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Anisoedessa, a new genus of Edessinae (Hemiptera: Heteroptera: Pentatomidae) and considerations on Edessinae relationships based on cladistic analysis

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Abstract. We tested the monophyly of a new genus *Anisoedessa*, which includes six new species: *A. proctocarinata* sp.n., *A. bispinosa* sp.n., *A. proctolabiata* sp.n., *A. flavomaculata* sp.n., *A. calodorsata* sp.n. and *A. ypsilonlineata* sp.n. The monophyly of *Anisoedessa* was supported by four synapomorphies: presence of dorsoposterior ridge on the proctiger; presence of ventroposterior margin, forming a lip on the proctiger, except in *A. flavomaculata*; proctiger excavated latero-posteriorly, except in *A. flavomaculata*; and ventral metallic sheen on abdominal intersegments. Forty-eight characters were selected from 28 taxa, 22 of which form the ingroup, including *Anisoedessa* (6 spp.), *Ascra* (1 sp.), *Brachystethus* (1 sp.), *Doesburgedessa* (2 spp.), *Edessa* (4 spp.), *Grammedessa* (2 spp.), *Olbia* (1 sp.), *Paraedessa* (2 spp.), *Pantochlora* (1 sp.), *Peromatus* (1 sp.), *Plagaedessa* (2 spp.), and *Pygoda* (1 sp.); and four outgroup taxa, *Neotibilis* sp., *Serdia*, and *Lopadusa* spp. (2 spp.). Phylogenetic analyses were conducted using TNT. Bootstrap and Bremer support in TNT showed statistical support for the monophyly of Edessinae and *Anisoedessa*; indicated *Edessa* as polyphyletic; and some support for natural groupings of *Doesburgedessa*, *Grammedessa*, and *Paraedessa*, although further analysis is needed in testing the monophyly of these genera. A key, diagnoses, descriptions as well as select images and illustrations of morphological features are provided for all species of *Anisoedessa*, as are geographical distributions on an illustrated map.

Key words. Pentatomoidea, taxonomy, phylogeny, Neotropics, new species, *Edessa*, key to species.

1. Introduction

Edessinae is predominately Neotropical in distribution, with the exception of *Ascra bifida* Say, 1832 restricted to the southern United States (Santos et al. 2015). The subfamily can be recognized by the presence of a raised metasternal process projecting anteriorly on the mesosternum (with the apex bifurcating or not); and by the mesosternal carina being lower than the metasternal process (Barcellos & Grazia 2003). Currently, Edessinae includes ten genera: *Ascra* Say, 1832 (14 species); *Brachystethus* Laporte, 1832 (10 species); *Doesburgedessa* Fernandes, 2010 (5 species); *Edessa* Fabricius, 1803 (around 300 species); *Grammedessa* Correia & Fernandes, 2016 (12 species); *Olbia* Stål, 1862 (3 species); *Pantochlora* Stål, 1870 (1 species); *Paraedessa* Silva & Fernandes, 2013 (9 species); *Peromatus* Amyot & Serville, 1843 (8 species); *Plagaedessa* Almeida & Fernandes, 2018 (4 species); and *Pygoda* Amyot & Serville, 1843 (9 species). This composition of Edessinae is widely accepted (i.e. Stål 1872; Kirkaldy 1909; Rolston & Mcdonald 1979; Fernandes & Van Doesburg 2000a,b,c; Barcellos & Grazia 2003; Santos et al. 2015), but a consensus has not been reached (Rider et al. 2018). Six additional genera are hypothesized to be part of Edessinae: *Lopadusa* Stål, 1860; *Pharnus* Stål, 1867; *Neopharnus* Van Duzee, 1910; *Praepharnus* Barber & Bruner, 1932; *Mediocampus* Thomas, 1994; and *Platistocoris* Rider,

1998. However, phylogenetic analyses are needed to test these placements.

Among the ten recognized genera of Edessinae, *Edessa* has no exclusive diagnostic characteristics, which pushes its limits close to the ones of the subfamily, resulting in considerable confusion between both taxa. This has led over the decades to an accumulation of approximately 300 species (Fernandes pers. comm.) within *Edessa*, transforming it into a "reservoir" of taxa (FERNANDES & VAN DOESBURG 2000c).

Some authors have attempted to reclassify *Edessa*. STÅL (1872) recognized species groups based on morphological characteristics for 60% of the included species. However, subsequent authors seldom followed his hypothesized groups (i.e. BREDDIN 1907). Most of the subsequent work consisted of isolated descriptions of species (DISTANT 1880; BERGROTH 1891; BREDDIN 1901, 1904; BARBER 1935), producing an inchoate classification framework of *Edessa*. KIRKALDY (1909) elevated Stål's species groups to subgenera of *Edessa*, including *Aceratodes* De Geer, 1773; *Ascra* Say, 1832; *Dorypleura* Lepeletier & Serville, 1825; *Edessa* Fabricius, 1787; *Hypoxys* Fabricius, 1803; and *Pygoda* Lepeletier & Serville, 1825. In recent years, J.A.M. Fernandes and colleagues have begun revising *Edessa*, proposing new species groups and genera based on likely putative synapomorphies (FERNANDES & VAN DOESBURG 2000a,b,c; FERNANDES et al. 2001; ELY E SILVA et al. 2006; FERNANDES 2010; FERNANDES & CAMPOS 2011; SILVA & FERNANDES 2012; SILVA et al. 2013; SANTOS et al. 2014; SANTOS et al. 2015; CORREIA & FERNANDES 2016; NASCIMENTO et al. 2017; ALMEIDA et al. 2018; FERNANDES et al. 2018). However, the monophyly of these species groups and genera were not tested phylogenetically, with the exception of *Brachystethus* (BARCELLOS & GRAZIA 2003).

Other species groups of Edessinae even lack the "dumpster" treatment of *Edessa*. In fact, J.A.M. Fernandes (based on his unpublished data) estimates an additional 300 species of Edessinae yet to be described. One such group is hypothesized to be related to the subgenus *Hypoxys* by the presence of the humeral angle shape and 7th abdominal segment projected posteriorly. We are naming this proposed new genus *Anisoedessa*, which presently includes six new species. The focus of this study is to 1) test the monophyly of the species group proposed as *Anisoedessa*; 2) examine the relationships of *Anisoedessa* with other Edessinae genera and *Edessa* species groups or subgenera; and 3) provide a key, diagnosis, and description of all species of *Anisoedessa*.

2. Material and methods

2.1. Taxonomy of *Anisoedessa*

We examined 55 specimens. The terminology follows DUPUIS (1970) and KMENT & VILÍMOVÁ (2010) for genitalia and scent apparatus respectively. Measurements were taken with a Zeiss Discovery V8 stereomicroscope presented in millimeters. Digital images were created using Leica DFC 450 camera, Leica M205A stereomicroscope, and multiple images were stacked with Leica LAS suite. Illustrations were made using a drawing tube attached to a Leica M205C stereomicroscope. Maps were made in QUANTUN GIS (2009).

2.2. Phylogenetic analyses

2.2.1. Taxon sampling. A total of 28 taxa were included in the analysis, 24 of which are ingroup taxa, including all six species of the proposed new genus *Anisoedessa*, and four outgroup taxa (Table 1).

2.2.2. Character sampling. A total of 49 morphological characters were established, 38 from general morphology of the body and 11 from male genitalia (section 3.1. and Table 1; 4 were adapted from BARCELLOS & GRAZIA 2003). The data matrix was edited in Mesquite (MADDISON & MADDISON 2011).

2.2.3. Analysis. All characters were treated as discrete and unordered. Phylogenetic relationships were tested using maximum parsimony in TNT 1.1 (GOLOBOFF et al. 2008). Character polarization followed the outgroup method (NIXON & CARPENTER 1993). Trees were calculated using TNT 1.1 (GOLOBOFF et al. 2008). Heuristic searches used 10000 replications and 100 trees saved per replication, RAS mechanism (Random addition sequence) and TBR (Tree-bisection Reconnection). We selected implied weighting (GOLOBOFF 1993) using the K=3 setting (default of the program). We summarized the analysis into a strict consensus tree. Branch support was calculated using TNT script BREMER RUN and expressed in the tree by Bremer support (BREMER 1994). Bootstrap analyses (FELSENSTEIN 1985) used TBR branch-swapping and consisted of 100 pseudoreplicates. Tree statistics (steps, retention index and consistency index) were calculated using WinClada 1:00:08 (NIXON 2002) and were also calculated for each character.

2.3. Abbreviations

Morphology. ch – chitinellipsen; **dr** – dorsal rim; **drc** – ductus receptaculi; **drg** – dorsal ridge of proctiger; **gc8** – gonocoxite 8; **gc9** – gonocoxite 9; **la8** – laterotergite 8; **la9** – laterotergite 9; **pa** – paramere; **pc –** pars communis; **pm –** metasternal process; **proc** – proctiger; **pyg** – pygophore; **tvi** – thickening of vaginal intima; **vr** – ventral rim; **X** – tenth segment.

Depositories. CAS – California Academy of Science, São Francisco, USA (Norman Penny); **DRC –** David Rider Collection, Fargo, USA (David Rider); **INPA –** Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (J. Albertino Rafael); **JEE –** Joseph Eger collec-

tion, Tampa, USA (Joseph Eger); **LRC –** Lupoli Roland Collection, Paris, France (Lupoli Roland); **MNHN** – Musée National d'Histoire Naturelle, Paris, France (Dr. Eric Guilbert); **UFRGS –** Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil (Jocélia Grazia); **RMNH –** National Museum of Natural History, Leiden, Nederland (Yvonne van Nierop); **USNM –** National Museum of Natural History, Smithsonian Institution, Washington, D.C, USA (Thomas Henry).

3. Results and discussion

3.1. List of characters

1 Head, ratio length of buccula: length of eye: **(0)** ≤ 1 (Fig. 1A); **(1)** > 1.5 (Fig. 1B). — CI = 100, RI = 100.

2 Head, black longitudinal stripes: **(0)** absent (Fig. 1C); **(1)** present (Fig. 1D). — There are 6 or 8 stripes in state (1); CI = 100, RI = 100.

3 Head, rows of punctures: **(0)** absent (Fig. 1C); **(1)** present (Fig. 1D). — There are 6 or 8 rows in state (1); CI = 100, RI = 100.

4 Head, antennae, first segment black with a ventral yellow spot: **(0)** absent (Fig. 1A); **(1)** present (Fig. 1B). — CI = 100, RI = 100.

5 Pronotum, humeral angles, shape of apex: **(0)** rounded (Fig. 1E); **(1)** dentiform (Fig. 1F); **(2)** globose (Fig. 1G); **(3)** laminar (Fig. 1D). — CI = 100, RI = 100.

6 Pronotum, humeral angle, transversal section: **(0)** flat (Fig. 1F); **(1)** rounded (Fig. 1G). — CI = 100, RI = 100.

7 Pronotum, humeral angle, slant: **(0)** level (Fig. 1H); **(1)** slanting dorsally (Fig. 1I). — CI = 100, RI = 100.

8 Pronotum, humeral angle, orientation: **(0)** lateral (Fig. 2A); **(1)** anteriorly bent (Fig. 2B). — CI = 50, RI = 50.

9 Pronotum, lateral margin, shape: **(0)** straight (Fig. 2C); **(1)** concave (Fig. 2B). — CI = 100, RI = 100.

10 Pronotum, humeral angle, length compared to width: **(0)** wider than long (Fig. 1F); **(1)** longer than wide (Fig. 1G, dashed line cuts the angle). — CI = 100, RI = 100.

11 Pronotum, humeral angle, color of apex: **(0)** concolorous with pronotum, but never black (Fig. 1C); **(1)** black, in contrast to green to dark green pronotum (Fig. 1D). — CI = 100, RI = 100.

12 Pronotum, humeral angle, length of the dark spot: **(0)** shorter than head width (Fig. 1H); **(1)** equal to or longer than head width (Fig. 1I). — CI = 100, RI = 100.

13 Pronotum, humeral angle, punctuation of apex: **(0)** present (Fig. 1H); **(1)** absent (Fig. 1I). — CI = 33, RI = 84.

14 Pronotum, humeral angle, length compared to head width: **(0)** shorter than head width (Fig. 1H); **(1)** longer than head width (Fig. 1I). — CI = 100, RI = 100.

15 Width of abdomen compared to width of pronotum: **(0)** abdomen wider than pronotum (Fig. 1E); **(1)** abdomen narrower than pronotum (Fig. 1G). — CI = 100, RI = 100.

16 Scutellum, apex form: **(0)** acute (Fig. 3C); **(1)** rounded (Fig. 3D). — CI = 50, RI = 75.

17 Corium, color: **(0)** concolorous with pronotum (Fig. 1E); **(1)** uniformly brown, in contrast to pronotum (Fig. 1G); **(2)** variegated (Fig. 1F). — CI = 40, RI = 70.

18 Thorax, ventral side, metallic sheen on stained areas: **(0)** absent (Fig. 2C); **(1)** present (Fig. 2D). — CI = 100, RI = 100.

19 Mesosternal keel, height: **(0)** equal to metasternal process (Fig. 1A); **(1)** lower than metasternal process (Fig. 1B). — CI = 100, RI = 100. Adapted from Barcellos & Grazia (2003).

20 Metasternal process, anterior margin: **(0)** undivided and truncate (Fig. 2E); **(1)** slightly notched and touching mesosternum (Fig. 2F); **(2)** deeply notched and touching mesosternum (Fig. 2G); **(3)** undivided, rounded, and touching mesosternum (Fig. 2H); **(4)** undivided, conical, and free (Fig. 2I). — CI = 100, RI = 100. Adapted from Barcellos & Grazia (2003).

21 Metasternal process, extension relative to anterior margin of mesocoxa: **(0)** not exceeding anterior margin (Fig. 2E); **(1)** exceeding anterior margin (Fig. 2G). — CI = 100, RI = 100.

22 Metasternal process, anterior bifurcation, apex: **(0)** rounded (Fig. 2G); **(1)** acute (Fig. 2C). — CI = 50, RI = 66.

23 Femur, apex, dorsal surface, color of margin: **(0)** concolorous with surrounding area (Fig. 2J); **(1)** solid black, in contrast to yellow to dark brown (Fig. 2C). — CI = 50, RI = 90.

24 Femur, dorsal surface, distal margin: **(0)** not projected (Fig. 2J); **(1)** projected in a flap (Fig. 2C). — CI = 50, RI = 90.

25 Femur, dorsal surface, tooth on distal margin: **(0)** absent (Fig. 2J); **(1)** present (Fig. 2K). — CI = 50, RI = 75.

26 Femur, apex, lateral surface, color of margin: **(0)** concolorous with surrounding area (Fig. 2J); **(1)** solid black, in contrast to yellow to dark brown (Fig. 2K). — CI = 33, RI = 77.

27 Femur, apex, lateral surface, tooth: **(0)** absent (Fig. 2J); **(1)** present (Fig. 2K). — CI = 50, RI = 90.

28 Femur, ventral surface, yellow spot: **(0)** absent (Fig. 2C); **(1)** present (Fig. 2D). — CI = 50, RI = 66.

29 Femur and tibia, longitudinal black stripes: **(0)** absent (Fig. 1A); **(1)** present (Fig. 1B). — CI = 100, RI = 100.

