

***Oreiallagma* gen. nov. with a redefinition of *Cyanallagma* Kennedy 1920 and *Mesamphiagrion* Kennedy 1920, and the description of *M. dunklei* sp. nov. and *M. ecuatoriale* sp. nov. from Ecuador (Odonata: Coenagrionidae)**

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Table of contents

Abstract	1
Introduction	2
Results	5
Taxonomic treatment	10
<i>Cyanallagma</i> Kennedy 1920	10
Key to males of <i>Cyanallagma</i>	14
Key to females of <i>Cyanallagma</i>	15
<i>Mesamphiagrion</i> Kennedy 1920 stat. rev.	15
Key to males of <i>Mesamphiagrion</i>	22
Key to females of <i>Mesamphiagrion</i>	23
<i>Mesamphiagrion dunklei</i> sp. nov.	24
<i>Mesamphiagrion ecuatoriale</i> sp. nov.	34
<i>Oreiallagma</i> gen. nov.	42
Key to males of <i>Oreiallagma</i>	44
Key to known females of <i>Oreiallagma</i>	44
<i>Oreiallagma acutum</i> (Ris 1918) comb. nov.	44
<i>Oreiallagma oreas</i> (Ris 1918) comb. nov.	45
<i>Oreiallagma prothoracicum</i> (Kimmins 1945) comb. nov.	46
<i>Oreiallagma quadricolor</i> (Ris 1918) comb. nov.	47
<i>Oreiallagma thelakterion</i> (De Marmels 1997) comb. nov.	48
Acknowledgments	49
References	49

Abstract

In this paper we re-evaluate *Cyanallagma* Kennedy 1920, which currently includes 15 species, and we address another five species that share diagnostic characters with some of them but are currently placed within *Leptagrion* Selys 1876, *Mesamphiagrion* Kennedy 1920, and *Telagrion* Selys 1876. A new genus, *Oreiallagma*, is described to include five species originally placed in *Acanthagrion* Selys 1876, *Cyanallagma*, and *Telagrion*. These species are *O. thelakterion* (De Marmels 1997) (type species), *O. acutum* (Ris 1918), *O. oreas* (Ris 1918), *O. prothoracicum* (Kimmins 1945), and *O. quadricolor* (Ris 1918). The last stadium larva of *O. quadricolor* is described. The remaining species currently included

in *Cyanallagma* are allocated to two separate genera: *Cyanallagma sensu stricto* and *Mesamphiagrion*. *Cyanallagma sensu stricto* comprises southern South American species including the type species, *Cyanallagma interruptum* (Selys 1876). *Mesamphiagrion* Kennedy 1920 includes a cluster of species from northwestern South America that are considered congeneric with the type species *Mesamphiagrion occultum* (Ris 1918). Two new species from Ecuador, *M. dunklei* and *M. ecuatoriale*, are described and *Argia hebdomatica* Navás 1934 is found to be a junior synonym of *M. ovigerum* (Calvert 1909). Synonymic lists, diagnoses, illustrations, keys, and distribution maps for the three genera are provided.

Key words: Zygoptera, new genus, new species, South America

Introduction

Generic concepts within neotropical Coenagrionidae are plagued by a lack of diagnostic characters. The abundance of recently discovered taxa coupled with a lack of review of generic concepts often precludes a meaningful classification and analysis within this diverse family. Until these problems are resolved little progress will be possible allowing for meaningful diagnostics and phylogenetic considerations. Past literature dealing with species we treat here has often involved generic transfers reflecting the inadequacy of their generic diagnoses.

Here we redefine *Cyanallagma* Kennedy 1920, currently including 15 species. We also address another five species that share diagnostic characters with some species of *Cyanallagma* but are currently placed within *Leptagrion* Selys 1876, *Mesamphiagrion* Kennedy 1920, and *Telagrion* Selys 1876. Several of these species have previously been included in or shifted among other genera, including *Acanthagrion* Selys 1876, *Archaeallagma* Kennedy 1920, *Argentagrion* Fraser 1948, *Argia* Rambur 1842, and *Enallagma* Charpentier 1840. Some of these species, known only from types, have not been re-examined since their original descriptions almost 90 years ago.

History. As the following historical account will show, the species treated here have not easily yielded to generic assignments often due to lack of material and addition of new species that have gradually broadened generic concepts. This has obscured their original definitions resulting in disagreement on cohesive character suites that may be used to define genera.

From the Andes, Ris (1918) described *Acanthagrion acutum*, *Telagrion oreas*, and *T. quadricolor*, and Kimmins (1945) described *T. prothoracicum*. None have been rediscovered since.

Kennedy (1920) erected *Cyanallagma* for species of Selys' (1876) '*Acanthagrion interruptum*' group, designating *Acanthagrion interruptum* as type species and including also *A. laterale* Selys, *A. acutum*, and "perhaps [*A.*] *cheliferum* Selys". His diagnosis (Kennedy 1920) was extremely brief: "as *Acanthagrion* but with male cerci not decumbent and usually forked". Leonard (1977) revised *Acanthagrion*, agreed with Kennedy's (1920) earlier actions, and transferred the following additional species to *Cyanallagma*: *Acanthagrion nigri-nuchale* Selys 1876, *A. trimaculatum* Selys 1876, *A. lindneri* Ris 1928, and *A. ambiguum* Ris 1904. His work was written in the 1930s and published posthumously. Fraser (1948) erected *Argentagrion* for reception of *Acanthagrion ambiguum*. Rácenis (1958) placed species of Selys' second ('*Acanthagrion interruptum*') section into two genera: *Cyanallagma* (including *Acanthagrion interruptum*, *A. bonariense* Ris 1913, and *A. laterale* Selys) and *Argentagrion* (including *A. ambiguum*, *A. cheliferum*, and *A. lindneri*). Bulla (1973) redescribed *Cyanallagma bonariense* and *C. interruptum*, and indicated that Rácenis (1958) diagnoses needed to be corrected to include variability observed within *C. interruptum* and *A. ambiguum*.

Cruz (1986) described *Cyanallagma* [*sic*] *demarmelsi*. De Marmels (1989) provided a complete characterization of *Cyanallagma* and redescription of the poorly known *A. acutum* and *Mesamphiagrion occultum* (Ris 1918). Later De Marmels described three new species, *C. risi*, *C. tepuianum*, and *C. thelktion*, redefined the genus, and referred his previous records of *C. ovigerum* to *C. risi* (De Marmels 1997). He also provided illustrations and keys for all species of *Cyanallagma* inhabiting the Andean cordillera of northern South

America and the single species so far known from Pantepui. Lencioni (2001) described *C. angelae* and provided keys for the species of *Cyanallagma* from southern South America and De Marmels (2003) described *C. ferenigrum*.

We have partitioned the 15 species currently included in *Cyanallagma* among three different genera (Table 1) and each is diagnosed based on unique characters and/or unique character sets.

Methodology. Adults of all described species of *Cyanallagma sensu lato*, except *C. risi* and *C. tepuianum*, were studied. All original descriptions and revisions were analyzed. Additionally, most species of other New World coenagrionid genera were examined to establish generic boundaries.

Diagnostic characters were illustrated with the aid of camera lucidae coupled to Wild M-8 and Nikon SMZ1500 microscopes. Figures are not to scale except where indicated. Specimens for SEM were cleaned in acetone, air dried and mounted on SEM stubs with carbon conductive adhesive tabs, and then sputter coated with gold/palladium alloy and examined with a JEOL SEM 6300 scanning electron microscope.

Total length and abdominal length do not include appendages. Wing terminology follows Riek & Kukalová-Peck (1984), genital ligula terminology Kennedy (1916), and larval mandibular formula Watson (1956). Abbreviations for structures used throughout the text are as follows: FW: forewing; HW: hindwing; pt: pterostigma; Ax: antenodals; Px: postnodals; S1–10: abdominal segments 1 to 10. Maps represent distribution records from collections and reliable literature records, and were created electronically from the Digital Chart of the World (1:1,000,000) using ArcView 9.1. Elevation data and longitude/latitude coordinates were culled from the Global Gazetteer website (<<http://www.fallingrain.com/world/>>). Acronyms used for collections are as follows:

ABM	Angelo Machado collection, Belo Horizonte, Minas Gerais, Brazil
BMNH	British Museum of Natural History, London, Great Britain
DRP	Dennis Paulson personal collection, Seattle, Washington, United States of America
FNS	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States of America
MIZA	Museo del Instituto de Zoología Agrícola, Maracay, Venezuela
MLP	Museo de La Plata, Buenos Aires, Argentina
NHMP	Natural History Museum of Paris, France
RWG	Rosser Garrison personal collection, Sacramento, California, United States of America
SWD	Sidney Dunkle personal collection, Tucson, Arizona, United States of America
TWD	Thomas W. Donnelly personal collection, Binghamton, New York, United States of America
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor, Michigan, United States of America

Characters. We found following characters to be of diagnostic value (Table 1 shows states for all species treated here):

Head.

1. Location of most posterior point of head at: 0. eyes (Fig. 5), 1. postocular lobe (Figs. 3a–d).
2. Area surrounding occipital foramen: 0. dark (Fig. 1a), 1. pale (Fig. 1b).

Thorax.

3. Dark stripe on metapleural suture: 0. present (Figs. 2a–b; 3a–b, d–f; 5), 1. absent (Figs. 2c; 3c).
4. Pale antehumeral stripe: 0. complete (Figs. 2a–b; 3c–e), 1. interrupted (Figs. 2c; 3a–b; 5).
5. Medial lobe of posterior margin of male pronotum: 0. not projected (Fig. 19), 1. projected posteriorly (Figs. 9a–14a; 15; 16a; 17–18; 20a–21a; 22a–b; 23a–24a; 25–27; 28a–b; 29a).
6. Lateral lobes of male posterior prothoracic lobes: 0. smoothly curved (Figs. 26–27, 28a), 1. bilobate (Figs.

25; 29a).

7. Leg length (measured as ratio of femur 1 [fe] length/distance between eyes at level of antennifer [ey]): 0. long, ratio = 1.08 (Fig. 5), 1. short, ratio = 1.03 (Figs. 3a, d–e).
8. Width central disk/width female mesostigmal plate: 0. disk wider than plate (Fig. 28c), 1. disk as wide as or narrower than plate (Figs. 9c–14c; 16c; 20c–21c; 22d; 23c–24c).
9. Female mesostigmal plate: 0. broad, with maximum width/length ratio < 0.5 (Figs. 9c; 16c; 20c–21c; 22d; 23c–24c), 1. narrow, with maximum width/length ratio > 0.5 (Figs. 10c–14c; 28c).
10. Female mesepisternal carinae: 0. ending anteriorly to and between postero-medial edges of mesostigmal plates (Figs. 9c; 16c; 20c–21c; 22d; 23c–24c), 1. ending at posterior edges of mesostigmal plates (Figs. 10–14c), 2. absent (Fig. 28c).

