly expand our knowledge of the group's diversity and to enable other studies to be carried out effectively.

6. Competing interests

The authors have declared that no competing interests exist.

7. Acknowledgments

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Supplementary Material 1

Figures S1–S4

Authors: Meneghetti J, Biganzoli-Rangel AJ, Carvalho GS, Paladini A (2025)
Data type: .pdf
Explanation notes: Figure S1. Cluster analyses for *M.* (*I.*) *fortunata* (**syn. nov.**) and *M.* (*I.*) *vittata* based on linear morphometric characters: **A** Cluster analysis of females, **B** cluster analysis of females by geographic states, **C** cluster analysis of females by unique ID. — **Figure S2.** Cluster analyses for *M.* (*I.*) *fortunata* (**syn. nov.**) and *M.* (*I.*) *vittata* based on linear morphometric characters: **A** cluster analysis of males and females, **B** cluster analysis of males and females by geographic states, **C** cluster analysis of males and females by unique ID. — **Figure S3.** Plot of the PCA and Cluster analyses for *M.* (*I.*) *fortunata* (**syn. nov.**) and *M.* (*I.*) *vittata* based on linear morphometry: **A** Females, **B** males and females. — **Figure S4.** Strict consensus of 4 trees resulting from the equal weights analysis of morphological data matrix.

Link: https://doi.org/10.3897/asp.83.e130043.suppl1

Supplementary Material 2

Tables S1–S4

Authors: Meneghetti J, Biganzoli-Rangel AJ, Carvalho GS, Paladini A (2025)
Data type: .zip
Explanation notes: Table S1. Specimens examined, morphometric characters and geographic distribution. — **Table S2.** Data matrix based on morphological characters. The columns refer to characters and the lines refer to species. Missing and unobservable character states were scored with "-" and "?", respectively. Polymorphic character states were coded with "*". — **Table S3.** Summary of comparative analysis of cladograms using SPR distance, Farris' distortion coefficient and Robinson-Foulds index. EW, equal weight tree; Dist, distortion; K, concavity constant; Lenght, length; Trees, number of cladograms obtained; F, fit.; CI, consistency index; RI, retention index; SPR, SPR distance averages; DC, Farris' distortion coefficient averages; RF, Robinson-Foulds index averages. The blue highlighted values indicate the K range and cladograms used to discuss the results. — **Table S4.** Analysis for the twenty K values using SPR distance (SPR), Farris' distortion coefficient (DC) and Robinson-Foulds index (RF). The last column (highlighted in bold) indicates the average of values for each of the three parameters tested. The blue highlighted values indicate the cladograms most similar to each other.

Link: https://doi.org/10.3897/asp.83.e130043.suppl2