30 Abdomen, dorsal surface, metallic sheen: **(0)** absent (Fig. 3A); **(1)** present (Fig. 3B). — CI = 33, RI = 77.

31 Connexivum punctures: **(0)** uniformly punctured (Fig. 3C); **(1)** not punctured on a medial calloused spot (Fig. 3D). — CI = 25, RI = 70.

32 Connexivum, intersegmental stripes: **(0)** absent (Fig. 3C); **(1)** present (Fig. 3D). — Intersegmental stains are present in *Hypoxys* and *Plagaedessa*, but in both cases they do not cover the margin of segments and are associated with coarse punctures, in *Anisoedessa*

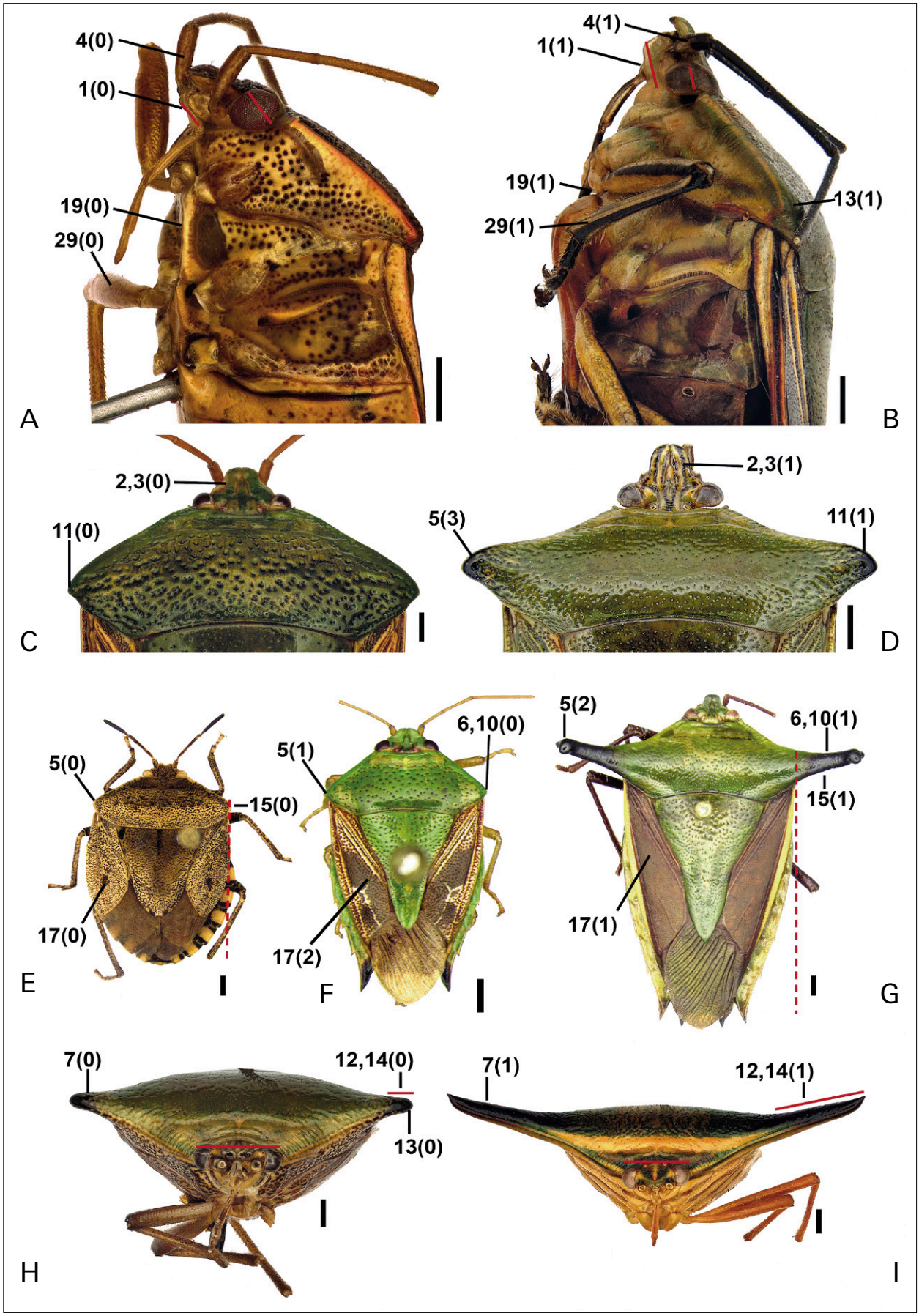

Fig. 1. Characters of Edessinae: **A**: Pronotum of *Neotibilis* sp. in lateral view; **B**: Pronotum of *Plagaedessa celsa* in lateral view; **C**: Pronotum of *Pygoda polita*; **D**: Pronotum of *Grammedessa pallicornis*; **E**: *Lopadusa* sp.; **F**: *Paraedessa* sp.; **G**: *Edessa cervus*; **H**: *Grammedessa pallicornis*; **I**: *Edessa bubalus*. — ***Scale bars***: 1 mm.

Table 1. Taxa included in the analysis (outgroup taxa in grey; ingroup taxa, i.e. Edessinae, in white) and data matrix of their morphological characters. The symbols '?' and '–' were used for lacking observations for a character and for cases of inapplicability of a character, respectively.

Character	**0000000001**	**1111111112**	**2222222223**	**3333333334**	**4444444444**
Taxon	**1234567890**	**1234567890**	**1234567890**	**1234567890**	**1234567890**
Neotibilis sp.	0000000000	0–00000000	0–00000000	000000000–	00–000000
Lopadusa (*Bothrocoris*) *fuscopuntacta* (Distant, 1880)	0000000000	0–00010010	0–00010000	000000000–	---0–0000
Lopadusa (*Bothrocoris*) *quinquedentata* (Spinola, 1837)	0000000000	0–00010010	0–00000000	000001000–	000000000
Serdia sp.	0000000000	0–00000000	0–00000001	000000000–	---0–0000
Anisoedessa calodorsata sp.n.	1000100000	0–10101112	1011011101	1111011112	111011001
Anisoedessa bispinosa sp.n.	1000100000	0–10101112	1011011001	1011011112	111001001
Anisoedessa flavomaculata sp.n.	1000100000	0–10101112	1011011101	1110011112	100001001
Anisoedessa ypsilonlineata sp.n.	1000100000	0–10101112	1011011101	1110011112	111011001
Anisoedessa proctocarinata sp.n.	1000100000	0–10101012	1011011101	0000011112	111001001
Anisoedessa proctolabiata sp.n.	1000100000	0–10101112	1011011001	1110011112	111001001
Ascra bifida (Say, 1832)	0000000000	0–00011012	1000000000	0000010012	000001001
Brachystethus cribrus (Fabricius, 1781)	0000000000	0–00010011	0–00000000	000001–012	000001001
Doesburgedessa nigrolimbata Fernandes, 2010	1000211011	1001101014	1–00000000	1001110212	000001001
Doesburgedessa rugifera (Stål, 1872)	1000211011	1001101014	1–00000000	1001110212	000001001
Edessa (*Dorypleura*) *bubalus* (Lepeletier & Serville, 1825)	1000211111	1101101012	1011111001	1001110212	000001001
Edessa (*Edessa*) *cervus* (Fabricius, 1787)	1000211111	1111101012	1011111000	1000010112	000001001
Edessa (*Hypoxys*) *quadridens* Fabricius, 1803	1000100000	0–10102012	1111011000	1001010112	000001001
Edessa (*Aceratodes*) *rufomarginata* (De Geer, 1773)	1000000000	0–00010012	1000000000	0000010012	000001001
Grammedessa pallicornis (Walker, 1868)	1110300010	1000100012	1111111000	1000010110	000001001
Grammedessa bugabensis (Distant, 1890)	1110300010	1000100012	1111111000	1000010110	000001001
Olbia elegans (Herrich-Schäffer, 1839)	1000211111	1001101012	1000000000	000001–110	000001001
Pantochlora vivida Stål, 1870	1000100000	0–00100013	1–00000000	000001–112	000001001
Paraedessa stolida (Linnaeus, 1758)	1000100000	0–10102012	1011011001	1001010112	000111101
Paraedessa albomaculata Silva & Fernandes, 2013	1000100000	0–10102012	1011011001	1001010112	000111101
Peromatus bolivianus Fallou, 1887	1000210011	1010101012	1011111000	0000010111	000001001
Plagaedessa celsa (Distant, 1890)	1001100000	0–10101012	1011011010	1001010112	000001011
Plagaedessa distanti Almeida & Fernandes, 2018	1001100000	0–10101012	1011011010	1001010112	000001011
Pygoda polita (Lepeletier & Serville, 1825)	1000100000	0–10101012	1111011000	1001010212	000001001

stripes cover the margins and are impunctate. Accordingly, we are considering these stains a case of analogy and not homology. CI = 100, RI = 100.

33 Connexivum punctures, metallic sheen: **(0)** absent (Fig. 3C); **(1)** present (Fig. 3D). — CI = 100, RI = 100.

34 Abdomen, segment VII, dorsal, black stain on distal half: **(0)** absent (Fig. 3A); **(1)** present (Fig. 3B). — CI = 16, RI = 50.

35 Abdomen, segment VII, 90° torsion of the projected part: **(0)** absent (Fig. 3H); **(1)** present (Fig. 3B). — CI = 50, RI = 50.

36 Abdomen, fusion of lateral parts of sternites II and III: **(0)** absent (Fig. 2J); **(1)** present (Fig. 2K). — This fusion occurs on the lateral margin near the connexivum. — CI = 100, RI = 100.

37 Abdomen, ventral surface, intersegmental stripes, metallic sheen: **(0)** absent (Fig. 3H); **(1)** present (Fig. 3I). — CI = 100, RI = 100.

38 Abdomen, segment VII, extension of the distal angle: **(0)** not reaching apex of laterotergites 9 (Fig. 3E); **(1)** level with laterotergites 9 (Fig. 3F); **(2)** surpassing apex of laterotergites 9 (Fig. 3G). — CI = 50, RI = 77.

39 Pygophore, superior process of genital cup: **(0)** absent (Fig. 4A); **(1)** present (Fig. 4B). — CI = 100, RI = 100.

40 Pygophore, superior process of genital cup, position: **(0)** adjacent to proctiger (Fig. 4B); **(1)** adjacent to base of parameres (Fig. 4C); **(2)** adjacent to dorsal rim of pygophore (Fig. 4D). — CI = 66, RI = 50.

41 Pygophore, proctiger, dorsoposterior ridge: **(0)** absent (Fig. 4C); **(1)** present (Figs. 4F, 7B). — CI = 100, RI = 100.

42 Pygophore, proctiger, ventroposterior margin expansion: **(0)** absent (Fig. 4C); **(1)** present, forming a lip (Fig. 4E). — CI = 50, RI = 75.

43 Pygophore, proctiger, excavation: **(0)** lateral (Fig. 4C); **(1)** lateroposterior (Fig. 4F). — CI = 50, RI = 75.

44 Pygophore, proctiger, lateral expansions of posterior surface: **(0)** absent (Fig. 4E); **(1)** present (Fig. 4D). — CI = 100, RI = 100.

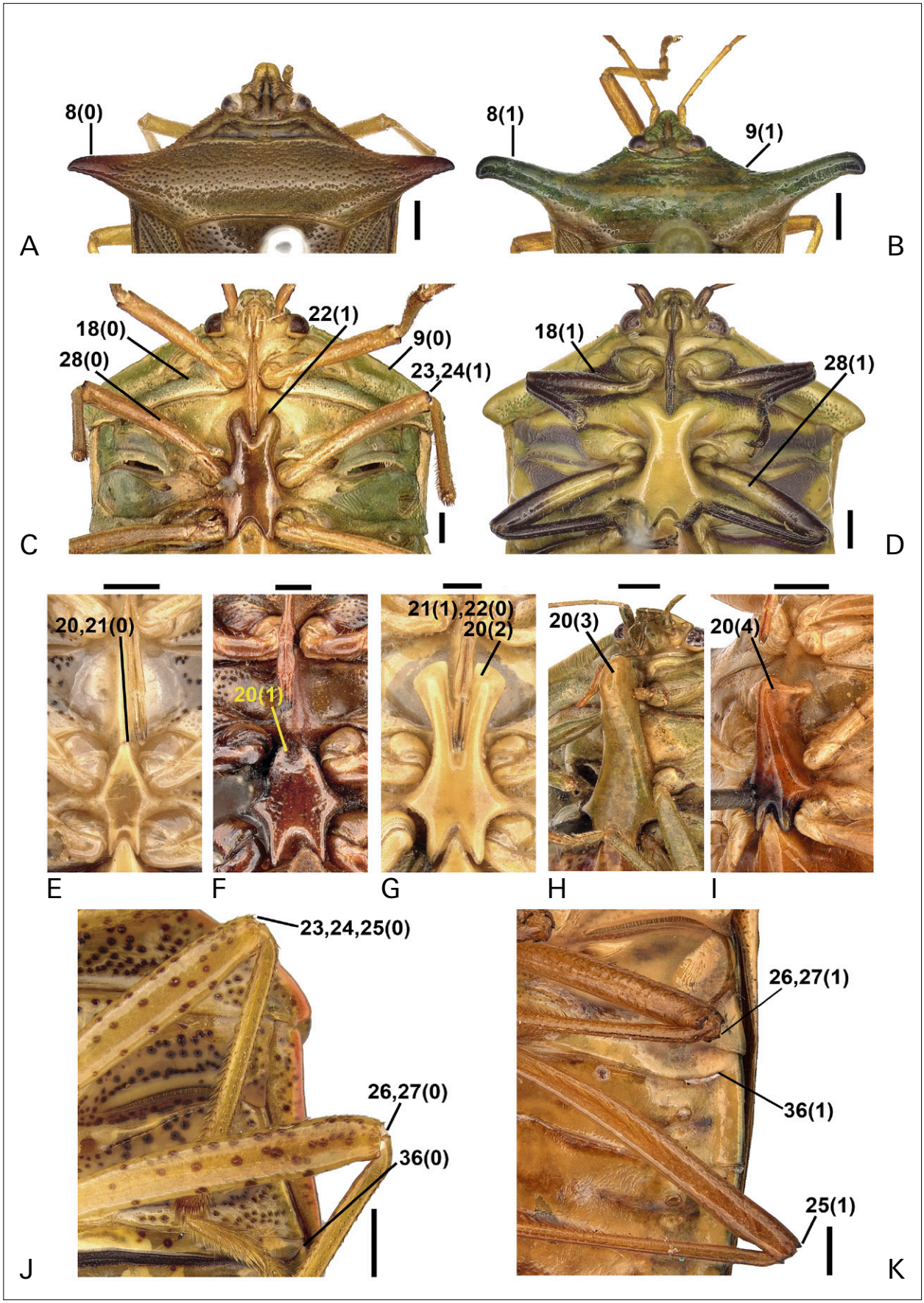

Fig. 2. Characters of Edessinae: **A**: Pronotum of *Doesburgedessa nigrolimbata*; **B**: Pronotum of *Olbia elegans*; **C**: Thorax of *Pygoda polita*, ventral view; **D**: Thorax of *Anisoedessa flavomaculata*, ventral view; **E**: Metasternal process of *Neotibilis* sp.; **F**: Metasternal process of *Brachystethus cribrus*; **G**: Metasternal process of *Edessa bubalus*; **H**: Metasternal process of *Pantochlora vivida*; **I**: Metasternal process of *Doesburgedessa nigrolimbata*; **J**: Mid and hind legs of *Neotibilis* sp.; **K**: Mid and hind legs of *Edessa bubalus*. — ***Scale bars***: 1 mm.