Abdomen.

11. Abdomen: 0. of regular length or short; abdomen length/head+thorax ratio = 4.3, 1. long; abdomen length/head + thorax ratio = 4.4.

Male genital ligula.

12. Ental transverse folds distal to genital ligula flexure present in number of one or two, extending either between medio-lateral lobes and/or between medio-lateral lobes and flexure (best seen in ento-lateral view with second segment of ligula flexed away from first segment): 0. lacking inner medial process (Figs. 50a–51a; 52c–53c), 1. with an inner medial process (Figs. 31, right white arrow; 32a, c–34a, c; 35a; 36a, c–37a, c; 38a; 40a, c–41a, c; 42a–48a; 49c). NOTE: when two transverse folds are present only one is projected into an inner medial process.
13. Lateral lobes (medial or apical) distal to genital ligula flexure: 0. one pair (Fig. 51), 1. two pairs (Figs. 30–50; 52–53).
14. Wide paired latero-apical folds with sclerotized margins on apex of genital ligula second segment: 0. absent (Figs. 30; 32–48), 1. present (Figs. 49–53).

Male S10.

15. Male S10 posterodorsal margin: 0. lacking paired tubercles (Figs. 55; 85–94), 1. with two lobe-like tubercles on sides of medial 'u'-shaped cleft (Figs. 54; 56–72; 76–84).
16. Male cercus: 0. lacking a ventro-apical process (Figs. 56–59), 1. with a broadly triangular ventro-apical process (Figs. 54–55), 2. with two short ventro-apical processes (Figs. 60–84); 3. with a long blade-like ventro-basal process (Figs. 85–94).
17. Male cercus: 0. lacking a ventro-basal process (Figs. 85–94), 1. with a short ventro-basal process (Figs. 54–79).
18. Male cercus: 0. lacking dorsal process (Figs. 54–59), 1. with a short dorsal process (Figs. 60–64; 70–74; 80–81; 88–89; 93–94), 2. with a long dorsal process (Figs. 65–69; 75–79; 82–87).
19. Patch of scalariform-like cuticle (differentiated scale-like integument) in male cercus: 0. absent (Figs. 55; 60–86; 90–91), 1. present (Figs. 95; 54; 56–59; 87–89; 92–94). NOTE: Presence or absence of scalariform-like cuticle can be confirmed by examination with SEM (Fig. 95); it is similar to but probably not homologous with scalariform cuticle described by Jurzitza (1975) for *Enallagma*, and depicted by May (2002) for *Enacantha* Donnelly & Alayo 1966, *Enallagma* and *Proischnura* Kennedy 1920.
20. Longitudinal carina on medial surface of male cercus: 0. absent (Figs. 54–55; 58–94), 1. present (Figs. 56–57).

Color.

21. Body: 0. lacking any red or bright orange (Figs. 105–106), 1. including some red or orange, at least during juvenile period (Figs. 108–109).

Larva.

22. Larva caudal lamellae: 0. approximately ovoid, ratio length/width of lateral lamella = 4 (Figs. 98–100), 1. lanceolate, ratio length/width of lateral lamella = 4.5 (Figs. 96–97).

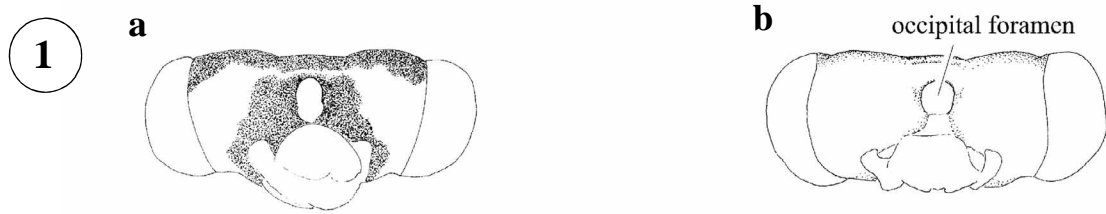


FIGURE 1. Head, posterior view. (a) *Cyanallagma interruptum*, male, Argentina, Queñi; (b) *Mesamphiagrion laterale*, male, Colombia, La Pica.

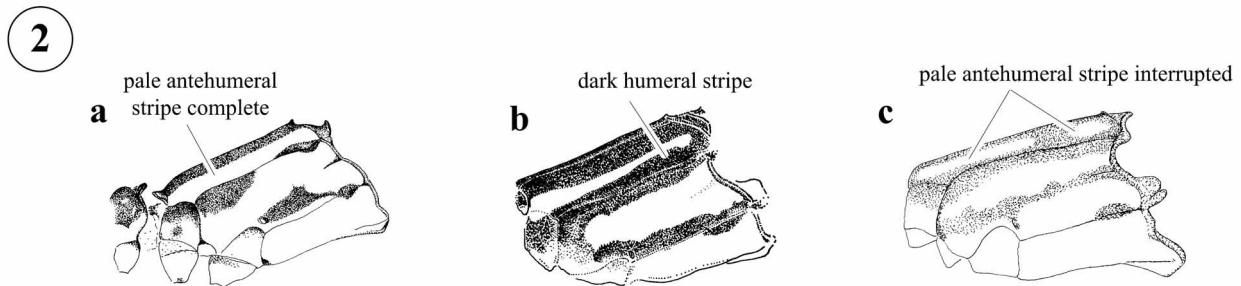


FIGURE 2. Thorax, lateral view. (a) *Cyanallagma trimaculatum*, male lectotype, Brazil, Santa Cruz; (b) *Mesamphiagrion gaianii*, male paratype, Venezuela, La Cristalina; (c) *M. tepuiantum*, male paratype, Venezuela, Mt. Duida (modified from De Marmels 1997).

We interpreted homologies for the various processes of male cercus (characters 16–18) based on their relative position on the cercus. We consider the ventral process of *Oreiallagma* to be homologous to the ventro-apical processes of *Cyanallagma* and *Mesamphiagrion* (Table 1). Alternatively it may be considered homologous to the ventro-basal process in these genera.

Results

Our analysis shows *Cyanallagma* as currently composed includes species belonging to three different genera: *Cyanallagma sensu stricto*, *Mesamphiagrion* stat. rev., and *Oreiallagma* gen. nov. (Tables 1–2). These three genera share a rounded frons, presence of pale postocular lobes, posterior lobe of prothorax trilobate, presence of mid-dorsal, and humeral dark stripes and male cerci are with processes of some kind. However, these processes occur in different number and position within each genus and they differ further in structure of the male genital ligula, the morphology of head, and the proportion of head size to leg and abdomen length (Table 2).

Kennedy's (1920) original diagnosis of *Mesamphiagrion*, based on *Enallagma occultum* Ris 1918, could be applied to all northern *Cyanallagma sensu lato* species: "Characters as in *Enallagma*, but body colors red, apex of segment 10 elevated and notched, body long haired and [ptero]stigma one-half cell long. Differs from *Amphiagrion* in male appendages being *Enallagma*-like, in postocular spots, in lacking the metasternal tubercles." In the material we examined, the thorax and S1–3 were red only in the juvenile male. The two mature males at our disposal lacked red, and dark areas on head and thorax were dark brown. In all northern species of *Cyanallagma sensu lato*, color includes red or ferruginous areas on head, thorax and/or S1–3 during the juvenile period of adult development (Calvert 1909; Ris 1918; De Marmels 1989, 1997); the apex of S10 is elevated and notched (Figs. 60; 70a; 80 for *M. occultum*; Figs. 61–69; 71a; 72; 76; 77b–79b; 81–84 for others); and pt is always short, from slightly shorter (as in *M. occultum*, Fig. 7c) to slightly longer than the underlying cell, with both states present, sometimes even within the same specimen (*i.e.* Fig. 7a). The body has long setae as in numerous Coenagrionidae of colder areas (*i.e.* North American *Amphiagrion* Selys, South American *Protallagma* Kennedy, and New Guinean *Oreagrion* Ris (Lieftinck 1949); *Protallagma* and *Oreagrion* inhabit mountainous areas above 3000 m). *Acanthagrion tepuiense* De Marmels 1985, is setose in specimens from tepuis and less so in specimens from the Gran Sabana lowland (De Marmels 1985: 13).

TABLE 1. Character states for studied species (characters listed and coded in the text); new combinations highlighted in *bold italic*. Question marks represent unknown character states.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Characters																							
Previous placement	New Placement																						
<i>Mesamphiagrion occultum</i>	1	1	1	0	1	0	1	0	1	?	?	0	1	1	0	1	2	1	1	0	0	1	?
<i>Mesamphiagrion laterale</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	2	1	2	0	0	1	0	0
<i>M. dunklei</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	2	1	2	0	0	1	?	?
<i>M. gaiani</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	2	1	2	0	0	1	0	0
<i>M. tamaense</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	2	1	2	0	0	1	0	0
<i>M. demarmelsi</i>	1	1	0	1	1	0	1	1	0	0	0	1	1	0	1	2	1	2	0	0	1	0	0
<i>M. tepuiatum</i>	1	1	0	1	1	0	1	1	0	0	0	1	1	0	1	2	1	2	0	0	1	?	?
<i>M. risi</i>	1	1	0	0	1	0	1	?	?	?	0	1	1	0	1	2	1	2	0	0	1	?	?
<i>M. ovigerum</i>	1	1	0	0	1	0	1	?	?	?	0	1	1	0	1	2	1	1	0	0	1	?	?
<i>M. ecuatoriale</i>	1	1	0	0	1	0	1	?	?	?	0	1	1	0	1	2	1	1	0	0	1	?	?
<i>M. ecuatoriale</i>	1	1	0	0	1	0	1	1	0	0	0,1	1	1	0	1	2	1	1	0	0	1	?	?
<i>Cyanallagma ferenigrum</i>	1	0	0	1	1	0	1	1	1	1	0	1	1	0	0	1	1	0	0	0	?	?	?
<i>C. interruptum</i>	1	0	0	1	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	?
<i>C. bonariense</i>	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	1	0	1	0	1	0	1
<i>C. angelae</i>	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	1	0	1	1	0	?	?
<i>C. nigrinuchale</i>	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	1	0	1	0	1	0	?
<i>C. trimaculatum</i>	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	1	0	1	0	0	?	?
<i>C. thelcterion</i>	1	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	1	0	1	0	0	?	?
<i>Oreialagma thelcterion</i>	0	1	0	1	1	1	0	?	?	?	1	1	1	1	0	3	0	2	0	0	1	?	?
<i>O. acutum</i>	0	1	0	1	1	0	0	?	?	?	1	0	0	1	0	3	0	2	0	0	1	?	?
<i>Leptagrion prothoracicum</i>	0	1	0	1	1	0	0	?	?	?	1	0	0	1	0	3	0	2	0	0	1	?	?
<i>Leptagrion oreas</i>	0	1	0	0	1	0	0	?	?	?	1	0	1	1	0	3	0	2	1	0	1	?	?
<i>T. quadricolor</i>	0	1	1	0	1	0	0	0	1	2	1	0	1	1	0	3	0	1	1	0	1	?	?

TABLE 2. Diagnostic characters of *Cyanallagma*, *Mesamphiagrion*, and *Oreiallagma*.

	<i>Cyanallagma</i>	<i>Mesamphiagrion</i>	<i>Oreiallagma</i>
Head (Figs. 1; 3a–e; 5)			
Location of most posterior point of head at	postocular lobes	postocular lobes	eyes
Area surrounding occipital foramen	dark	pale	pale
Thorax (Figs. 2–3; 5)			
Female mesostigmal plates	wide or narrow	wide	narrow
Female mesepisternal carinae ending at mesostigmal plates	posterior end or medial portion	medial portion	carinae absent
Legs (Figs. 3a–b, d–e)			
Length (ratio femur 1/distance between eyes)	short (= 1)	short (=1.03)	long (= 1.08)
Abdomen (Figs. 4–5; 54–94)			
Length (ratio abdomen/ head+ thorax)	short (3.27–4.3)	short (3.39–4.85)	long (4.4–6.5)
Tubercles on postero-dorsal cleft of male S10	present or absent	present	absent
Male cercus ventro-basal process	present	present	absent
Male cercus ventro-apical processes	absent or present, 1 short	present, 2 short	absent
Male cercus dorsal process	absent	present	present
Male genital ligula (Figs. 30–53)			
Pair of wide latero-apical folds on segment 2	absent	absent	present
Color (Figs. 105–109)			
Including red during juvenile period of adult life	no	yes	yes
Larva (Figs. 96–101; 111)			
Occipital lobes	prominent	prominent	not prominent
Premental setae	3–5	3–5	2
Postero-dorsal margin of S10	with 'u' cleft	with 'u' cleft	entire
Caudal lamellae	lanceolate	ovoid	ovoid

As De Marmels noted (1989), the shape of posterior lobe of prothorax and the male genital ligula of *Mesamphiagrion occultum* (Figs. 15; 38) are as in the northern species of *Cyanallagma sensu lato* (Figs. 16–24; 39–48). He refrained from synonymizing *Mesamphiagrion* with *Cyanallagma* based on two differences he observed between *M. occultum* and the species of *Cyanallagma* studied by him. These characters were a shorter abdomen in relation to head and thorax length (ratio = 3.4:1) and pt small relative to wing size and located more basally from wing tip. We found these character states are encompassed within the range of variability present in *Cyanallagma sensu lato*. For example, the ratio abdomen/ head + thorax length ranges in the southern cluster of species from 3.27 (*C. nigrinuchale*) to 4.27 (*C. angelae*) and in the northern cluster of species from 3.60 ('*C.* demarmelsi) to 4.28 ('*C.* tamaense). We attempted to quantify the distance of pt to wing tip by counting the number of cells present between them and found that number of cells between pt and apex of FW is intraspecifically variable, ranging from 3 to 6 (6 observed in *M. occultum* and also in *M. ecuatoriale*, '*C.* gaianii', '*C.* laterale', and '*C.* tamaense').

Based on the examination of three males of *M. occultum* kindly sent to us by J. De Marmels and their comparison with all described species of *Cyanallagma sensu lato* we conclude that *M. occultum* is congeneric with '*Cyanallagma*' *ovigerum* and with all other species of '*Cyanallagma*' from northwestern South America. Consequently we transfer all of them to *Mesamphiagrion* and redefine both genera. Main differences between *Mesamphiagrion* and *Cyanallagma sensu stricto* are found in the male cercus. In *Mesamphiagrion*, the cercus

has four processes: one dorsal, two short ventro-apical and one ventro-basal (Figs. 70–79). In *Cyanallagma sensu stricto*, including the type species *Cyanallagma interruptum* and another five species from southern South America (Table 1), there is always a short ventro-basal process, sometimes a broadly triangular ventro-apical process, and no dorsal process (Figs. 54–59). The two genera also differ in some color pattern characters. The body never includes red or reddish colors in *Cyanallagma* (Figs. 105–106) while it does include red or reddish color in juvenile adults of *Mesamphiagrion* (Figs. 108–109). The only species where red has not yet been observed is *M. ecuatoriale*, which is known only from six mature adults. Rear of head around the occipital foramen is dark in *Cyanallagma* (Fig. 1a) versus pale in *Mesamphiagrion* (Fig. 1b). Based on only the few larvae known, they also differ in the shape of the caudal lamellae, which are lanceolate in *Cyanallagma* (Figs. 96–97) and ovoid in *Mesamphiagrion* (Figs. 98–100).

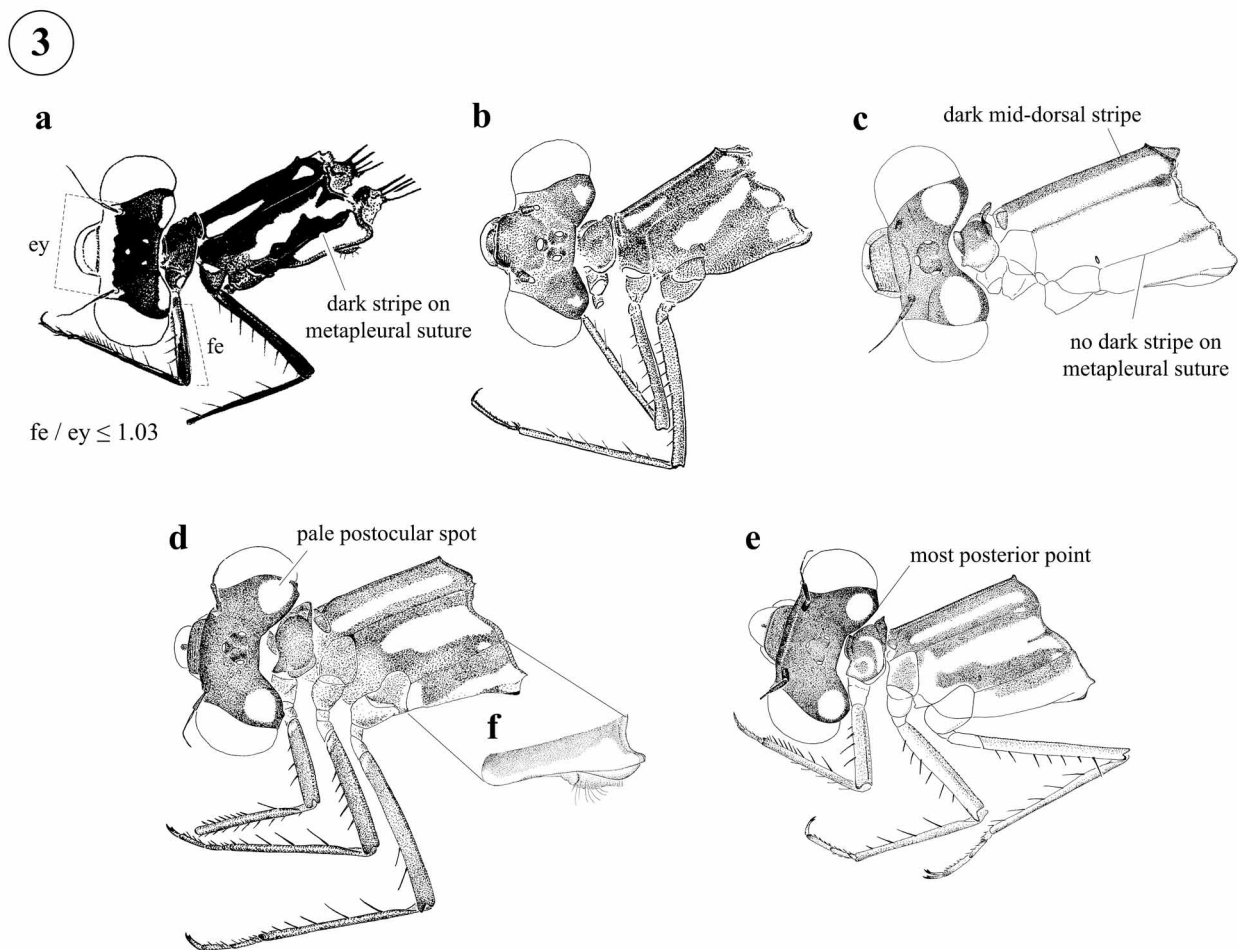


FIGURE 3. Head and thorax, dorsal and lateral view respectively (a–e), detail metepimeron, lateral view (f). (a) *Cyanallagma nigrinuchale*, male, Brazil, Lagoa dos Cordois; (b) *C. ferenigrum*, male holotype, Brazil, Utariti; (c) *Mesamphiagrion ecuatoriale*, male holotype, Ecuador, Archidona-Baeza; (d) *M. dunklei*, male paratype, Ecuador, Coyuja; (e) *M. dunklei*, female paratype, Ecuador, Coyuja; (f) *M. dunklei*, male holotype, Ecuador, Coyuja.

Distribution patterns of *Cyanallagma* and *Mesamphiagrion* (Figs. 102–103) also point to an independent evolution of these two genera, since they are broadly allopatric with two disjunct centers of diversity in northern and southern South America, and with no species recorded between southern Ecuador and central Brazil and northern Argentina.