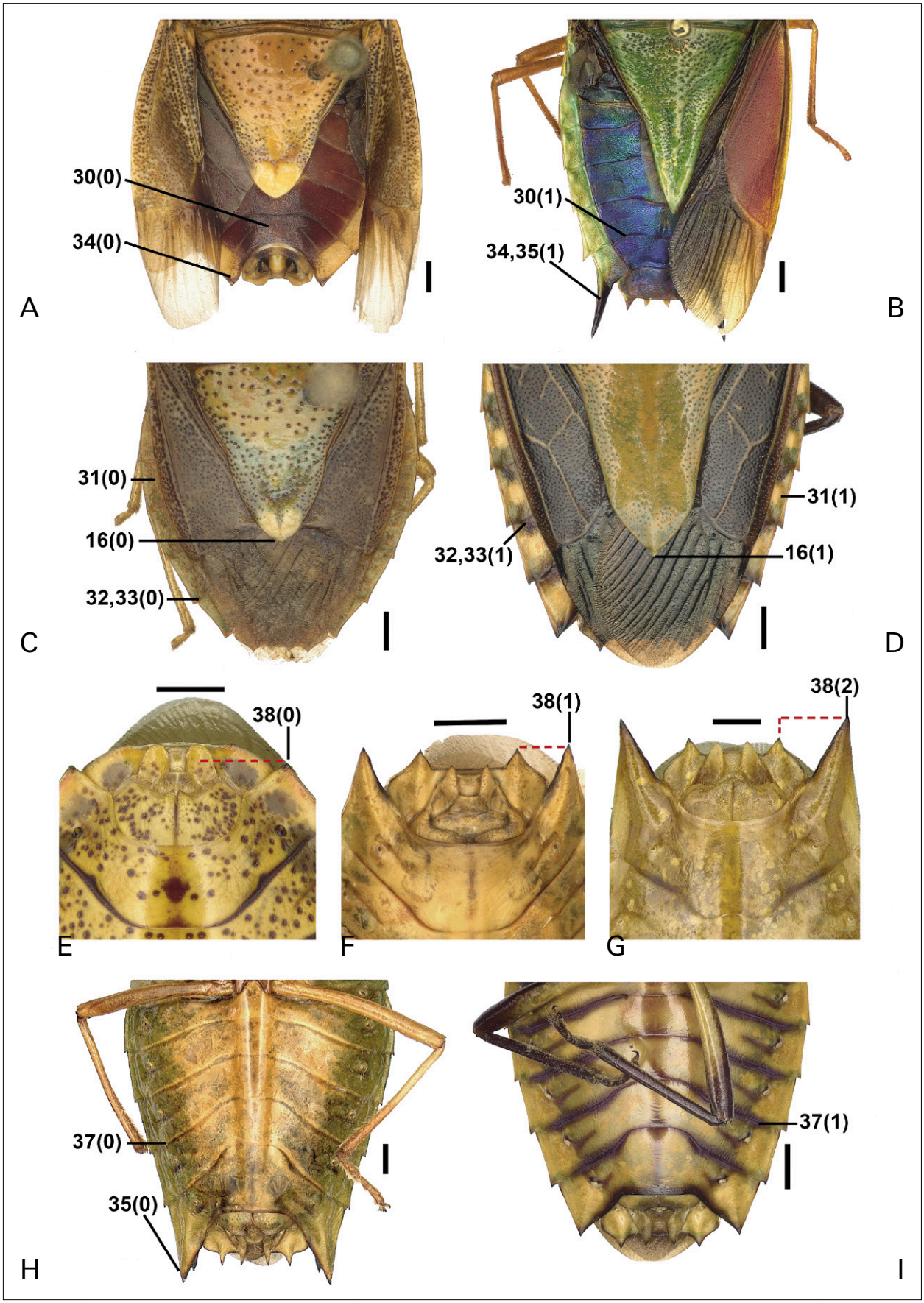

Fig. 3. Characters of Edessinae: **A**: Abdomen of *Ascra bifida*, dorsal view; **B**: Abdomen of *Edessa bubalus*, dorsal view; **C**: Apex of the scutellum and connexivum of *Ascra bifida*; **D**: Apex of the scutellum and connexivum of *Anisoedessa flavomaculata*; **E**: Genital plates of *Neotibilis* sp.; **F**: Genital plates of *Paraedessa stolida*; **G**: Genital plates of *Doesburgedessa nigrolimbata*; **H**: Abdomen of *Pygoda polita*, ventral view; **I**: Abdomen of *Anisoedessa flavomaculata*, ventral view. — ***Scale bars***: 1 mm.

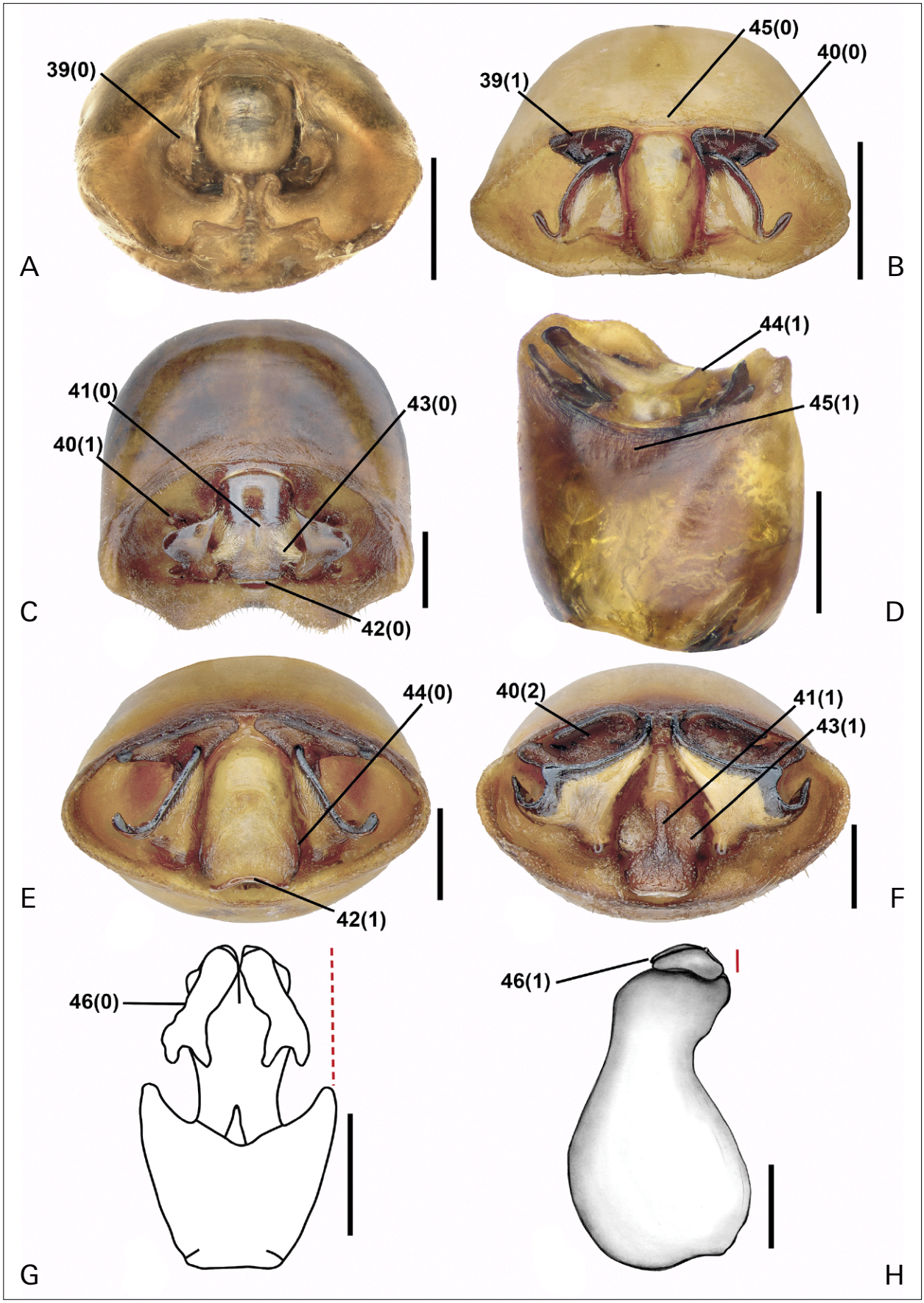

Fig. 4. Characters of Edessinae: **A**: Pygophore of *Neotibilis* sp., posterior view; **B**: Pygophore of *Olbia elegans*, posterior view; **C**: Pygophore of *Peromatus bolivianus* posterior view; **D**: Pygophore of *Paraedessa stolida* dorsolateral view; **E**: Pygophore of *Anisoedessa proctolabiata*, posterior view; **F**: Pygophore of *Anisoedessa proctocarinata* posterior view; **G**: Phallus of *Neotibilis fulvicornis*, redrawn from BARCELLOS & GRAZIA (2003); **H**: Phallus of *Pygoda polita*. — ***Scale bars***: 1 mm.

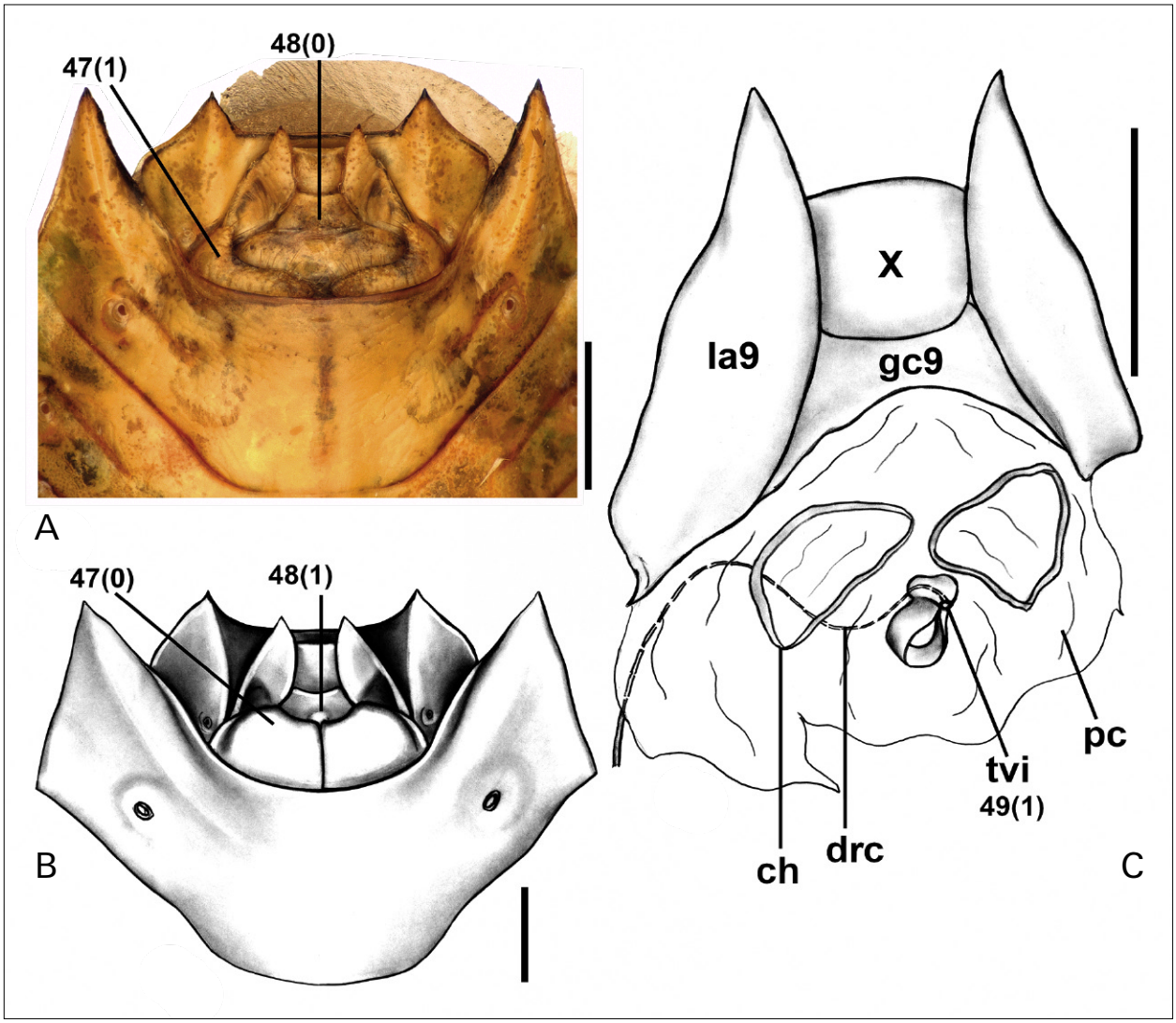

Fig. 5. Characters of Edessinae: **A**: Genital plates of *Paraedessa stolida*; **B**: Genital plates of *Plagaedessa celsa*; **C**: Female genitalia of *Pygoda expolita*. — ***Abbreviations***: ch – chitinellipsen; dr – ductus receptaculi; gc9 – gonocoxite 9; la9 – laterotergite 9; pc – pars communis; tvi – thickening of vaginal intima; X – abdominal segment X. — ***Scale bars***: 1 mm.

45 Pygophore, dorsal rim, small median notch: **(0)** absent (Fig. 4B); **(1)** present (Fig. 4D). — CI = 50, RI = 66.

46 Phallus, development of vesica: **(0)** well developed (Fig. 4G); **(1)** poorly developed (Fig. 4H). — CI = 100, RI = 100. Adapted from Barcellos & Grazia (2003).

47 Female genital plates, gonocoxites 8 development: **(0)** well developed (Fig. 5B); **(1)** poorly developed (Fig. 5A). — CI = 100, RI = 100.

48 Female genital plates, gonapophysis 9 sclerotized forming a protuberance at the base of gonocoxites 9: **(0)** absent (Fig. 5C); **(1)** present (Fig. 5B). — CI = 100, RI = 100.

49 Female genital plates, thickening of vaginal intima: **(0)** lack of a raised drop-like projection; **(1)** presence of a raised drop-like projection (see Barcellos & Grazia 2003: fig. 22). — The name beak-like was not used. — CI = 100, RI = 100. Adapted from Barcellos & Grazia (2003).