4

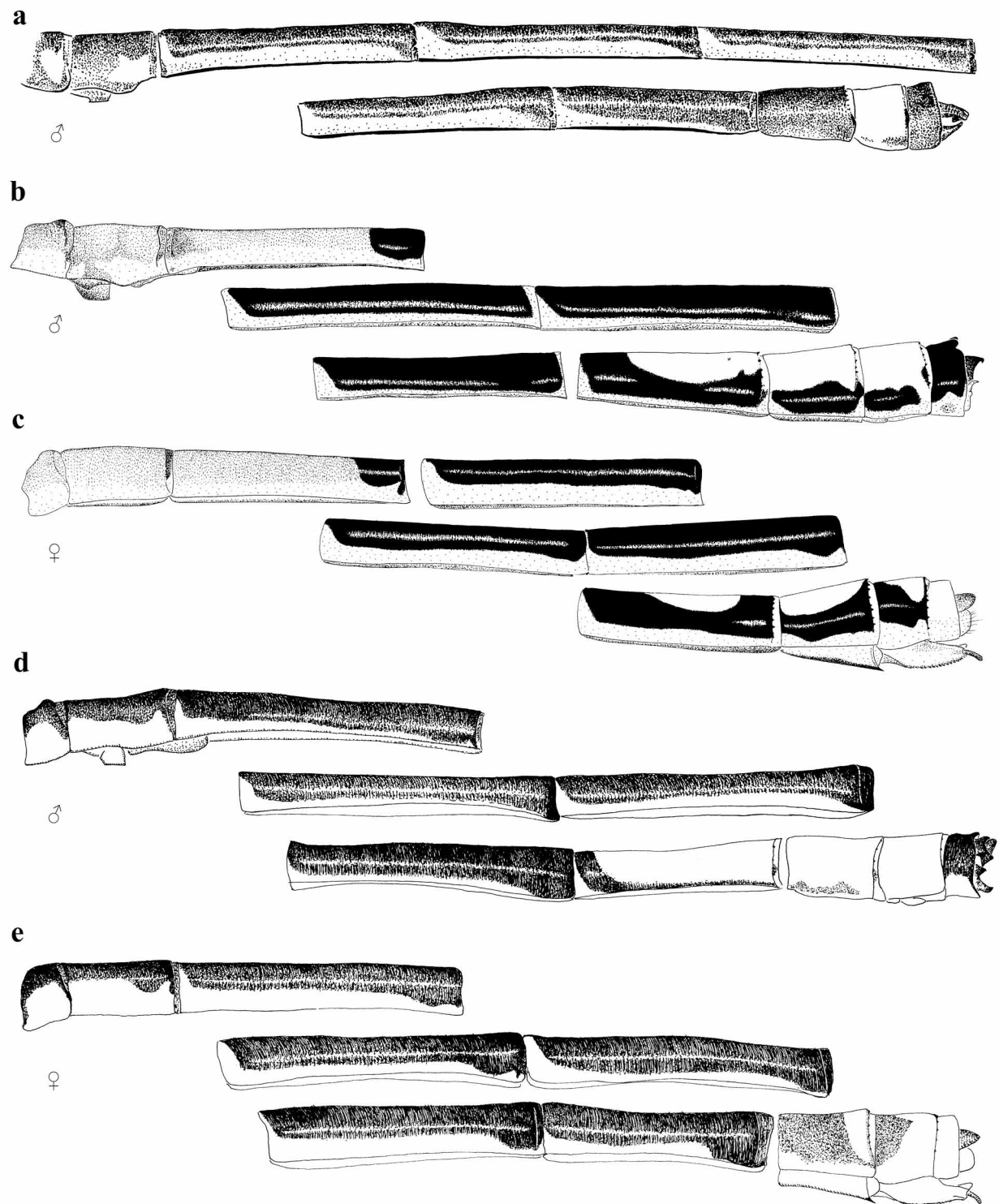


FIGURE 4. Abdomen, lateral view. (a) *Cyanallagma ferenigrum*, male holotype, Brazil, Utiariti; (b) *Mesamphiagrion dunklei*, male paratype, Ecuador, Coyuja; (c) *M. dunklei*, female paratype, Ecuador, Coyuja; (d) *M. ecuatoriale*, male holotype, Ecuador, Archidona-Baeza; (e) *M. ecuatoriale*, female allotype, Ecuador, Archidona-Baeza.

Navás (1934) described three *Argia* species, which according to examination of their types, belong to *Mesamphiagrion* as here redefined: *Argia ternaria*, *A. trina*, and *A. hebdomatica*. The first two were already synonymized with '*C. laterale*' by Donnelly & Alayo (1966: 113) and Garrison (1991: 11) respectively. We re-

examined their types and confirm their synonymy. The holotype of *A. hebdomatica*, an incomplete male lacking S6–10, agrees well with the generic definition of *Mesamphiagrion*, and shape of the posterior lobe of prothorax (Fig. 18b), genital ligula (Fig. 39) and color pattern demonstrate it is a junior synonym of *M. ovigerum*.

During a trip to Parque Nacional Manú, Peru in 1993 Dr. J.A. Louton reared a pair of Coenagrionidae larvae in the field from bromeliads that we later tentatively identified as *Cyanallagma*. The male was subsequently found to agree well with the description and holotype of *Telagrion quadricolor*. This led to examination of type material of poorly known *Telagrion* species, which revealed striking similarities among *T. oreas*, *T. quadricolor*, *T. prothoracicum*, *Acanthagrion acutum*, and *Cyanallagma thelcterion*. These five species are similar to *Mesamphiagrion* in color pattern (pale blue to olive postocular spots; thoracic striping; and combination of reddish-orange, black or brown and blue on body) and in having a projecting prominent medial lobe on the posterior margin of the prothorax. However, they differ from *Mesamphiagrion* in that each male cercus has a 'c'-shaped, blade-like ventral process as long as or longer than the cercus. Each of these processes converges medially with the one on the opposite cercus before diverging at its tip (Figs. 85–94). In *Mesamphiagrion*, the ventral processes are shorter than the cercus (Figs. 70–79). They differ from all known New World Coenagrionidae in that the genital ligula has a wide latero-apical pair of folds with sclerotized margins that converge medially at the distal end of the second segment (Figs. 49–53). They further differ from *Cyanallagma* and *Mesamphiagrion* (Table 2) in lacking protruding occipital lobes (Fig. 5) and in having relatively longer legs and abdomen. They also lack the marginal tubercles on sides of postero-dorsal cleft of S10 (Figs. 85–89), which is typical of *Cyanallagma* (*C. ferenigrum* is an exception) and *Mesamphiagrion*. Consequently a new genus, *Oreiallagma*, is described here for the reception of these five species.

Taxonomic treatment

Cyanallagma Kennedy 1920

Figures 1a–2a; 3a–b; 4a; 6; 9–14; 30–37; 54–59; 95–97; 102; 105–106

Cyanallagma Kennedy 1920: 87 (diagnosis; designation of *Acanthagrion interruptum* Selys 1876 as type species).

Bulla 1973: 95–104, figs. 1–21 (discussion of generic diagnosis, redescription of adults of *C. bonariense* and *C. interruptum* and description of larvae, illustration of diagnostic characters).

Davies 1981: 5 (generic listing with type species listed).

Davies & Tobin 1984: 66 (synonymic list).

De Marmels 1988: 100 (synonymy of *Archaeallagma*).

De Marmels 1989: 246–248 (generic characterization).

Bridges 1994: III.13 (synonymic list).

De Marmels 1997: 135–156, figs. 1–85 (generic diagnosis, keys, maps, and illustrations for northern species, description of the larva of *C. galianii*).

Steinmann 1997: 247 (synonymic list).

Tsuda 2000: 31 (synonymic list).

Lencioni 2001: 345–349, figs. 1–14 (generic key and illustrations for southern species).

De Marmels 2003: 103–106, figs. 8–16, 21 (description of *C. ferenigrum*, illustrations of male S10, genital ligula, head, thorax, and S1–2, S7–10, pt, male and female posterior prothoracic lobe, map, discussion of generic placement).

Lencioni 2006: 25, 33, fig. B7 (key to Brazilian genera; diagnosis).

Type species: *Acanthagrion interruptum* Selys 1876 by original designation (Kennedy 1920: 87).

Other species included: *C. angelae* Lencioni 2001, *C. bonariense* (Ris 1913), *C. ferenigrum* De Marmels 2003, *C. nigrinuchale* (Selys 1876), and *C. trimaculatum* (Selys 1876).

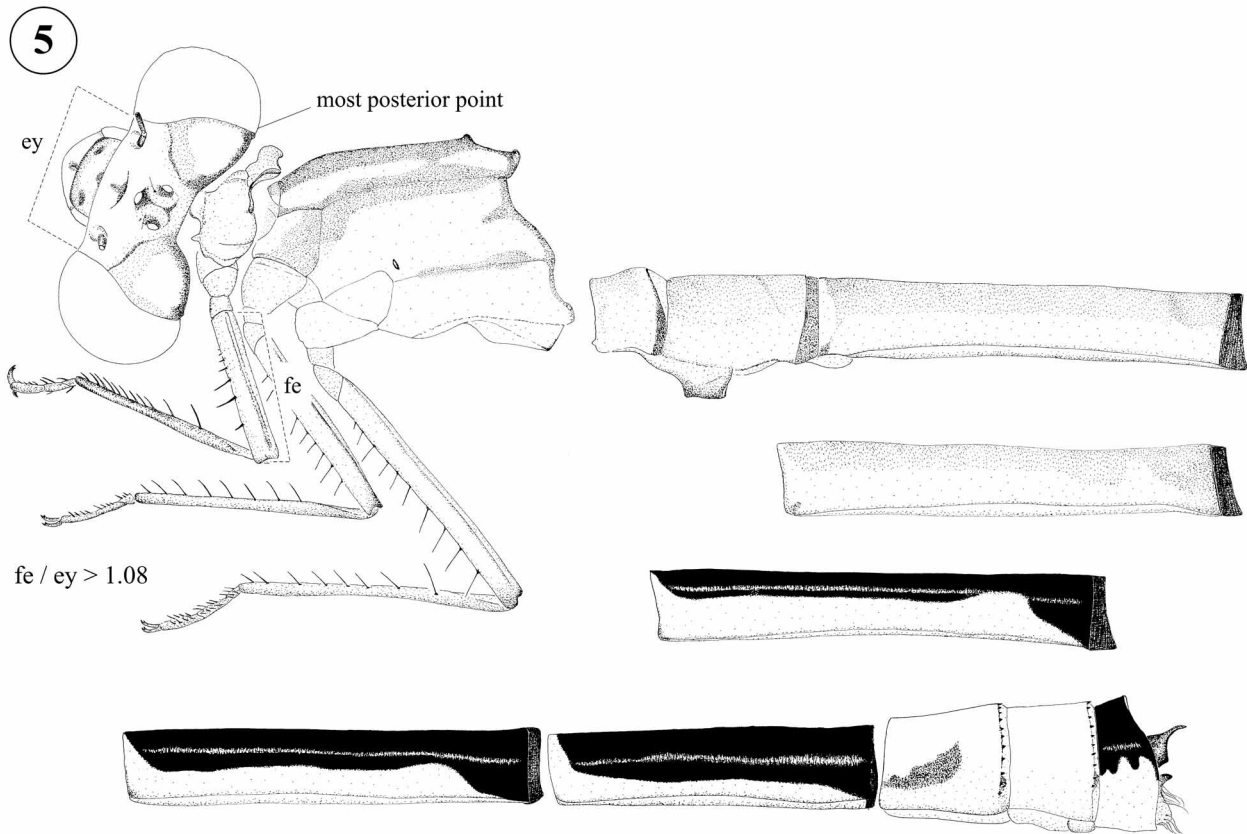


FIGURE 5. Color pattern of head, dorsal view, and body, lateral view, *Oreiallagma thekterion*, male paratype, Venezuela, Monte Zerpa.

Specimens examined. *C. angelae* (2 ♂, 1 ♀). BRAZIL. São Paulo State: Salesópolis, 2.xi.2001, F.A.A. Lencioni leg., 2 ♂, 1 ♀ (RWG).

C. bonariense (9 ♂, 3 ♀). ARGENTINA. Buenos Aires Prov.: Arroyo Caracol Chico, N of Berisso, 23.xi.1979, C.M. & O.S. Flint, Jr. leg., 1 ♂, 2 ♀ (RWG); Berisso, 24.ii.1989, G. Jurzitza leg., 1 ♂ (RWG); Villa Elisa, 26.xi.1979, C.M. & O.S. Flint, Jr. leg., 3 ♂ (RWG); Campana, Delta del Paraná, San Fernando, 8.i.1999, J. Muzón & N. von Ellenrieder leg., 3 ♂, 1 ♀ (MLP). Córdoba Prov.: Arroyo Las Vacas, Embalse Río Tercero, 24.xi.1981, A. Rodrigues Capítulo leg., 1 ♂ (MLP).

C. ferenigrum (1 ♂, 1 ♀). BRAZIL. Mato Grosso State: Utiariti, viii.1961, K. Lenko leg., 1 ♂ **holotype**, 1 ♀ **paratype** (ABMM).

C. interruptum (21 ♂, 10 ♀). CHILE. Aisén Region: 19 km N de Puerto Ibáñez, 590 m, 22.i.1992, J. Muzón leg., 2 ♂, 1 ♀ (RWG); same 1 ♂ (MLP). Osorno Region: Maicolpue, spring-fed pools, 22.xii.1993, C.M. & O.S. Flint, Jr. leg., 1 ♂ (RWG). de los Lagos Region: Cuesta Moraga, 9 km N Villa Santa Lucía, 24.i.1987, C.M. & O.S. Flint, Jr. leg., 3 ♂ (RWG); 10 km SW Futaleufú, 28.i.1987, C.M. & O.S. Flint, Jr. leg., 1 ♂, 1 ♀ (RWG); Lago Lonconao, just W of Futaleufú, 17.i.1987, R.W. Garrison leg., 10 ♂, 2 ♀ (RWG); Ensenada, 12-14.xii.1926, R.C. & E.S. Shannon leg., 1 ♂ (RWG). Malleco region: Cordillera de Nahuelbuta, marsh N of Coimalín, 16.xii.1993, C.M. & O.S. Flint, Jr. leg., 1 ♂, 1 ♀ (RWG). Maule Region: Reloca, S of Constitución, damp area near road, 16.xii.1976, Gurney & Barria leg., 3 ♂, 1 ♀ (RWG). Valparaiso region: Valparaiso, M. Mac Lachlan leg., 1 ♂ **lectotype** (BMNH); same data 1 ♂, 1 ♀ **paralectotypes** (IRSNB). ARGENTINA. Santa Cruz Prov.: El Calafate, Ayo. Los Perros (estepa extra-andina), 19.i.1992, J. Muzón leg., 1 ♂ (RWG). Chubut Prov.: Esquel, Laguna La Zeta, 19.i.1989, J. Muzón leg., 2 ♀ (RWG); Parque Nacional Nahuel Huapi, charca camino a Los Alerces, 24.i.1988, J. Muzón leg., 2 ♂ (RWG); Languineo, pond and

stream nr. Tecka, by route 62, 680 meters, 16.i.1995, R.W. Garrison leg., 11 ♂, 5 ♀ (RWG). Neuquen Prov.: Ruca Malén, 23 km N Villa La Angostura, 29.xii.1993, C.M. & O.S. Flint, Jr. leg., 1 ♀ (RWG); P.N. Lanín, Lago Queñi, 7.ii.1999, J. Muzón & P. Marino leg., 1 ♂, 1 ♀ (MLP). Río Negro Prov.: Meseta de Somuncurá, Valcheta, Ea. El Rincón, 28.i.1999, J. Muzón & N. von Ellenrieder leg., 1 ♂ (MLP); Laguna Cari Lafquen Chica, Aguada, 4.ii.1999, J. Muzón & P. Marino leg., 1 ♂, 1 ♀ (MLP).

C. nigrinuchale (3 ♂, 6 ♀). In order to clarify application of the name, we designate the syntype male from Brazil, Minas Gerais, São João del Rei, xi.1872, Walthère de Selys leg. as **lectotype**, and the 5 ♀ syntypes with the same data as **paralectotypes** (IRSNB). BRAZIL: São Paulo State: Fazenda Santana do Rio Abaixo, Jacareí, 1-6.xi.1999, F.A.A. Lencioni leg., 2 ♂ (RWG); same but 8.xii.1998, 1 ♀ (RWG). ARGENTINA. Misiones Prov.: Parque Nacional Iguazú, 13.iv.1991, J. Muzón leg., 1 ♀ (RWG); San Pedro, junction of Rt. Nac. 14 and 17, charca, 12.iv.1991, J. Muzón leg., 1 ♂ (RWG).

C. trimaculatum (4 ♂, 2 ♀). BRAZIL. Rio Grande do Sul State: Santa Cruz, 10.x., Walthère de Selys leg., 1 ♂ **lectotype**, 2 ♂ **paralectotypes** (IRSNB). Rio de Janeiro State: Teresópolis, 20.x., Walthère de Selys leg., 1 ♂, 2 ♀ **paralectotypes** (IRSNB).

Generic characterization. Head. Dorsum dark brown to black with pale blue postocular spots, pale postocular bar usually absent (present in some females of *C. interruptum* and *C. angelae*), rear of head surrounding occipital foramen black (Fig. 1a) to entirely dark brown in *C. ferenigrum* and black in *C. nigrinuchale*. Frons rounded, occipital lobes protruding posteriorly so that posterior most point of head is at their level (Figs. 3a–b).

Thorax. Posterior lobe of pronotum trilobate with medial lobe developed into a caudally projected plate, especially in males (Figs. 9a–14a), not projected beyond lateral lobes in females of *C. interruptum*, *C. nigrinuchale*, and *C. trimaculatum* (Figs. 9b; 13b–14b). Female mesostigmal plates triangular and wide, each with maximum width of less than 0.5 of maximum length (in *C. interruptum*, Fig. 9c) to rectangular and narrow, each with maximum width of more than 0.5 of maximum length (in *C. angelae*, *C. bonariense*, *C. ferenigrum*, *C. nigrinuchale*, and *C. trimaculatum*, Figs. 10c–14c); mesepisternal carinae arising between mesostigmal plates, anteriorly to their postero-medial edges in *C. interruptum* (Fig. 13c), at posterior edges of mesostigmal plates in *C. angelae*, *C. bonariense*, *C. ferenigrum*, *C. nigrinuchale*, and *C. trimaculatum* (Figs. 10c–14c). Pterothorax with dark brown to black mid-dorsal and humeral stripes and usually a dark brown to black stripe over metapleural (metepimeral-metepisternal) suture (absent in some specimens of *C. interruptum* and *C. bonariense*), with pale blue antehumeral stripe (occasionally lacking in some *C. interruptum*) usually interrupted distally (Figs. 105–106) but complete in *C. trimaculatum* and some females of *C. interruptum* and *C. angelae*. Legs short with femur 1 shorter than distance between eyes at level of antennifer (ratio = 1; Fig. 3a), tibial spurs shorter than or as long as distance between them (Figs. 3a–b), pretarsal claw with well developed supplementary tooth. Wings hyaline, CuP reaching CuPAA proximal to hind margin of wing for a distance as long as CuP or shorter, vein descending from quadrangle not forming a straight line to wing margin (Fig. 6).

Abdomen. Black and blue and pale yellow (Fig. 4a), relatively short with a ratio of 3.27–4.27 to length of head plus thorax. Genital ligula distal segment lacking inner fold, with paired latero-apical and latero-medial lobes (Figs. 30–37), with one or two ental membranous transverse folds distal to flexure, one between medio-lateral lobes and the second between medio-lateral lobes and flexure (Figs. 31; 34c), one of them usually projected into a medial membranous process, which might be folded and hidden in lateral view and is entire in *C. angelae*, *C. bonariense*, *C. interruptum*, *C. nigrinuchale*, and *C. trimaculatum* (Figs. 31; 33–37), and bifid in *C. ferenigrum* (Fig. 32). Second segment of genital ligula lacking wide latero-apical folds with sclerotized margins (Figs. 30–37). Postero-dorsal margin of male S10 with a 'u'-shaped cleft margined by a pair of tubercles in *C. angelae*, *C. bonariense*, *C. interruptum*, *C. nigrinuchale*, and *C. trimaculatum* (Figs. 54; 56–59), lacking tubercles in *C. ferenigrum* (Fig. 55). Male cercus always with a short ventro-basal process (Figs. 54–59); also with a broadly triangular ventro-apical process only in *C. ferenigrum* and *C. interruptum* (Figs. 54–55). Male paraproct with a branch ending on a sclerotized tip, dorsal in *C. angelae*, *C. bonariense*, *C. nigri-*

nuchale, and *C. trimaculatum* (Figs. 54a–b; 56–58b; 59c), and medial in *C. ferenigrum* (Fig. 55). Female with vulvar spine on S8; ovipositor slightly shorter to slightly longer than S10, not reaching tips of cerci.