3.2. Phylogenetic results

The analysis under the implied weighting resulted in one most parsimonious tree with 89 steps (L), consistency index (CI) 64 and retention index (RI) 86 (Fig. 6). A very similar topology was obtained as the strict consensus from three most parsimonious trees under traditional search. Four trends were observed from this tree: 1) support of *Anisoedessa* as monophyletic; 2) support for the monophyly of Edessinae; 3) polyphyly of *Edessa*; and 4) some support for the monophyly of genera described by Fernandes and colleagues (Silva et al. 2013; Correia & Fernandes 2016; Almeida et al. 2018) (Fig. 6). Four synapomorphies supported the new genus *Anisoedessa*: presence of a dorsoposterior ridge on the proctiger; presence of the ventroposterior margin, forming a lip on the proctiger, except in *A. flavomaculata*; proctiger excavated lateroposteriorly, except in *A. flavomaculata*; and ventral metallic sheen on abdominal intersegments (Fig. 6).

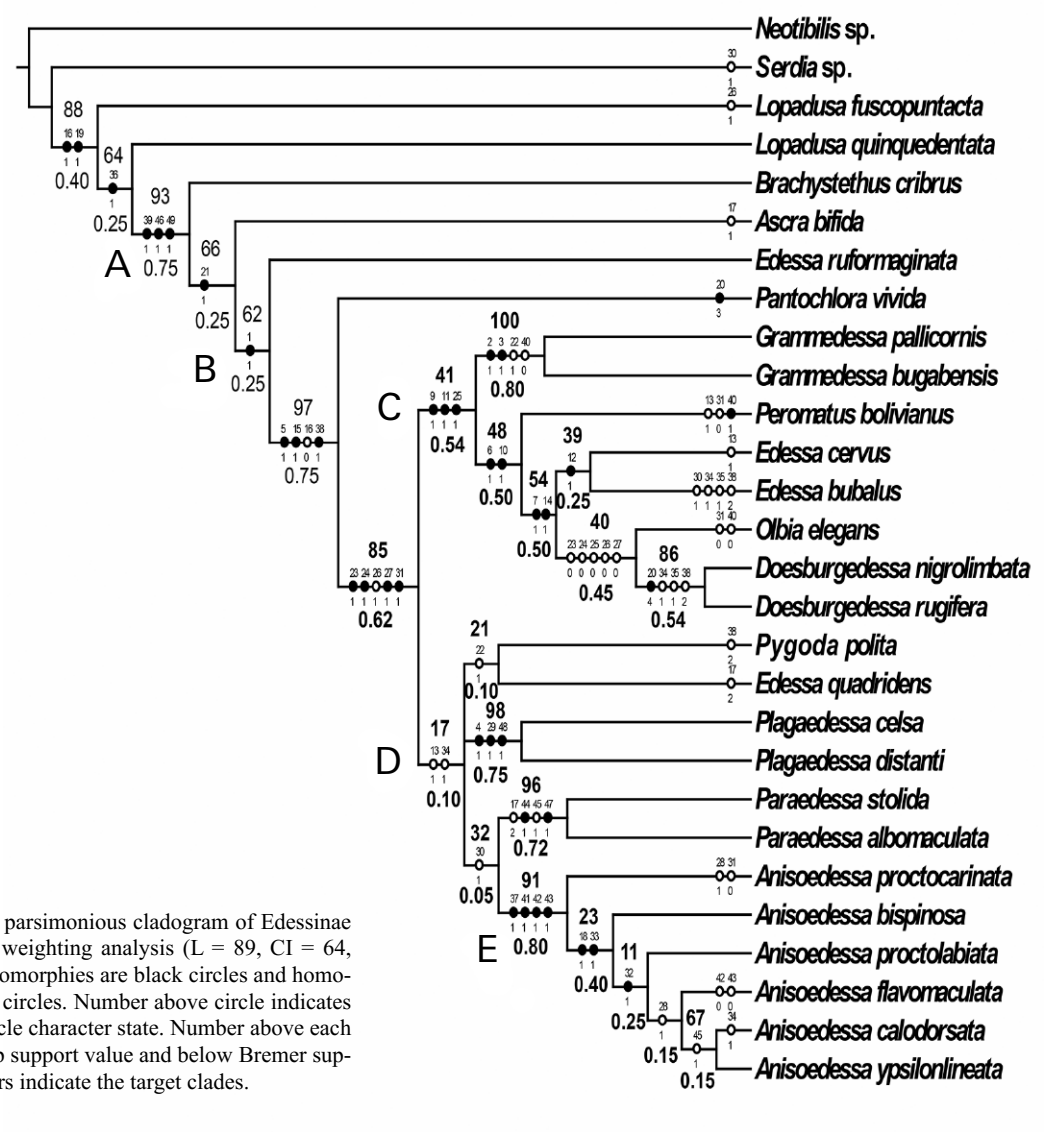

Fig. 6. The single most parsimonious cladogram of Edessinae obtained from implied weighting analysis (L = 89, CI = 64, RI = 86). Unique synapomorphies are black circles and homoplasious ones are white circles. Number above circle indicates character and below circle character state. Number above each node indicates bootstrap support value and below Bremer support value. Capital letters indicate the target clades.

Weak support between these species may also be a result of homoplasy. Minimizing the effects of homoplasy in this analysis may be improved by increasing taxon sampling (HEATH et al. 2008); data partitioning (NYLANDER et al. 2004) of genitalic and coloration characters; and increasing the taxa to character ratio, which was quite low at 1.76:1.

Maximum parsimony also supported *Brachystethus* as the sister taxon of all remaining Edessinae lineages (Fig. 6 Clade A) agreeing with BARCELLOS & GRAZIA (2003). This analysis tested the monophyly of this taxon in a more robust scenario using more taxa representing morphological diversity of Edessinae and Pentatomini, and a new synapomorphy for this clade (abdominal sternites II and III fused laterally) never used before.

Our phylogeny also showed *Edessa* to be polyphyletic (Fig. 6). The monophyly of *Edessa* was not tested by BARCELLOS & GRAZIA (2003), making this analysis the first attempt in examining the natural condition of *Edessa*. The idea that *Edessa* is not a monophyletic taxon was first mentioned by FERNANDES & DOESBURG (2000a). Species currently included in the genus appeared in Clades B, C, and D (Fig. 6). In Clade B, *E. rufomarginata* is sister to the *Pantochlora-Anisoedessa* clade supported by three synapomorphies (Fig. 6). This clade is well supported (Bootstrap: 62; Bremer: 0,25) and comprises most of the species of Edessinae included in this analysis. Clade D shows a polytomy with weak support, but in all analysis composition and topology of the polytomy was stable (Fig. 6). This low statistical support is consequence of lack of more characters.

Recently described Edessinae genera (*Doesburgedessa*, *Paraedessa*, *Grammedessa*, and *Plagaedessa*) showed statistical support in our phylogenetic tree (Fig. 6). All synapomorphies or homoplasies supporting these genera are mentioned in their original descriptions and are used to separate them from other genera of Edessinae. In clade D, except for *Pygoda*, all other taxa are historically part of the subgenus *Hypoxys* due to diagnostic features identified by STÅL (1872). A more comprehensive study involving species with acute and short pronotal angle, including all taxa from clade D+E, is under development. This study will include a larger number of species (around 100) and new characters to increase the taxa to character ratio (GRAYBEAL 1998); and possible insufficient taxa sampling, which may decrease branch and node support (HEATH et al. 2008).

Testing the monophyly and relationships of *Hypoxys* with other Edessinae genera will improve our understanding of Edessinae evolution and biodiversity as whole.

3.3. Identification key of *Anisoedessa*

1 Venter green; abdominal sternites with intersegmental vittae light metallic violet (Fig. 13B,L) **2**
1' Venter yellow or greenish yellow, abdominal sternites with intersegmental vittae unmuted metallic violet (Fig. 13F,H) **3**
2 Punctures on connexivum with metallic sheen; posterior surface of the proctiger without a median carina (Fig. 12B); gonocoxites 8 convex (Fig. 12D) ..... ***A. ypsilonlineata***
2' Punctures on connexivum without metallic sheen; posterior surface of proctiger with large median carina (Fig. 7B); gonocoxites 8 with distinct transvers and medial fold (Fig. 7D) ..... ***A. proctocarinata***
3 Legs dark brown with ventral yellow stain on femora (Fig. 13H) **4**
3' Legs unicolorous (Fig. 13F) **5**
4 Ventral rim of pygophore with pair of bifurcated expansions (Fig. 8B); superior process of the genital cup almost fused with the diaphragm; proctiger with a strongly developed lip on posterior surface (Fig. 8A–C); posterior margin of gonocoxite 8 straight or slightly concave (Fig. 8D) ..... ***A. bispinosa***
4' Ventral rim of pygophore without developed expansions; superior process of the genital cup well developed, and hastate; proctiger with a somewhat developed lip on posterior face (Fig. 9A–C); posterior margin of gonocoxite 8 distinctly arched (Fig. 9D) ..... ***A. proctolabiata***
5 Dorsal rim of pygophore with small lateral protuberances near posterolateral angles; superior process of the genital cup elliptical, pedunculate, and oblique to dorsal rim (Fig. 10A–B); gonocoxites 9 as wide as laterotergite 9 (Fig. 10D) ..... ***A. flavomaculata***
5' Dorsal rim of pygophore without protuberances; superior process of the genital cup subtriangular, flat and contiguous to dorsal rim (Fig. 11A–B); gonocoxites 9 almost 2 x wider than laterotergite 9 (Fig. 11D) ..... ***A. calodorsata***

3.4. *Anisoedessa* Nunes & Fernandes gen.n.

(Figs. 7–14)

Description. ***Head***: Mandibular plates with outer margin yellow anterior to the eyes; and surpassing clypeus. Inner margin of mandibular plates darker than cephalic disc. Clypeus seldom punctate. Ventral surface yellow, green or orange. Bucculae subtriangular. First rostral segment surpassing bucculae. Rostrum dark brown to black, except yellow base of first rostral segment. Rostral segment I < II > III > IV. Antennae orange or brown. ***Thorax***: Pronotum with scattered coarse punctures among dense small punctures; cicatrices and lateral margins not punctured; anterolateral margins yellow and almost straight; anterolateral angles with small yellow tooth. Scutellum with scattered coarse punctures among dense small punctures on anterior half, posterior half with dense, small, dark punctures; punctures brown or concolorous; apex acute. Hemelytra with shallow, dense and concolorous punctures (Fig. 13A,C,E,G,I,K). Venter yellow, orange, pale green or green. Propleuron with metallic violet vittae or metallic violet to reddish brown punctures. Evaporatorium darker than surrounding area, completely rugulose, coated by translucid whitish and dull texture. Mesopleural margin raised and yellow. Peritreme ruga-like and yellow. Metasternal process (mp) yellow with anterior half of the bifurcation raised; arms of the bifurcation anteriorly rounded and evanescent (e.g. Fig. 7E). Tibiae and tarsi densely setose, setae yellow and short. ***Abdomen***: Connexival segments III–VI green with yellow or light green median spot between shallow, densely punctate excavations on each segment, except flat, sparsely punctate segments in *A. proctocarinata*; excavations with metallic sheen; and lateral angles spinose. Connexivum segment VII dark brown to black with medial yellow or light green median spot, except entirely black segment of *A. proctocarinata*. Venter with intersegmental vittae wide and plainly metallic or reduced to a shallow reddish-brown line with metallic sheen. Elliptical spiracles within tumid area and somewhat posteriorly directed. Abdominal pseudosutures darker than surrounding area, metallic sheen variable (e.g. Fig. 13B). Pair of trichobothria in line with spiracles. ***Male terminalia***: Pygophore trapezoidal in dorsal view. Posterolateral angles rounded or truncate (e.g. Figs. 7A, 11A). Parameres (pa) large, long and anteriorly directed, almost reaching base of proctiger (proc). Proctiger cylindrical. Ventral rim of pygophore shallowly excavated and slightly tumid. Expansions of the ventral rim (vr) somewhat tumid and developed. Punctures distributed in a "V" pattern on ventral surface. ***Female terminalia***: Genital plates (Fig. 7D): Gonocoxites 8 (gc8) punctured and slightly convex, except folded in *A. proctocarinata*. Gonocoxites 9 (gc9) trapezoidal. Laterotergites 8 (la8) convex with a few concolorous punctures, distal margin black, projected and acute. Laterotergites 9 (la9) excavated or flat on basal half, remaining tumid; apex black and spinose surpassing the dorsal tergite uniting laterotergites 8. Tenth segment (X) square.

Diagnosis. Medium-sized species (10.2–17.7 mm). Dorsum green to dark green on head, pronotum and scutellum; corium dark brown; connexivum green, usually spotted. Venter yellow or brown or variegated yellow and green with transverse dark vittae. Dark stripes on thorax usually with metallic sheen, at least on propleura. Posterolateral angles of pronotum acute and not projected. Hemelytra brown to dark brown with corial veins yellow to green, medial one branched forming a "Y". Legs mostly dark brown with yellow area on femora or completely yellow. Dorsal surface of abdomen, dark spots on connexivum and intersegmental area of abdominal sternites