Generic diagnosis. No unique characters are known for *Cyanallagma*. The combination of a rounded frons, presence of pale postocular spots, a trilobate prothoracic posterior lobe, striped pterothorax, and male cerci armed with some kind of process is common to *Apanisagrion* Kennedy 1920, *Chrysobasis* Rácenis 1959a, *Hesperagrion* Calvert 1902, *Homeoura* Kennedy 1920, some species of *Ischnura* Charpentier 1840, *Leptobasis* Selys 1877, *Mesamphiagrion*, *Oreiallagma*, and *Telagrion*.

Cyanallagma differs from *Mesamphiagrion* and *Oreiallagma* by having the rear of head surrounding occipital foramen dark (Fig. 1a) and by the male cercus lacking a dorsal process (Figs. 54–59). The three genera are further diagnosed in Table 2. *Cyanallagma* can be separated from all the remaining genera mentioned above except *Hesperagrion* and some *Ischnura* species by its most posterior point of the head located at the level of the postocular lobes (Figs. 3a–b) rather than at the level of eyes (as in Fig. 5).

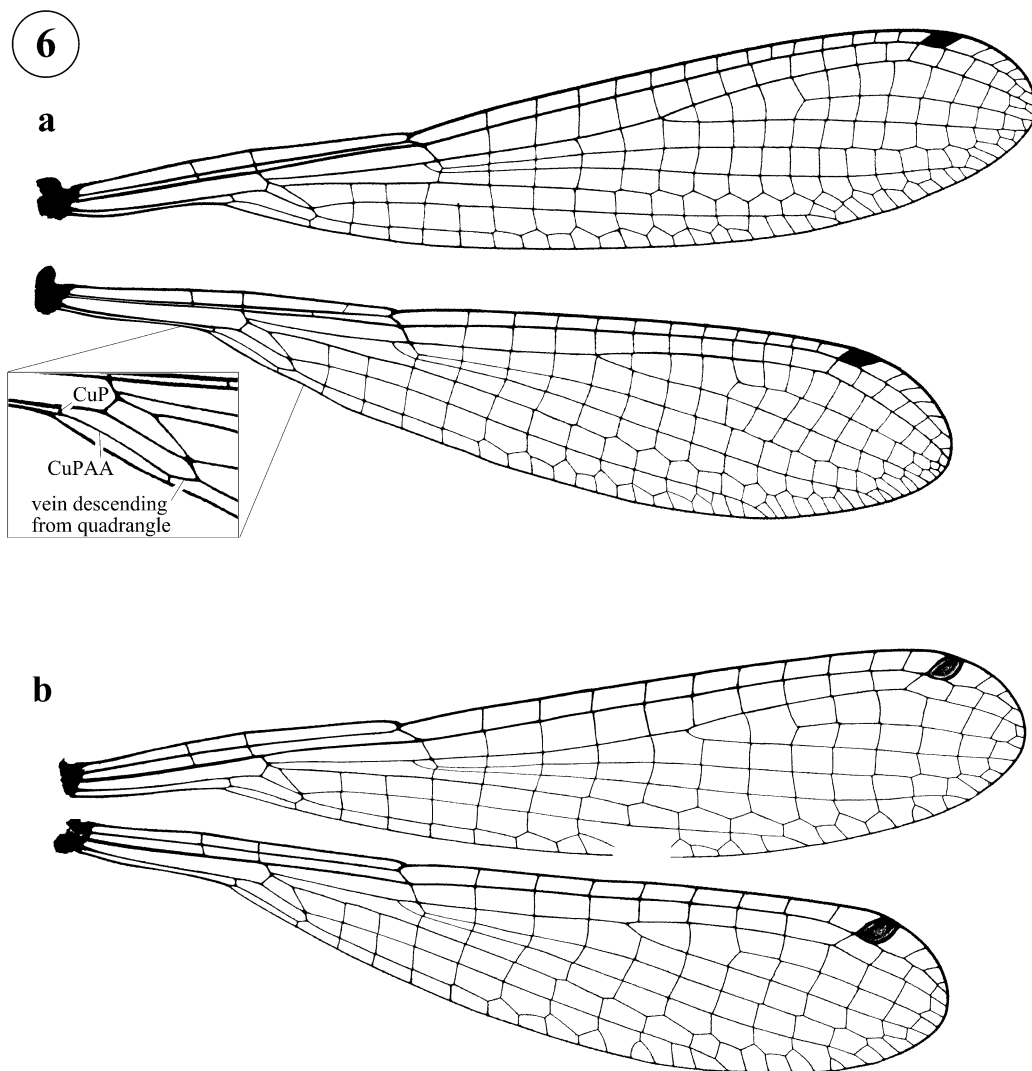


FIGURE 6. Wings. (a) *Cyanallagma interruptum*, male, Argentina, Queñi; (b) *C. ferenigrum*, male holotype, Brazil, Utiariti.

The following characters will separate *Cyanallagma* from *Hesperagrion*: male cercus lacking a dorsal process, postero-dorsal margin of S10 with a 'u'-shaped cleft margined by a pair of tubercles (Figs. 54–59), genital ligula lacking a pair of large lateral chitinized spines (Figs. 30–37), and female mesanepisterna with

well developed carinae forming distinct ridges (Figs. 9c–14c). *Cyanallagma* differs from *Ischnura* by having a ventro-basal process in male cercus (Figs. 54–59), genital ligula distal segment with paired latero-apical and latero-medial lobes, lacking an inner fold, with distal corners not projected into flagellae (Figs. 30–37), and female mesanepisterna with well developed carinae forming distinct ridges (Figs. 9c–14c).

Remarks. A patch of differentiated scalariform-like cuticle apparently occurs in all species except *C. ferenigrum*. We confirmed its presence in *C. interruptum* with SEM (Fig. 95) and the same appears as a pale corrugated area surrounded by dense setation when viewed at high magnification (>100x) under a binocular microscope in *C. angelae*, *C. bonariense*, *C. nigrinuchale*, and *C. trimaculatum* as well as in *Oreiallagma oreas*, *O. prothoracicum*, and *O. quadricolor* (Figs. 52; 56–59; 87–89). Since the only available male of *C. ferenigrum* was the holotype, we did not subject it to SEM examination. However, the appearance of its cercus under the binocular microscope with a pale spot lacking dense setation and with no evident corrugation (Fig. 55) is like the cerci of *Mesamphiagrion laterale* and *Acanthagrion lancea* Selys, both of which we examined with SEM, and confirmed a lack of any differentiated scalariform-like cuticular areas.

According to Lencioni (*pers. comm.*) immature adults of *C. angelae* are purplish for some hours after emergence before acquiring the blue color characteristic of adults.

Distribution. Southern South America from southern Chile and Argentina to central Brazil, from 0 to 1450 m above sea level (Fig. 102).

Key to males of *Cyanallagma*

1. Pale area on metepimeron restricted to posterior 0.3 (Fig. 3b); S10 lacking postero-dorsal tubercles (Fig. 55); inner process of genital ligula transverse fold bifid (Figs. 32a, c); Mato Grosso and Bahia States, Brazil (Fig. 102) *C. ferenigrum*
- 1'. Pale area on metepimeron occupying posterior 0.6 or more (Figs. 2a–b; 3a); S10 with a pair of postero-dorsal tubercles (Figs. 54; 56–59); inner process of genital ligula transverse fold entire (Figs. 31; 33c; 34c; 36c–37c) 2
2. (1'.) Cercus with a large broadly based ventro-apical process (Fig. 54b); S half of Chile and Argentina (Fig. 102) *C. interruptum*
- 2'. Cercus lacking a ventro-apical process (Figs. 56b–59b) 3
3. (2'.) Cercus with a longitudinal carina on inner surface (Figs. 56a–57a); medial lobe of posterior prothoracic lobe smoothly rounded (Figs. 11a–12a) 4
- 3'. Cercus lacking a longitudinal carina on inner surface (Figs. 58a–59a); medial lobe of posterior prothoracic lobe bilobate (Figs. 13a–14a) 5
4. (3.) Medial lobe of posterior prothoracic lobe arising on ventral surface of pronotum, separated from lateral lobes by a carina (Fig. 12a); ventro-basal tooth of cercus directed antero-ventrally (Fig. 57a), longitudinal carina at about mid-width of cercus, ending dorso-apically at posterior margin (Figs. 57a–b); latero-apical processes of genital ligula small and directed posteriorly (Fig. 36); São Paulo State, Brazil (Fig. 102) *C. angelae*
- 4'. Medial lobe of posterior prothoracic lobe arising on dorsal surface of pronotum, continuous with lateral lobes (Fig. 11a); ventro-basal tooth of cercus directed postero-ventrally (Fig. 56a), longitudinal carina along ventral margin of cercus, ending ventro-apically at posterior margin (Figs. 56a–b); latero-apical processes of genital ligula large and recurved ventro-anteriorly (Fig. 33); central E Argentina and Uruguay (Fig. 102) *C. bonariense*
5. (3'.) Pale antehumeral stripe interrupted, black of humeral suture confluent with black of metapleural suture anteriorly (Fig. 3a); Misiones Province, Argentina to Minas Gerais and Goiás States, Brazil (Fig. 102) *C. nigrinuchale*

- 5'. Pale antehumeral stripe complete, black of humeral suture separated from black of metapleural suture (Fig. 2a); Rio Grande do Sul to Rio de Janeiro States, Brazil (Fig. 102) *C. trimaculatum*

Key to females of *Cyanallagma*

1. Pale area on metepimeron restricted to posterior 0.3 (Fig. 3b); Mato Grosso and Bahia States, Brazil (Fig. 102) *C. ferenigrum*
- 1'. Pale area on metepimeron occupying posterior 0.6 or more (Figs. 2a; 3a) 2
2. (1'.) Mesostigmal plates broad and triangular, mesepisternal carinae arising proximal to postero-medial margin of mesostigmal plates (Fig. 9c); S half of Chile and Argentina (Fig. 102) *C. interruptum*
- 2'. Mesostigmal plates narrow and rectangular, mesepisternal carinae arising at postero-medial margin of mesostigmal plates (Figs. 10c–14c).....3
3. (2'.) Medial lobe of posterior prothoracic lobe well developed (Figs. 11b–12b) 4
- 3'. Medial lobe of posterior prothoracic lobe very small (Figs. 13b–14b) 5
4. (3.) Lateral margin of female mesostigmal plates linear (Fig. 12c); São Paulo State, Brazil (Fig. 102)
..... *C. angelae*
- 4'. Lateral margin of female mesostigmal plates rounded (Fig. 11c); central E Argentina and Uruguay (Fig. 102) *C. bonariense*
5. (3'.) Pale antehumeral stripe interrupted, black of humeral suture confluent with black of metapleural suture anteriorly (Fig. 3a); medial lobe of prothoracic posterior lobe represented by a small point continuous with lateral lobes (Fig. 13b); Misiones Province, Argentina to Minas Gerais and Goias States, Brazil (Fig. 102) *C. nigrinuchale*
- 5'. Pale antehumeral stripe complete, black of humeral suture separated from black of metapleural suture (Fig. 2a); medial lobe of prothoracic posterior lobe rounded and separated from lateral lobes by a marked concavity on each side (Fig. 14b); Rio Grande do Sul to Rio de Janeiro States, Brazil (Fig. 102) *C. trimaculatum*

***Mesamphiagrion* Kennedy 1920 stat. rev.**

Figures 1b; 2b–c; 3c–f; 4b–e; 7; 15–24; 38–48; 60–84; 98–100; 103; 107–109

Mesamphiagrion Kennedy 1920: 87 (diagnosis; designation of *Enallagma occultum* Ris 1918 as type species).

St. Quentin 1960: 52 (key).

Davies 1981: 6 (generic listing with type species listed).

Davies & Tobin 1984: 75 (synonymic list).

De Marmels 1989 (redefinition).

Bridges 1994: III.29 (synonymic list).

Steinmann 1997: 278 (synonymic list).

Tsuda 2000: 39 (synonymic list).

Archaeallagma Kennedy 1920: 87 (diagnosis; designation of *Enallagma ovigerum* Calvert 1909 as type species). — **syn.**

nov.

Lieftinck 1949: 204 (summary of similarities among *Protallagma*/ *Archaeallagma*/ *Oreagrion*).

Davies 1981: 5 (as synonym of *Enallagma*).

Davies & Tobin 1984: 65 (synonymic list).

De Marmels 1988: 100 (synonymy with *Cyanallagma*).

De Marmels 1989: 250 (discussion of synonymy with *Cyanallagma*).

Bridges 1994: III.5 (as synonym of *Cyanallagma*).

Steinmann 1997: 245 (synonymic list as valid genus).

Tsuda 2000: 202 (as synonym of *Cyanallagma*).

Cyanallagma Kennedy 1920: 87 (in part; inclusion of *Acanthagrion laterale* Selys 1876).

Davies & Tobin 1984: 66 (in part, synonymic list).

De Marmels 1989: 246–248 (generic characterization).

Bridges 1994: III.13 (in part, synonymic list).

Steinmann 1997: 247 (in part, synonymic list).

De Marmels 1997: 135–156, figs. 1–85 (in part, generic diagnosis, keys, maps, and illustrations for northern species, description of the larva of '*C.*' *gaianii*).

Tsuda 2000: 31 (in part, synonymic list).

De Marmels 2007: 96–110, figs. 111–122 (description of larvae of '*C.*' *laterale* and '*C.*' *tamaense*).

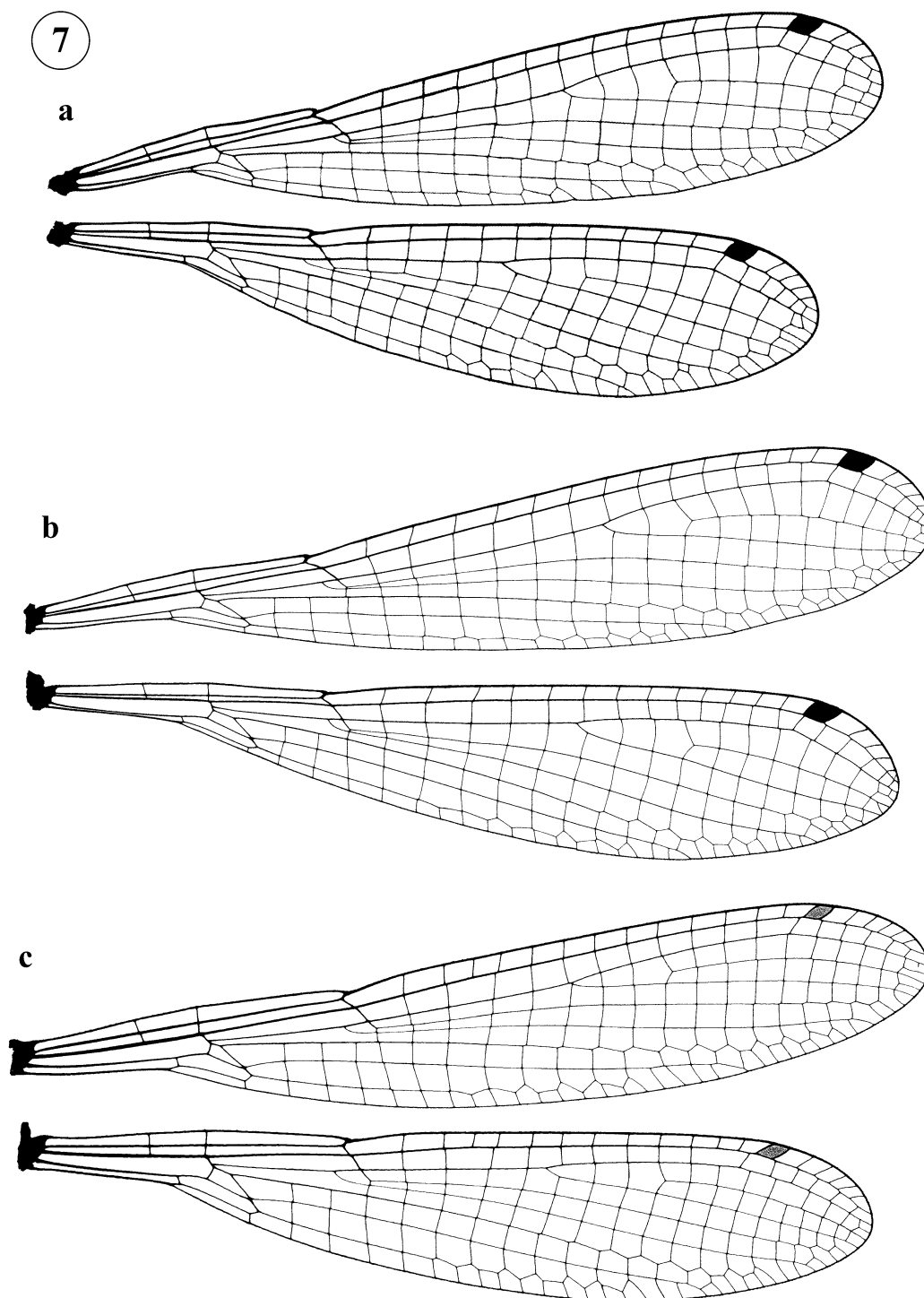


FIGURE 7. Wings. (a) *Mesamphiagrion dunklei*, male paratype, Ecuador, Coyuja; (b) *M. ecuatoriale*, male holotype, Ecuador, Archidona-Baeza; (c) *M. occultum*, male, Colombia, Chingaza.

Type species: *Enallagma occultum* Ris 1918 by original designation (Kennedy 1920: 87).

Other species included: *M. demarmelsi* (Cruz 1986) **comb. nov.**, *M. dunklei* **sp. nov.**, *M. ecuatoriale* **sp. nov.**, *M. gaianii* (De Marmels 1997) **comb. nov.**, *M. laterale* (Selys 1876) **comb. nov.** [syn *Argia ternaria* Navás 1934, syn *Argia trina* Navás 1934], *M. ovigerum* (Calvert 1909) **comb. nov.** [*Argia hebdomatica* Navás 1934, **syn. nov.**], *M. risi* (De Marmels 1997) **comb. nov.**, *M. tamaense* (De Marmels 1988) **comb. nov.**, and *M. tepuiantum* (De Marmels 1997) **comb. nov.**.

Specimens examined. *M. demarmelsi* (1 ♂). COLOMBIA. Cundinamarca Dept.: 11 km N of Bogotá, 8.iii.1969, P.P. Spangler leg., 1 ♂ (RWG).

M. dunklei (31 ♂, 11 ♀). ECUADOR. Napo Prov. See details under species account.

M. ecuatoriale (4 ♂, 2 ♀). ECUADOR. Napo Prov. See details under species account.

M. gaianii (2 ♂). VENEZUELA. Trujillo State: Ancient road Boconó-Trujillo, Páramo La Cristalina, 29.viii.1991, J. De Marmels leg., 2 ♂ **paratypes** (RWG).

M. laterale (26 ♂, 8 ♀). VENEZUELA. Mérida State: 17 km E of La Azulita, 26.vii.1989, T.W. Donnelly leg., 3 ♂ (TWD); same data but 1 ♂ (RWG); same data but 3 ♂ (FSCA); Carbonera, 31.xii.1960, J. Rácenis leg., 1 ♂ (FSCA). COLOMBIA. Boyacá Dept.: La Pica, 13.ii/3.iii.1917, M.A. Carriker leg., 12 ♂, 3 ♀ (RWG); Santuario de Fauna y Flora de IGUAQUE, near Arcabuco, 1.viii. 1991, J. Delgado leg., 2 ♀ (TWD, RWG); same data but 1.ix.1991, 1 ♀ (TWD); same data but 1.x.1991 (C. Rodrigues), 1 ♀ (TWD); Cauca Dept.: Nueva Granada, M. Mac Lachlan leg., 1 ♂ **lectotype** (BMNH); same data 2 ♂ **paralectotypes** (IRSNB). Santander Dept.: La Unión, 1 ♂ **holotype** of *Argia trina* Navás 1934 (FSCA). Cundinamarca Dept.: Quetame, vii.1912, 1 ♂ **syntype** of *Argia ternaria* Navás 1934 (UMMZ); Pensilvania, 1913, 1 ♂ **syntype** of *Argia ternaria* Navás 1934 (NHMP); Choachí, viii.1916, 1 ♀ **syntype** of *Argia ternaria* Navás 1934 (NHMP).

M. occultum (3 ♂). COLOMBIA. Cundinamarca Dept.: Parque Nacional Chingaza, Quebrada La Playa, 9.xi.2003, O. Realpe & M. Beltrán leg., 1 ♂ (RWG); same data but Churca Ludeck, 20.ix.2003, 2 ♂ (RWG).