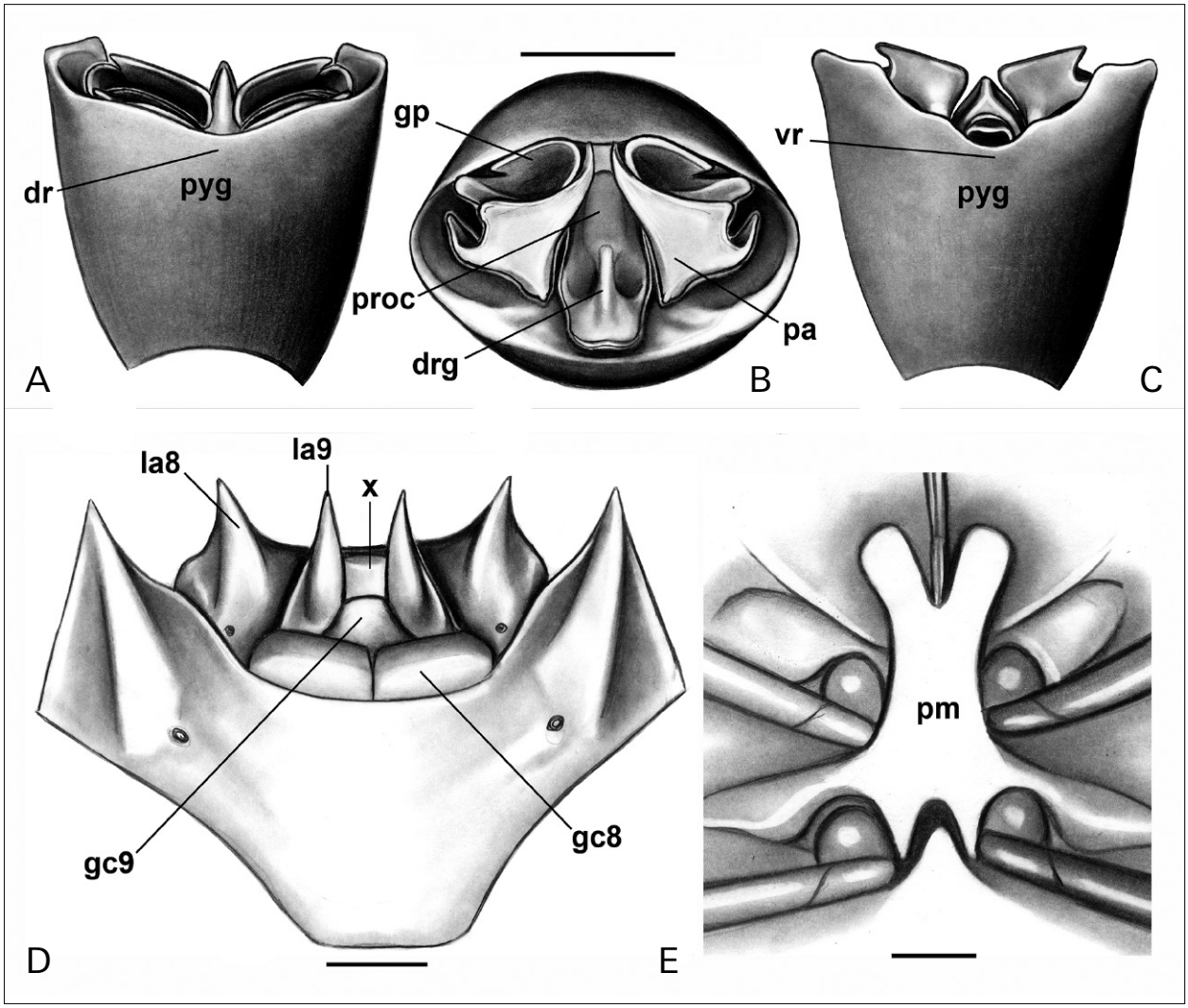

Fig. 7. *Anisoedessa proctocarinata* sp.n. **A**–**C**: male, pygophore, dorsal (**A**), posterior (**B**), and ventral (**C**) views; **D**: female, genital plates; **E**: metasternal process. — ***Abbreviations***: dr – dorsal rim; drg – dorsal ridge of proctiger; gp – genital cup process; gc8 – gonocoxite 8; gc9 – gonocoxite 9; la8 – laterotergite 8; la9 – laterotergite 9; pa – paramere; pyg – pygophore; VII – tergite VII; vr – ventral rim; X – abdominal segment X. — ***Scale bars***: 1 mm.

with metallic sheen. Pygophore wider than long. Parameres and superior processes of the genital cup proximal to proctiger. Proctiger with a dorsoposterior ridge variable in size; ventral margin of posterior face tumid and emarginated, sometimes forming a distinct curved directed posteriorly lip. Gonocoxites 8 subrectangular, wider than long and laterally slanting.

Etymology. Aniso = different, unequal. Gender feminine.

Type species. *Anisoedessa calodorsata* sp.n.

Remarks. *Anisoedessa* can be readily separated from other closely related Edessinae genera by the dorsoposterior ridge on the proctiger; presence of the ventroposterior margin, forming a lip on the proctiger, except in *A. flavomaculata*; proctiger excavated lateral-posteriorly, except in *A. flavomaculata*; and ventral metallic sheen on abdominal intersegments. *Anisoedessa* can be separated from *Paraedessa* by the monochromatic corium (variegated), dorsal side of abdomen uniformly dark metallic green or violet (metallic violet with large median yellow spots); *Anisoedessa* can be separated from *Edessa* (*Hypoxys*) by the monochromatic corium (variegated), humeral angles concolorous with pronotum (dark brown or black), and pygophore wider than long (longer than wide). An illustrated key separating all genera from Clade C can be found in ALMEIDA et al. (2018).

3.5. *Anisoedessa proctocarinata* Nunes & Fernandes sp.n.

(Figs. 7, 13 A,B, 14)

Description. ***Measurements***: Head length: 1.3–1.4 mm; head width: 2.7–3.0 mm; pronotal length: 3.3–3.6 mm; pronotal width: 7.6–9.4 mm; length of antennal segments: I: 1.0 mm; II: 1.4–1.5 mm; III: 2.5–2.9 mm; IV: missing; V: missing; total length: 13.3–17.7 mm; abdominal width: 6.7–8.4 mm. ***Head***: Bucculae punctate.

Fourth rostral segment resting between arms of metasternal process. ***Thorax***: Pronotum with concolorous punctures (Fig. 13A). Anterolateral margins green, anterior 1/3 rugulose. Corium brown with veins yellow or light green. Ventrally, prothorax with two brown sulcate lines. First line parallel to anterolateral margin (Fig. 13B); second line punctured, extending from base of coxa to lateral margin of propleuron, with faint metallic sheen. Small brown small punctures concentrated between second line and intersegmental brown margin. Mesepisternum with a narrow brown line. Evaporatorium mostly green with shallow grooves; mesepimerum greenish-yellow with a groove between margins, lacks rugulose ridge. Metepisternum with brown coloration concentrated near peritreme. Peritreme reaching 2/3 of the distance between ostiole of the scent gland and margin of metepleuron. Metasternal process with arms of the anterior bifurcation flat and subrectangular (Fig. 7E), somewhat divergent. ***Abdomen***: Dorsal surface metallic green or violet. Intersegmental stripes of abdominal sternites narrow and dark green with faint metallic reddish sheen. Spiracles without brown ring. Abdominal pseudosutures concolorous with ventral surface (Fig. 13B). ***Male terminalia***: Pygophore dorsal rim rugulose, punctate and fuscous. Posterolateral angles truncate and slightly projected (Fig. 7A). Superior process of the genital cup black, large, elliptical, dorsal margin touching dorsal rim; ventral lobe laterally directed (Fig. 7B). Paramere yellow with margin black; anteriorly directed lobe triangular and long; dorsal margin forming a small triangular lobe; posterior lobe digitiform curved lateral-dorsal; base cylindrical with a conical projection posteriorly directed (Fig. 7B). Proctiger strongly excavated laterally, forming a rounded concavity covered by dense short setae (Fig. 7B); posterior surface small and shallowly concave, ventral margin slightly projected. Ventral rim of pygophore sinuous; expansion laterally contiguous with posterolateral angle and acuminated (Fig. 7C), covered with long setae. Ventral punctures dense and coarse. ***Female terminalia***: Genital plates (Fig. 7D): Gonocoxites 8 densely punctate, not tumid, with slight transverse fold. Posterior margin straight. Gonapophysis 8 not visible. Gonocoxites 9 slightly convex and polished. Laterotergites 8 with distal spine strongly projected. Laterotergites 9 with base weakly excavated; posteriorly conical, extending past tergite connecting laterotergites 8.

Diagnosis. Each segment of connexivum flat with a medial small tumid concolorous area; no metallic color on connexivum. Body ventrally green with light transversal brown stripes only on thorax, faint metallic violet sheen only on propleural stripe (Fig. 13A,B). Antennae brown. Legs dark brown, ventral side of femora mostly dark yellow. Seventh abdominal segment of connexivum black. Intersegmental bands of abdominal sternites and metallic sheen weakly visible. Superior process of genital cup notched dorsally. Posterior surface of proctiger with large longitudinal median carina. Gonocoxites 8 with a median transverse fold (Fig. 7D).

Etymology. Name refers to the conspicuous carina on posterior surface of proctiger.

Distribution. French Guiana: Cayenne, Saint Laurent du Maroni; Guyana: Georgetown; Brazil: Pará (Fig. 14).

Material examined. ***Type material:*** Holotype male. 'FRENCH GUIANA, Saint Laurent du Maroni: Maripasoula, Massif Mitaraka | 01.iii.2015 Light trap | Coll R. Lupoli | MNHN (EH) 24487' (MNHN). – Paratypes. FRENCH GUIANA, Cayenne: 1 ♂ | Cabassou | Jan 1981 | G. Tavakilian leg. | Collection ORSTOM, D. Rider coll. (DRC); 2 ♀ Matiti ZA wayabo | 1–31.x.2013 | J. Giuglaris leg. | Flight interception trap. (JEE); 1 ♂ 5 km E Tonnegrande, 45 m | 04°48.176′N 052°25.525′W | MV Light, J. E. Eger Coll. (JEE); 1 ♂ 4 ♀ vic. Amazon Nature Lodge | 30 km SE Roura on Kaw Rd., 4–14.i.2016 | J. Eger, R. Morris, J. Wappes, 300 m, 04°33.570′N 052°12.433′W | MV Lights (JEE); 1 ♀ Saint-Élie, Inselberg HTE Koursibo, Savane-roche | 03.iii.2013 | Light trap | S. E. A. G. Coll R. Lupoli (RLC); Saint Laurent du Maroni: 1 ♀ Maripasoula, Massif Mitaraka | 24.ii.2015 Light trap | Coll R. Lupoli (RLC); GUYANA, Georgetown: 1 ♀ Demerara | R.J.Crew | 23.v.1901, EPVan Duzee Collection (CAS). BRAZIL, Pará: 1 ♀ Paragominas | 10–V–2018 | Al2 Arm. luminosa | Equipe entomologia Col. (UFRGS).

3.6. *Anisoedessa bispinosa* Nunes & Fernandes sp.n.

(Figs. 8, 13C,D, 14)

Description. ***Measurements***: Head length: 1.3–1.8 mm; head width: 2.2–2.3 mm; pronotal length: 2.6–3.1 mm; pronotal width: 6.5–8.0 mm; length of antennal segments: I: 0.8–1.0 mm; II: 1.0–1.7 mm; III: 2.5–3.2 mm; IV: 2.8 mm; V: missing; total length: 10.2–13.3 mm; abdominal width: 5.8–6.8 mm. ***Head***: Bucculae punctate. First rostral segment yellow and segments two, three and four brown. Fourth and part of the third rostral segment resting between arms of metasternal process. ***Thorax***: Concolorous punctures on pronotum (Fig. 13C). Anterolateral margins greenish, anterior 1/4 rugulose. Corium with green veins. Ventrally, first thoracic segment punctate, punctures concentrated on posterior half, punctures brown on a medial stripe; some punctures with metallic green sheen. Anterior margin of mesopleuron punctate, with a faint metallic sheen and a small spot proximal to coxa. Evaporatorium mostly brown, greenish yellow around thoracic spiracle. Peritreme reaching almost 3/4 of the distance between ostiole of the scent gland and margin of metepleuron. Bifurcating arms of metasternal process digitiform (Fig. 8E), and slightly divergent. ***Abdomen***: Dorsal surface variegated with metallic violet and green. Intersegmental stripes of abdominal sternites dark brown and narrow, sometimes medial region of first three visible segments without stripes. Stripes absent on median ventral longitudinal line of segments III and IV (Fig. 13D). Stripes with faint metallic reddish sheen. Spiracles in yellow tumid spots. Abdominal pseudosutures light brown with faint metallic sheen between spiracles and trichobothria. ***Male terminalia***: Pygophore dorsal rim projected posteriorly and medially excavated (Fig. 8B). Borders of the excavation black; margin arcuate and black, and distally with lateral acuminate expan-

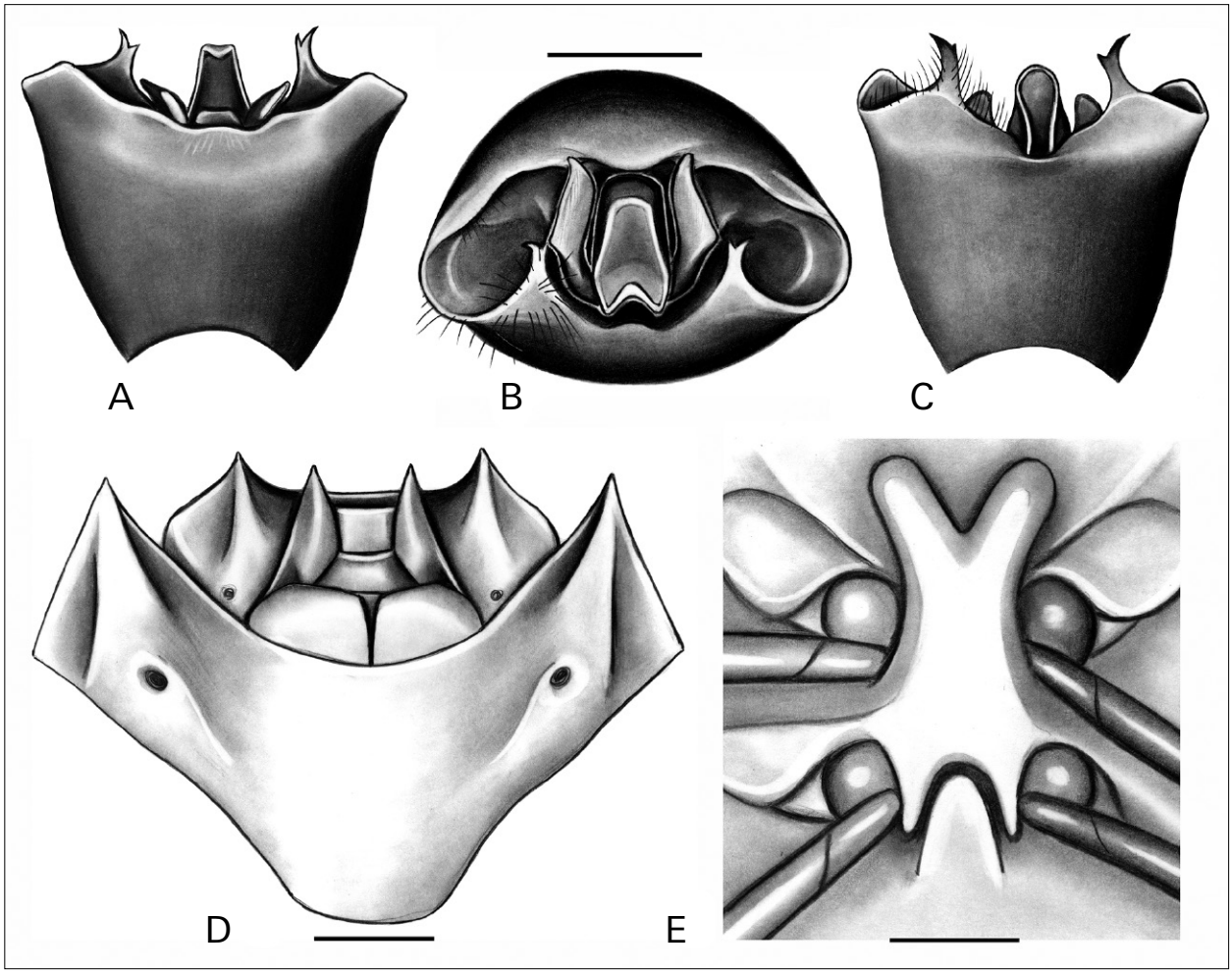

Fig. 8. *Anisoedessa bispinosa* sp.n. **A**–**C**: male, pygophore, dorsal (**A**), posterior (**B**), and ventral (**C**) views; **D**: female, genital plates; **E**: metasternal process. — ***Scale bars***: 1 mm.

sions extending beyond posterolateral angles (Fig. 8B). Posterolateral angles truncate (Fig. 8A). Superior process of genital cup triangular and brown. Paramere square, apically acute; dorsally acicular, yellow with margin black, dorsally directed touching dorsal rim; posterior margin with a small triangular process; base long and cylindrical (Fig. 8B). Proctiger very short; lateral surface with shallow excavation, setae sparse; posterior surface membranous and flat; ventral margin strongly projected into a membranous lip imbedded in sclerotized rim (Fig. 8B). Ventral rim of pygophore projected posteriorly, expansions strongly developed and projected posterodorsally (Fig. 8C). ***Female terminalia***: Genital plates (Fig. 8D): Posterior margin of gonocoxites 8 dark brown and truncate; black punctures concentrated on inner half; sutural borders slightly divergent distally. Gonocoxites 9 slightly convex and rugulose. Laterotergites 9 tumid, basally flat.

Diagnosis. Each segment of connexivum with a small medial yellow tumid spot and another small, anterior, punctured, rounded spot with faint metallic blue sheen. Body ventrally greenish-yellow with light brown transverse maculae showing faint metallic blue-green sheen. Antennae dark yellow. Legs dark brown, femora with ventral narrow brown maculae (Fig. 13D). Pygophore with dorsal rim projecting over genital cup; superior process of the genital cup almost completely fused with diaphragm (Fig. 8B). Proctiger with distal margin developed into concave lip. Ventral rim of pygophore expanded into bifurcated projections (Fig. 8C).

Etymology. Name refers to the bifurcated expansions of the ventral rim.

Distribution. Brazil: Amazonas; Peru: Madre de Dios (Fig. 14)**.**

Material examined. ***Type material***: Holotype male. 'BRAZIL. Amazonas: Coari | Rio Urucu Ig. [Igarapé] Marta | 3.4°50′0.73″S 65°02′37″W | 14–25.viii.1993, P.F. | Bührnheim et.al. col.' (INPA). – Paratypes. BRAZIL. Amazonas: 1 ♀ Coari, Rio Urucu | 4°51′56.5″S 65°0.4′56.6″W | 11–18.v.1991, P. Bührnheim | N.O Aguiar & F.A. Fé col (INPA); PERU: 1 ♂ Madre de Dios: Rio Tambopata Res. 30 air km. | SW Pto. Maldonado, 290 m. | 6–10. xi.1979, J.B. Heppner | subtropical moist forest (USNM).

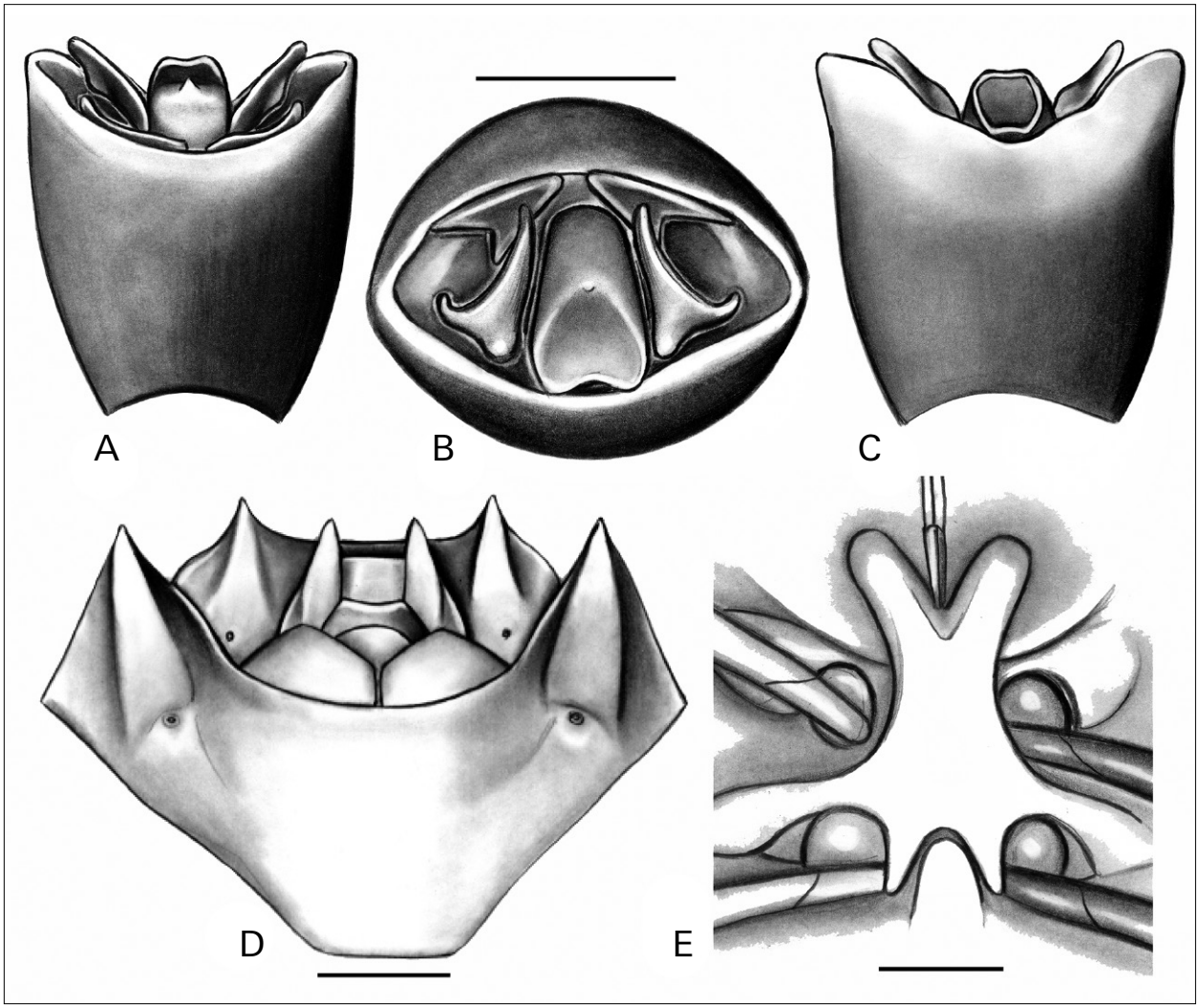

Fig. 9. *Anisoedessa proctolabiata* sp.n. **A**–**C**: male, pygophore, dorsal (**A**), posterior (**B**), and ventral (**C**) views; **D**: female, genital plates; **E**: metasternal process. — ***Scale bars***: 1 mm.

3.7. *Anisoedessa proctolabiata* Nunes & Fernandes sp.n.

(Figs. 9, 13 E,F, 14)

Description. ***Measurements***: Head length: 1.3–1.4 mm; head width: 2.3–2.4 mm; pronotal length: 2.2–2.6 mm; pronotal width: 6.3–7.2 mm; length of antennal segments: I: 0.7 mm; II: 1.0 mm; III: 2.4–2.5 mm; IV: 2.4 mm; V: missing; total length: 10.3–11.5 mm; abdominal width: 5.6–6.5 mm. ***Head***: Bucculae rugulose and punctate. Fourth rostral segment resting between arms of metasternal process. ***Thorax***: Pronotum with brown punctures. Anterolateral margin yellow, anterior 1/4 rugulose. Pale yellow veins on corium (Fig. 13E). Ventrally, first thoracic segment with fuscous punctures, concentrated on posterior half. Punctures and small spot proximal to coxa with metallic blue sheen. Anterior margin of mesopleuron punctate, dark green with metallic blue sheen. Evaporatorium mostly dark brown, except green and yellow posterior margin of mesepimeron. Mesepimeron with shallow furrow between margin and rugulose crest. Peritreme reaching 3/4 distance between ostiole of the scent gland and margin of metepleuron. Bifurcating arms of metasternal process ventrally flat, digitiform (Fig. 9E) and diverging. ***Abdomen***: Dorsal surface metallic, violet-green. Intersegmental stripes of abdominal sternites dark brown with metallic reddish sheen; narrow or absent on median ventral longitudinal line (Fig. 13F). Spiracles within yellowish, tumid spot. Abdominal pseudosutures brown with metallic reddish sheen. ***Male terminalia***: Pygophore dorsal rim fuscous and rugulose medially. Posterolateral angles rounded and slightly projected (Fig. 9A). Superior process of genital cup fuscous, adjacent to dorsal rim, and projected over proctiger (Fig. 9B). Paramere yellow, triangular, posterior lobe curved dorsally; base cylindrical (Fig. 9B). Proctiger with lateral surface smooth with few short setae; posterior surface coarse and shallowly concave; ventral margin posteriorly projected into lip with margin bilobate and brown (Fig. 9A,B); dorsal ridge minute, and conical. Ventral rim of pygophore sinuous, slightly expanded, rounded, setose adjacent to posterolateral angles (Fig. 9C). ***Female terminalia***: Genital plates (Fig. 9D): Gonocoxites 8 acuminate; posterior half mostly brown and punctate; sutural border slightly

diverging. Gonapophysis 8 overlapping base of gonocoxites 9. Gonocoxites 9 flat and broad. Laterotergites 9 mostly tumid, except a small, basal, flat area.

Diagnosis. Each segment of connexivum with a median yellow calloused spot and two concave brown spots with black punctures and metallic violet sheen. Body ventrally yellow with light green stripes on thorax and abdomen (Fig. 13E,F); green stripes with metallic violet blue sheen on middle of propleuron, anterior margin of metepleuron, and intersegmental area of abdominal sternites. Antennae and legs dark yellow. Pygophore with superior process of genital cup hastate (Fig. 9B). Female with gonapophysis 8 overlapping base of gonocoxites 9 (Fig. 9D).

Etymology. Name refers to the development of the posterior margin of the proctiger forming a lip.

Distribution. French Guiana: Cayenne, Saint-Laurent-du-Maroni (Fig. 14).

Material examined. ***Type material***: Holotype male. 'FRENCH GUIANA, Saint Laurent du Maroni: Mana Laussat P8 | 13.v.2010 | 05°28′31.6N 053°35′07.3W | Light trap | S. E. A. G,. leg. Coll R. Lupoli | MNHN (EH) 24488' (MNHN). – Paratypes. FRENCH GUIANA, Cayenne: 2 ♂ 2 ♀ 41 km SE Roura on Kaw Rd | 8.xii.2002, 04°32. 214′N 052°07.420′W | 272 m MV Light, J. E. Eger, Coll' (JEE); 1 ♂ 1 ♀ same data (UFRGS); 1 ♂ HWY N2 to Regina | 15 km. S. of Cayenne | 2.vi.1986 | E.G. Riley e D.A. Rider (DRC); 1 ♀ Hwy N2 to Regina | 67 Km. S. of Cayenne | 4.vi.1986 | E.G. Riley e D.A. Rider (DRC); 1 ♀ Patawa Mt. | 3.iii.1995 | 4.42N 53.54W, elev 650 m | at mercury vapor lights | coll. J. A. Levis (USNM); Saint Laurent du Maroni: 1 ♀ same data as holotype | MNHN (EH) 24489 (MNHN); 1 ♀ Route d' Apatou PK25 | 05.xii.2013. PolyVie trap | S. E. A. G. leg. Coll R. Lupoli (RLC).

3.8. *Anisoedessa flavomaculata* Nunes & Fernandes sp.n.

(Figs. 10, 13 G,H, 14)

Description. ***Measurements***: Head length: 1.6–2.0 mm; head width: 3.0 mm; pronotal length: 4.0–4.2 mm; pronotal width: 9.3–10.1 mm; length of antennal segments: I: 1.1 mm; II: 1.5 mm; III: 3.2–3.6 mm; IV: 3.6 mm; V: missing; total length: 14.7–16.4 mm; abdominal width: 8.1–8.6 mm. ***Head***: Bucculae rugulose and punctate. First rostral segment dark yellow and remaining segments dark brown. ***Thorax***: Pronotum with brown punctures. Anterolateral margin yellow, anterior 1/3 rugulose. Veins of corium green (Fig. 13G). Ventrally, prothorax with metallic green and violet vittae; punctuation coarse and concolorous. Anterior margin of mesopleuron mostly dark brown with metallic, green sheen; punctate, dark brown, metallic stripe on base of coxae. Evaporatorium bluish brown. Mesepimeron with deep groove between yellow margin and raised rugulose crest. Peritreme reaching 2/3 distance between ostiole of scent gland and dorsal-lateral margin of metepleuron. Bifurcating arms of metasternal process acuminate and laterad (Fig.10E). ***Abdomen***: Dorsal surface metallic violet. Connexivum with posterior angles black-capped spines. Dark brown intersegmental stripes of abdominal sternites narrowed medially and metallic violet (Fig. 13H). Brown coloration encircling spiracles. Pseudosutures fuscous with metallic violet sheen. ***Male terminalia***: Pygophore dorsal rim fuscous and densely punctate, medially. Posterolateral angles rounded and somewhat projected (Fig. 10A). Superior process of genital cup black, elliptical, concave, oblique to proctiger and pedunculate. Paramere with triangular lobe directed anterior-laterad (Fig. 10B); base conical. Proctiger with lateral surface strongly excavated covered by dense tufts of short setae; posterior surface shagreen and flat, ventral margin not projected; dorsal ridge narrowed (Fig. 10B). Ventral rim of pygophore concave with expansions inconspicuous, detectable only by the different texture of surface Fig. 10C). Punctures on ventral surface dense and coarse. ***Female terminalia***: Genital plates (Fig. 10D): Gonocoxites 8 medial area with black punctures with faint metallic, violet sheen. Gonapophysis 8 slightly exposed. Gonocoxites 9 rugulose. Laterotergites 8 with spiracles encircled by brown coloration. Laterotergites 9 tumid, except excavated base.

Diagnosis. Each segment of connexivum with a large medial yellow tumid spot, and an anterior dark, punctured, and rounded spot with metallic violet or green sheen. Body ventrally greenish-yellow with transversal dark maculae, most of them with metallic sheen (Figs. 13G,H). Antennae with antennal tubercle and first segment light brown, second to fourth orange. Legs dark brown, femora with a large ventral dark yellow spot. Pygophore with a lateral lobe on dorsal rim (Fig. 10A). Posterior surface of proctiger triangular. Parameres bilobed laterally (Fig. 10B). Gonocoxites 8 with rounded excavation, posteriorly (Fig. 10D).

Etymology. Name refers to a yellow spot in the ventral surface of the femora.

Distribution. Brazil: Amazonas (Fig. 14).

Material examined. ***Type material***: Holotype male. 'BRAZIL. Amazonas: Reserva Ducke | 30 km N. of Manaus | iii.1998 | K. Vulinec D. Mellow' (INPA). – Paratype. BRAZIL. Amazonas: 1 ♀ same data | 30.v.1998 | J.E. Eger Collection (JEE).

3.9. *Anisoedessa calodorsata* Nunes & Fernandes sp.n.

(Figs. 11, 13 I,J, 14)

Description. ***Measurements***: Head length: 1.3–1.6 mm; head width: 2.3–2.5 mm; pronotal length: 2.5–3.1 mm; pronotal width: 6.8–8.0 mm; length of antennal segments: I: 0.9–1.1 mm; II: 1.3–1.5 mm; III: 2.6–3.1 mm; IV: 3.0–3.5 mm; V: missing; total length: 10.7–13.7 mm; abdominal width: 6.0–7.2 mm. ***Head***: Bucculae punctured. Fourth rostral segment resting between arms of metasternal process. ***Thorax***: Pronotum with

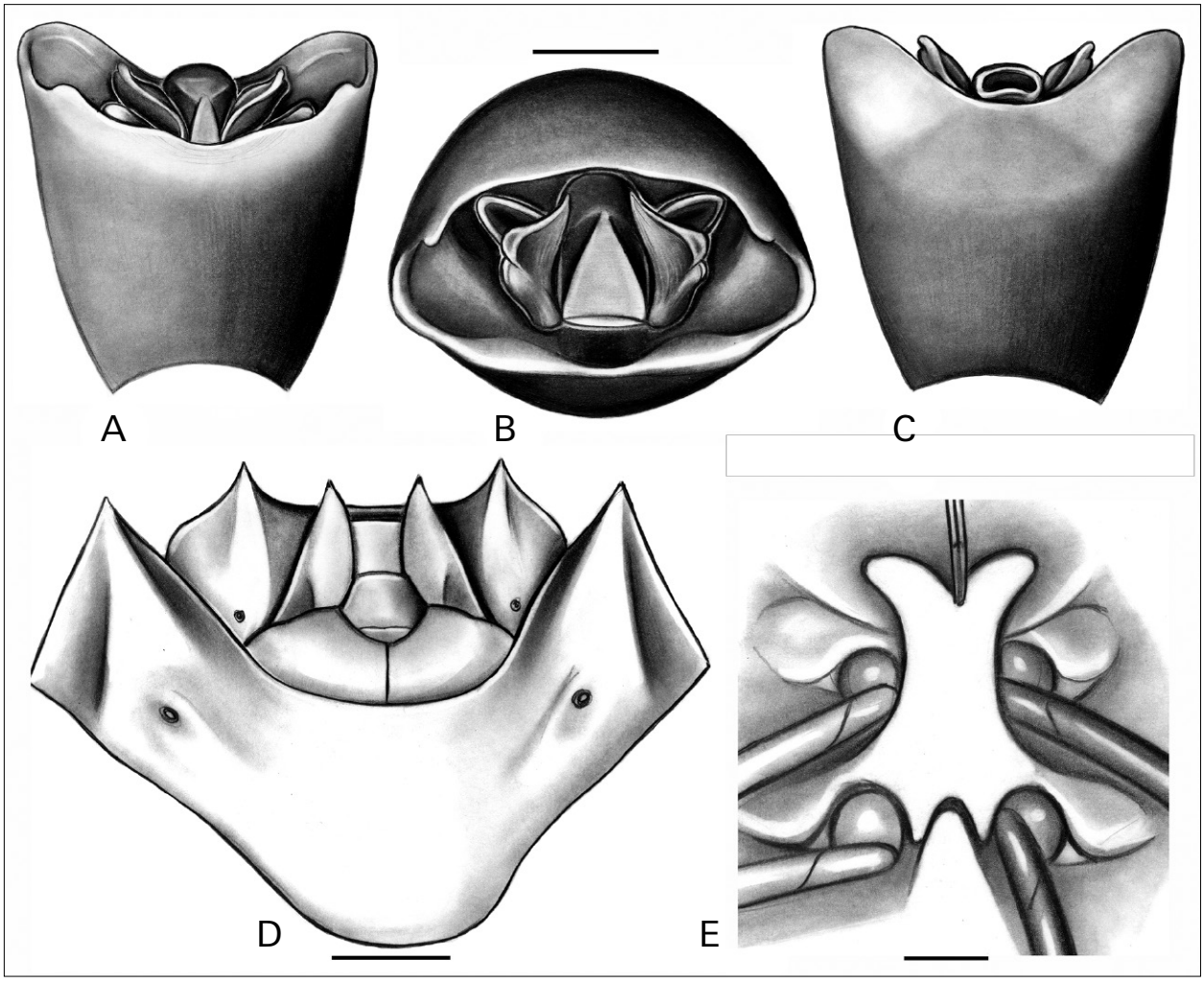

Fig. 10. *Anisoedessa flavomaculata* sp.n. **A**–**C**: male, pygophore, dorsal (**A**), posterior (**B**), and ventral (**C**) views; **D**: female, genital plates; **E**: metasternal process. — ***Scale bars***: 1 mm.

brown punctures. Anterolateral margin yellow, anterior 1/4 rugulose. Corium with veins pale yellow (Fig. 13I). Ventrally, first thoracic segment with punctures concentrated posteriorly and fuscous. Metallic, blue sheen on most of dark green stripes and punctures. Anterior margin of mesopleuron brown and punctured. Evaporatorium mostly dark brown, except green and yellow posteriorly on margin of mesepimeron. Mesepimeron with deep furrow between margin and small ridge. Peritreme reaching 4/5 of the distance between ostiole of the scent gland and margin of metepleuron. Anterior bifurcating arms of metasternal flat and digitiform (Fig. 11E), somewhat diverging. ***Abdomen***: Dorsal surface metallic green. Intersegmental stripes of the abdominal sternites dark brown, broad medially and metallic reddish or blue (Fig. 13J). Spiracles within a yellowish tumid spot. Abdominal pseudosutures dark brown with metallic blue sheen. ***Male terminalia***: Pygophore dorsal rim fuscous and rugulose. Posterolateral angles rounded, somewhat projected (Fig. 11A). Superior process of genital cup fuscous, subtriangular, flat and touching dorsal rim (Fig. 11B). Paramere yellow with margin black; anterior lobe digitiform, posterior lobe short, narrowed and curved laterally; base cylindrical (Fig. 11B). Proctiger lateral excavations with few short setae; posterior surface shagreened and shallowly concave, ventral margin projecting over ventral rim of pygophore. Proctiger lip with expanded sinuous margin (Fig. 11B). Dorsal ridge of proctiger small, conical and brown. Ventral rim of pygophore sinuous; expansions rudimentarily developed, rounded, tumid and setose and adjacent to posterolateral angles (Fig. 11B,C). ***Female terminalia***: Genital plates (Fig. 11D): Gonocoxite 8 with posterior margin acuminate adjacent to base of laterotergite 9; margin black and densely punctate; punctures sparse and uniformly spaced on disc; and sutural border slightly separated, medially. Gonapophysis 8 barely visible. Gonocoxites 9 slightly tumid and wide. Laterotergites 9 mostly tumid, except of a small flat basal area.

Diagnosis. Each segment of connexivum with a yellow tumid small medial spot and two small punctured concavities. Body ventrally yellow (thorax greenish yellow) with transversal dark green stripes, mesial vittae on propleuron and intersegmental area between pro- and mesopleuron with metallic blue green sheen. Antennae light

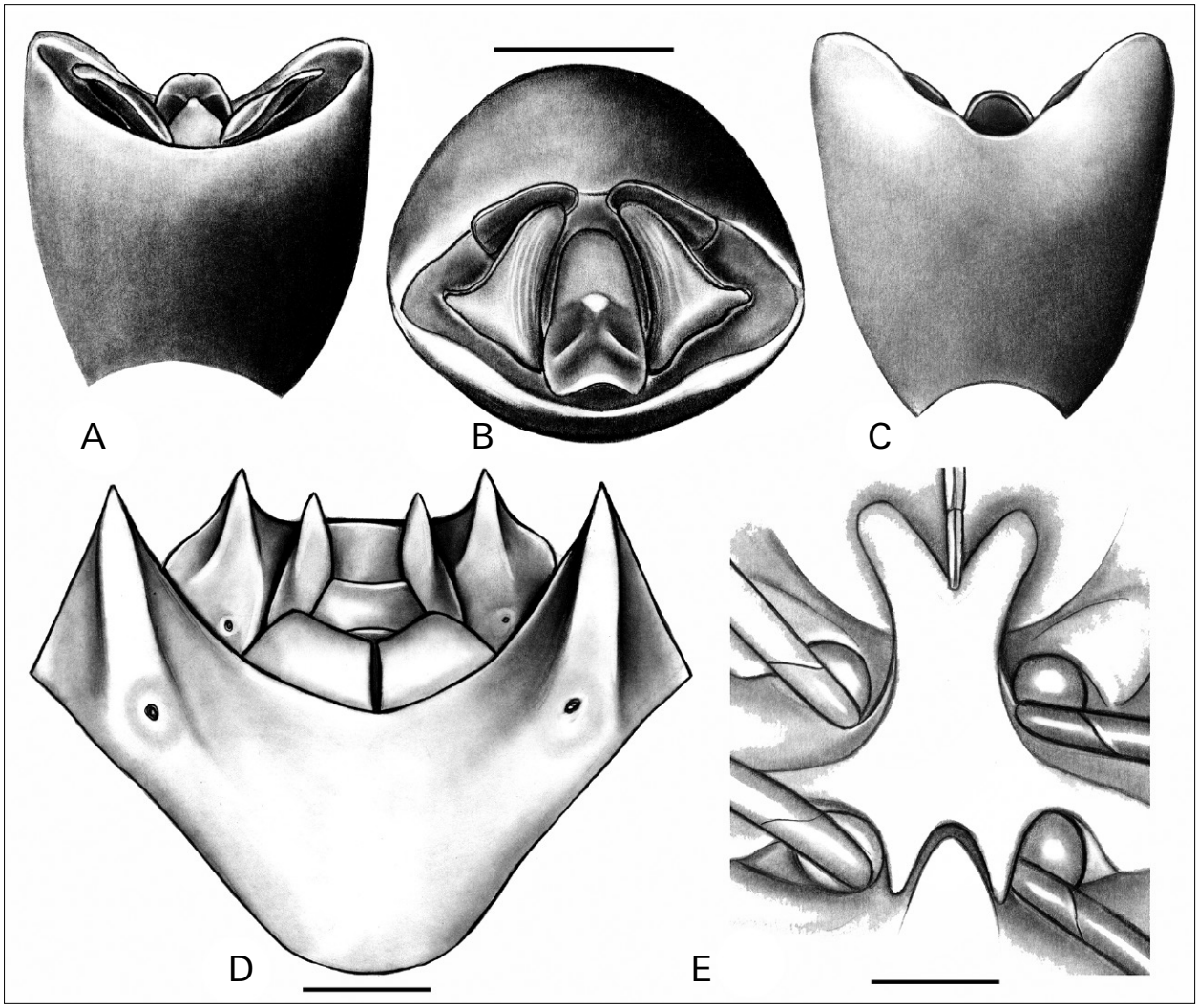

Fig. 11. *Anisoedessa calodorsata* sp.n. **A**–**C**: male, pygophore, dorsal (**A**), posterior (**B**), and ventral (**C**) views; **D**: female, genital plates; **E**: metasternal process. — ***Scale bars***: 1 mm.

brown. Legs brown, except yellow ventral side of femora (Fig. 13I,J). Dorsal rim of pygophore with a median, shallow concavity. Proctiger with two lateral-posterior excavations (Fig. 11B). Paramere triangular, lateral surface striate, dorsal margin sinuate (Fig. 11B). Gonocoxite 8 quadriangular (Fig. 11D).

Etymology. Kalos: Sublime. Name refers to the beautiful green metallic sheen of the dorsal surface of abdomen.

Distribution. Brazil: Rondonia; Peru: Madre de Dios (Fig. 14).

Material examined. ***Type material***: Holotype male. 'PERU, Madre de Dios: Rio Tambopata Res. 30 air km SW | Pto. Maldonado, 290 m. | 6–10.xi.1979 J. B. Heppner | subtropical moist forest' (USNM). – Paratypes. BRAZIL, Rondônia: 4 ♂ 1 ♀ 62 km SW Ariquemes | nr Fzda Rancho Grande | 4–16.xi.1997 JE. Eger | MV & UV Lights (JEE); 1 ♂ 1 ♀ same data (UFRGS). PERU, Madre de Dios: 3 ♂ 1 ♀ Rio Tambopata Res, 30 air km SW | Pto. Maldonado, 290 m. | 16–20.xi.1979 J. B. Heppner | subtropical moist forest (USNM); 1 ♂ 1 ♀, same data | 11–15.xi.1979 (USNM).

3.10. *Anisoedessa ypsilonlineata* Nunes & Fernandes sp.n.

(Figs. 12, 13K,L, 14)

Description. ***Measurements***: Head length: 1.4–1.7 mm; head width: 2.3–2.7 mm; pronotal length: 2.6–3.1 mm; pronotal width: 6.6–7.9 mm; length of antennal segments: I: 1.0–1.1 mm; II: 1.2–1.8 mm; III: 2.4–3.5 mm; IV: 2.8 mm; V: missing; total length: 10.7–12.4 mm; abdominal width: 5.7–7.2 mm. ***Head***: Bucculae rugulose and punctured. Fourth and part of the third rostral segment resting between arms of metasternal process. ***Thorax***: Pronotum with brown punctures. Anterolateral margin pale yellow, anterior 1/3 rugulose. Corium with veins greenish yellow (Fig. 13K). Ventrally, first thoracic segment with punctures concentrated on a median impressed narrow stripe, punctures fuscous; small dark green spot with metallic blue sheen adjacent to coxa (Fig. 13L). Anterior margin of mesopleuron green, punctate, with metallic blue sheen. Evaporatorium concolorous or greenish-brown. Posterior margin of mesepimeron green and yellow; mesepimeron with shal-

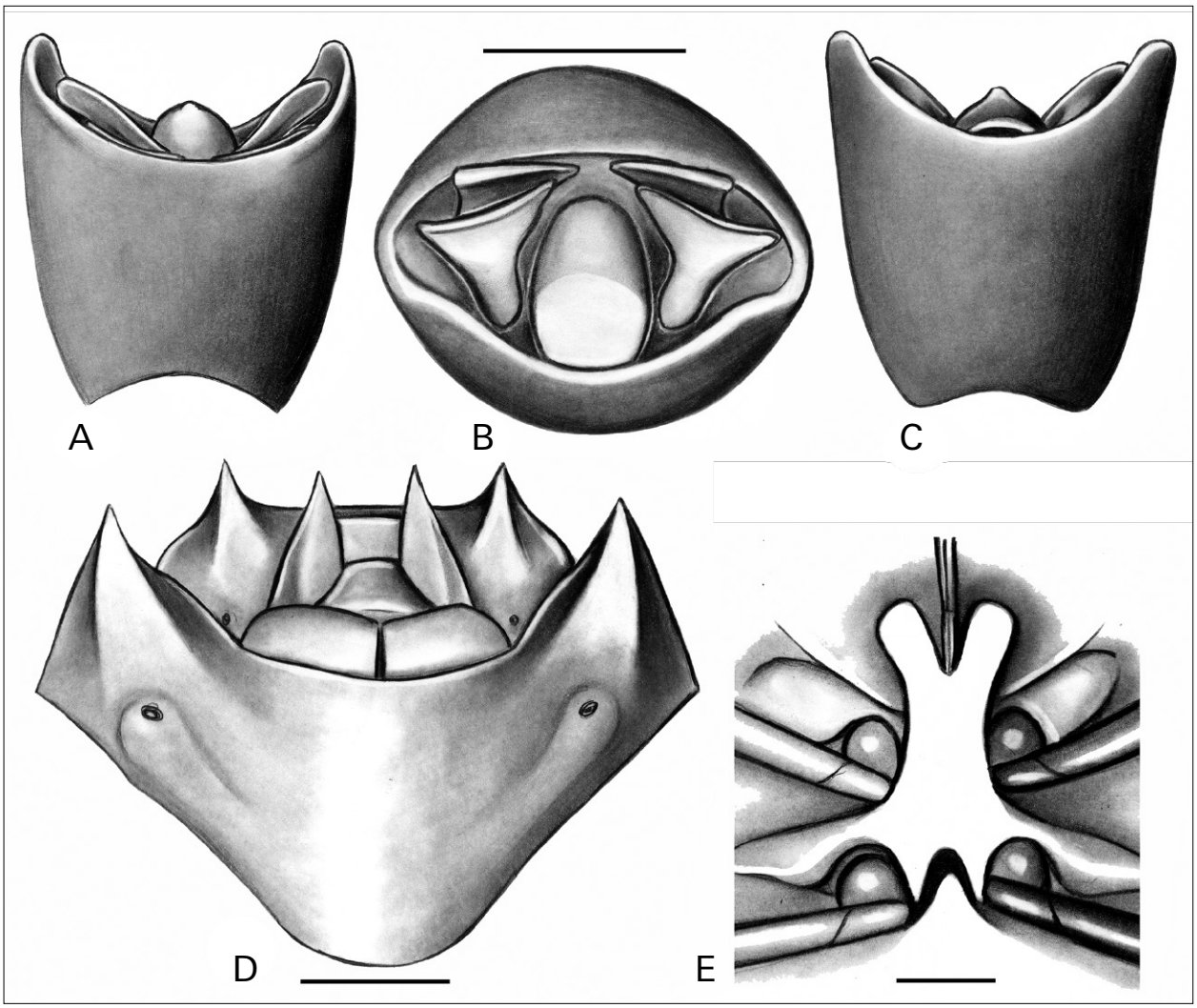

Fig. 12. *Anisoedessa ypsilonlineata* sp.n. **A**–**C**: male, pygophore, dorsal (**A**), posterior (**B**), and ventral (**C**) views; **D**: female, genital plates; **E**: metasternal process. — ***Scale bars***: 1 mm.

low furrow between margin and small rugulose ridge. Peritreme reaching 3/4 of the distance between ostiole of the scent gland and margin of metepleuron. Bifurcating arms of metasternal process subrectangular (Fig. 13L), somewhat diverging. ***Abdomen***: Dorsal surface metallic blue or green. Narrow dark brown intersegmental stripes on abdominal sternites, with metallic reddish sheen (Fig. 13L). Yellowish tumid spot encircling spiracles. Abdominal pseudosutures light brown with faint metallic, reddish sheen. ***Male terminalia***: Pygophore with dorsal rim fuscous and rugulose medially. Posterolateral angles rounded and posteriorly projected (Fig. 12A). Superior process of genital cup triangular, deeply furrowed, medially; and partially contiguous with dorsal rim (Fig. 12B). Paramere asymmetrically triangular, small, posterior lobe, slightly curved laterally (Fig. 12B); base cylindrical. Proctiger with tiny tuft of short setae on ventral margin; posterior surface shagreen and shallowly concave; and ventral margin smooth, but not projected (Fig. 12B). Dorsal ridge of proctiger reduced to small conical projection (Fig. 12A). Ventral rim of pygophore concave and setose, with expansions inconspicuous, detectable only by different texture of surface (Fig. 12C). ***Female terminalia***: Genital plates (Fig. 12D): Gonocoxites 8 uniformly punctured; basal half slightly concave; posterior margin arched. Gonocoxites 9 slightly convex. Laterotergites 9 mostly tumid, except for minute flat basal and lateral areas.

Diagnosis. Each segment of connexivum with greenish yellow, tumid, small, median spot and two small, punctured concavities. Body ventrally green with transverse dark green stripes; middle of propleuron, margin of mesopleuron and intersegmental area between pro and mesopleuron metallic blue or green (Fig. 13K,L). Antennae light brown with first two segments slightly darker than the others. Legs dark brown, except yellow large spot on ventral side of the femora. Proctiger cylindrical, lacks carina and excavations (Fig. 12B). Parameres triangular (Fig. 12B). Gonocoxite 8 rectangular and tumid (Fig. 12D).

Etymology. In reference to the yellow veins of the corium forming a "Y".

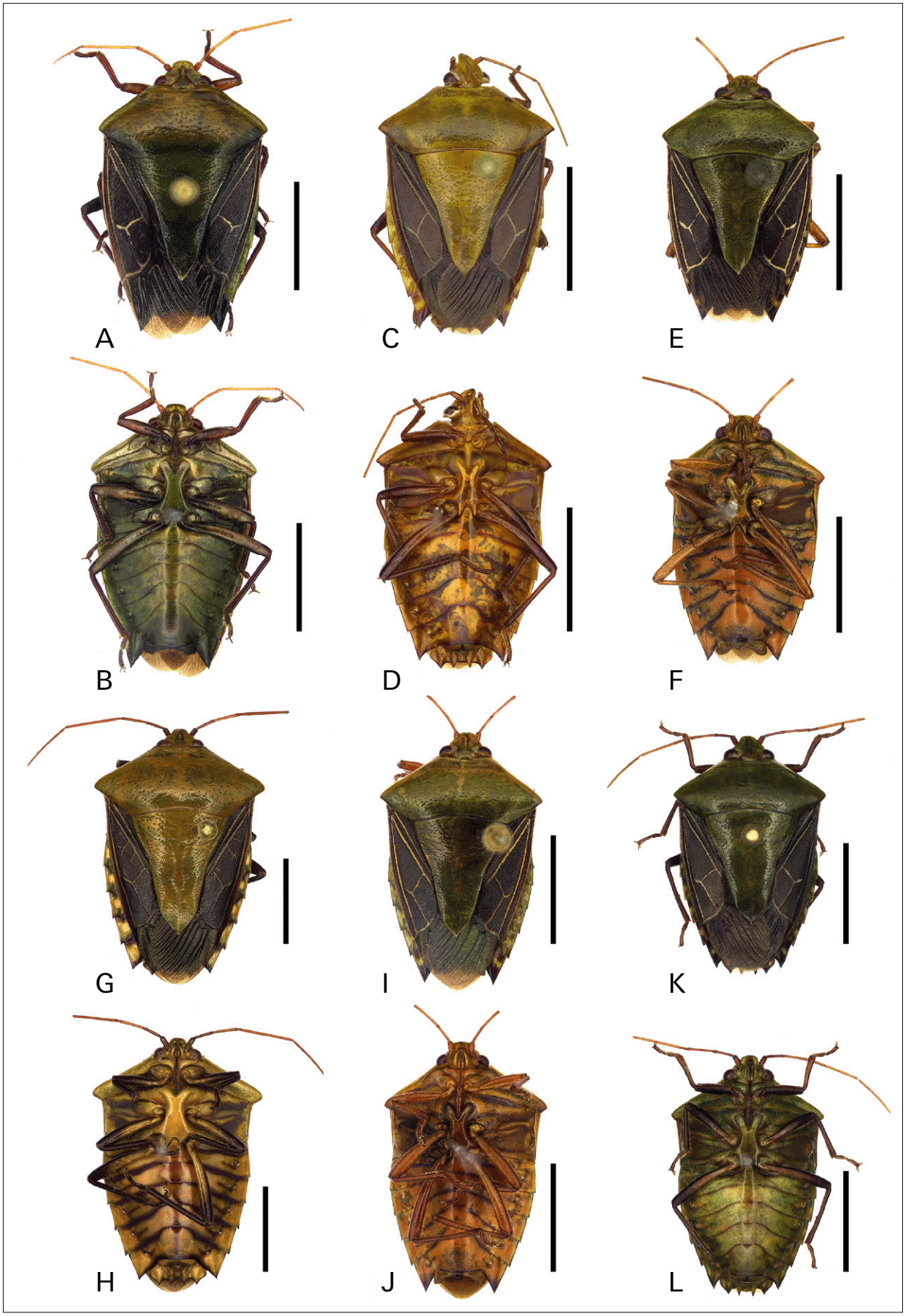

Fig. 13. Habitus, dorsal (top) and ventral (bottom) views. **A**,**B**: *Anisoedessa proctocarinata*; **C**,**D**: *Anisoedessa bispinosa*; **E**,**F**: *Anisoedessa proctolabiata*; **G**,**H**: *Anisoedessa flavomaculata*; **I**,**J**: *Anisoedessa calodorsata*; **K**,**L**: *Anisoedessa ypsilonlineata*. — ***Scale bars***: 5 mm.

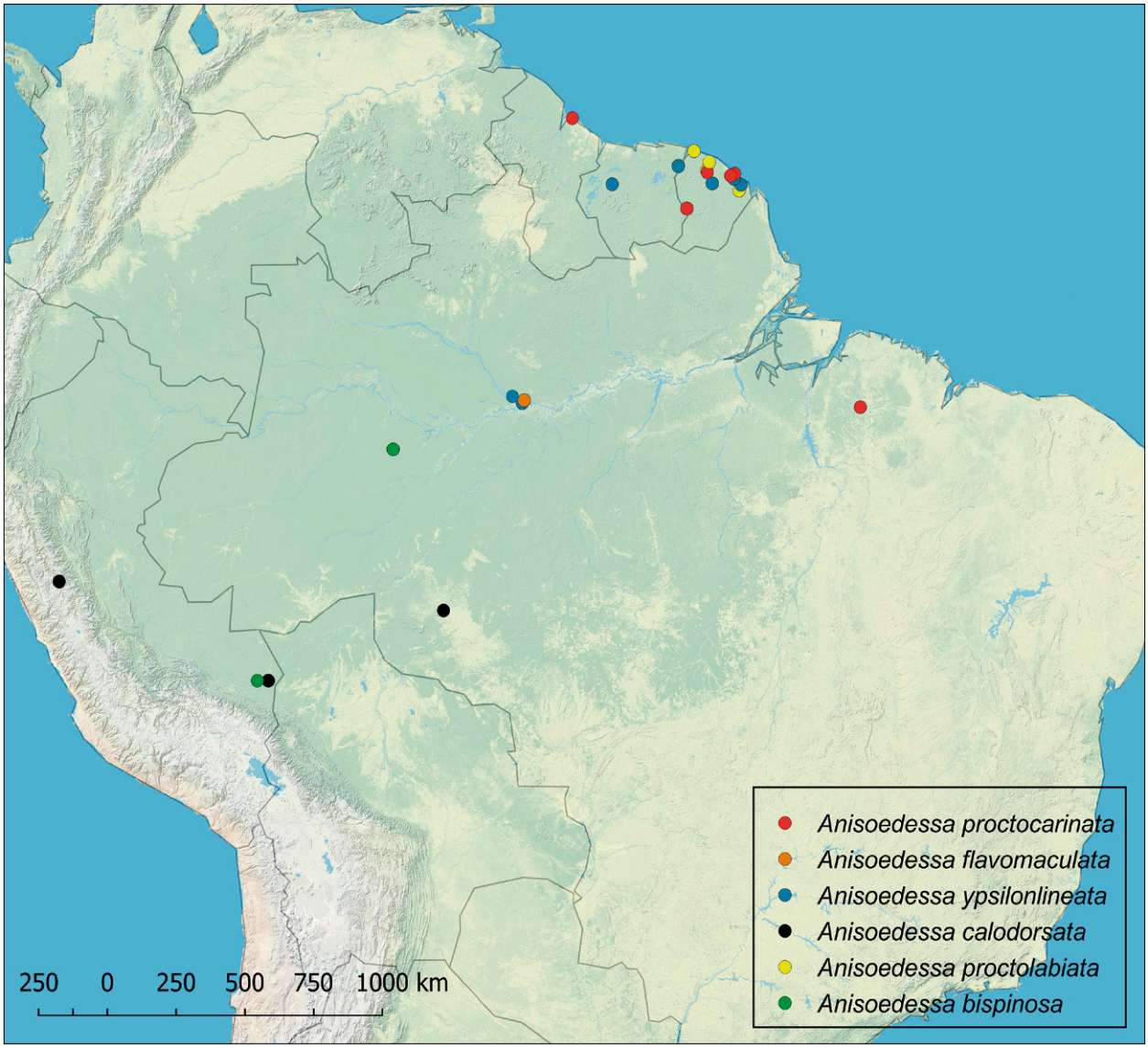

Fig. 14. Distribution of the species of *Anisoedessa* gen.n.

Distribution. French Guiana: Cayenne; Suriname: Sipaliwini; Brazil: Amazonas (Fig. 14).

Material examined. ***Type material***: Holotype male. 'FRENCH GUIANA, Cayenne: Roura RN2 pK22 | Montagne des Chevaux | 04.i.2014. GemLight trap | S. E. A. G. leg. | MNHN (EH) 24490' (MNHN). – Paratypes. FRENCH GUIANA, Cayenne: 1 ♀ Grand Matoury | v.1982 | G. Tavakilian | MNHN (EH) 24491 (MNHN); 1 ♂ Entomotech Lodge | 30 km SE Roura on Kaw Rd | xi.2004 – ii.2005 | F. Goulbert, 04°33. 570′N 052°12.433′W | 300 km MV Light. J. E. Eger (JEE); 1 ♀ Roura, RN2 pK22 Montagne des Chevaux | 24.ii.2013. GemLight trap | S. E. A. G. leg. (RLC); 1 ♀ same data | 10.viii.2013 (UFRGS); 1 ♀ same data | 08.iii.2014 (RLC); 1 ♂ Route de Kaw Pk 40 | 31.xii.1983 | G. Tavakilian | MNHN (EH) 24492 (MNHN). 1 ♂ 12 km W of Risquetout | 5.xii.2002 J. E. Eger | 04°54.673′N 052°11.150′W | 58 m MV Light (UFRGS); Saint Laurent du Maroni: 1 ♀ Route d' Apatou pK25 | 25.vii.2011. Light Trap | S. E. A. G. leg. Coll R. Lupoli (RLC); SURINAME, Sipaliwini: 1 ♀ Bakhuisgebergte | Kamp III, 20.ii.1965 | P.A. Florschütz (RMNH); BRAZIL, Amazonas: 1 ♂ Manaus | i – ii.1978 | B. C. Ratcliffe (INPA).

4. Conclusions

Our phylogenetic analysis corroborated the monophyly of Edessinae, of the new genus *Anisoedessa*, and of recently described genera (*Doesburgedessa* Fernandes, 2010; *Paraedessa* Silva & Fernandes, 2013; *Grammedessa* Correia & Fernandes, 2016; and *Plagaedessa* Almeida & Fernandes, 2018). The analysis also supports the non-monophyly of *Edessa* (Fig. 6). Further mining of morphological and molecular characters combined with rigorous phylogenetic testing may also improve the branch support of the previously described Edessinae genera and lead to taxonomical changes in the subfamily, especially in *Edessa*. Evidence from this study also shows the value of phylogenetics in testing Edessinae as a whole.

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