M. ovigerum (3 ♂). COLOMBIA. Cundinamarca Dept.: Santa Fe de Bogotá, 1863, Lindig leg., 1 ♂ **holotype** (MCZ); Pensilvania, 1913, 1 ♂ **lectotype** *A. hebdomatica* (MNHP); Boyacá Dept.: Arcabuco, Santuario de Flora y Fauna de Iguaque, 2400–3600 m, 16.xi.1991, M. Roa leg., 1 ♂ (DRP).

M. tamaense (11 ♂, 1 ♀). COLOMBIA. Boyacá Dept.: La Pica, 9–14.ii.1917, M.A. Carriker leg., 11 ♂, 1 ♀ (RWG).

Generic characterization. Head. Color of dorsum dark reddish brown to black with pale blue to olive postocular spots, usually no pale postocular bar but present in some specimens of *M. laterale*; rear of head surrounding occipital foramen pale (Fig. 1b). Frons rounded, occipital lobes protruding posteriorly so that most posterior point of head is at their level (Figs. 3c–e). **Thorax.** Posterior lobe of prothorax trilobate, usually with medial lobe developed into a caudally projected plate (Figs. 15; 16a; 17–18; 20a, b–22a, b; 23a; 24a–b) especially in males, but only slightly projected in male *M. tepuiantum* (Fig. 19) and female *M. ecuatoriale* (Fig. 16b) or not projected in females of *M. dunklei* and *M. gaianii* (Figs. 22c; 23b). Female mesostigmal plates broadly triangular and wide, each with ratio of maximum width/length of less than 0.5; mesanepisternal carinae arising between mesostigmal plates anteriorly to their postero-medial edges (Figs. 16c; 20c–21c; 22d; 23c–24c). Pterothorax (Figs. 2b–c; 3c–e) with dark mid-dorsal and humeral stripes, usually with a dark stripe over metapleural suture (Figs. 2b; 3d–f) that is absent in *M. ecuatoriale*, *M. occultum*, *M. ovigerum*, and *M. tepuiantum* (Figs. 2c–3c); with pale blue antehumeral stripe usually complete (Figs. 2b; 3c–e), but interrupted distally in *M. tepuiantum* and some *M. demarmelsi* (Fig. 2c). Legs short with femur 1 usually shorter than distance between eyes at level of antennifer (Figs. 3d–e; ratio = 1.03), tibial spurs shorter to slightly longer than distance between them (Figs. 3d–e); pretarsal claw with well developed supplementary tooth. Wings hyaline to smoky in some tenerals (*i.e.* in *M. laterale* and *M. tamaense*), CuP reaching CuPAA proximal to hind margin of wing for a distance as long as CuP or shorter, vein descending from quadrangle not forming a straight line to wing margin (Fig. 7).

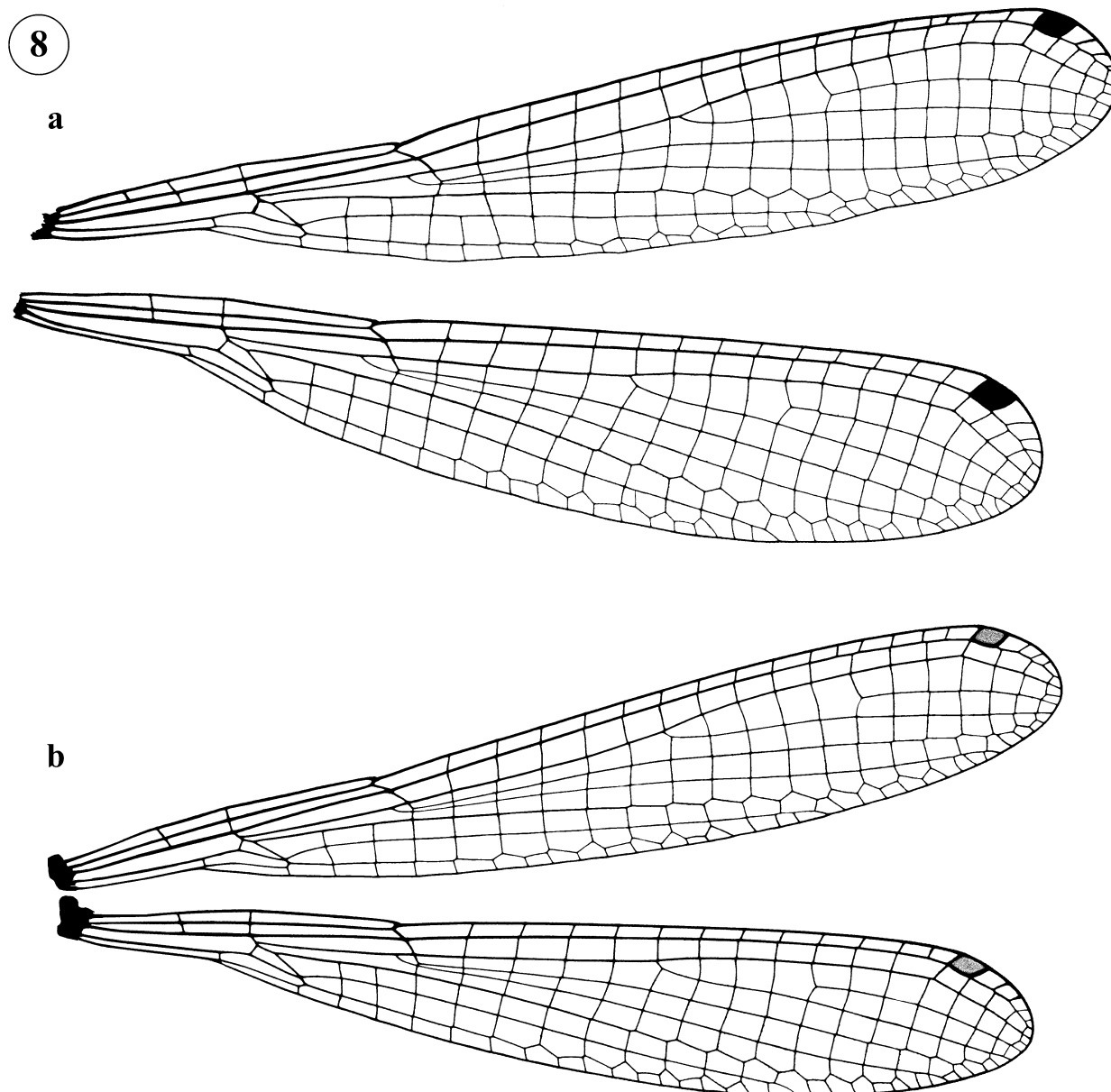
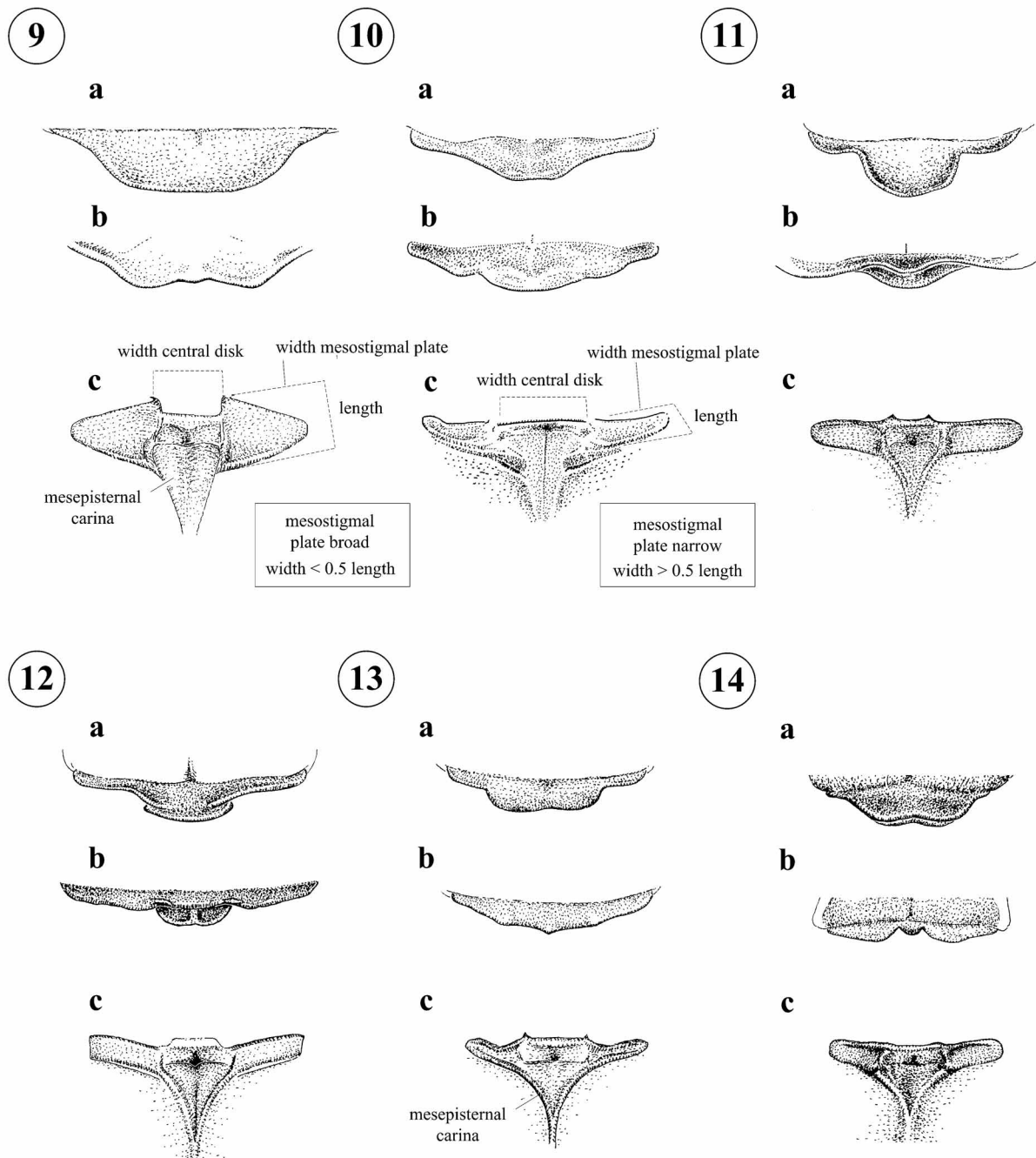


FIGURE 8. Wings. (a). *Oreiallagma thelcterion*, male paratype, Venezuela, Monte Zerpa; (b) *O. prothoracicum*, male paratype, Ecuador, Intaj.

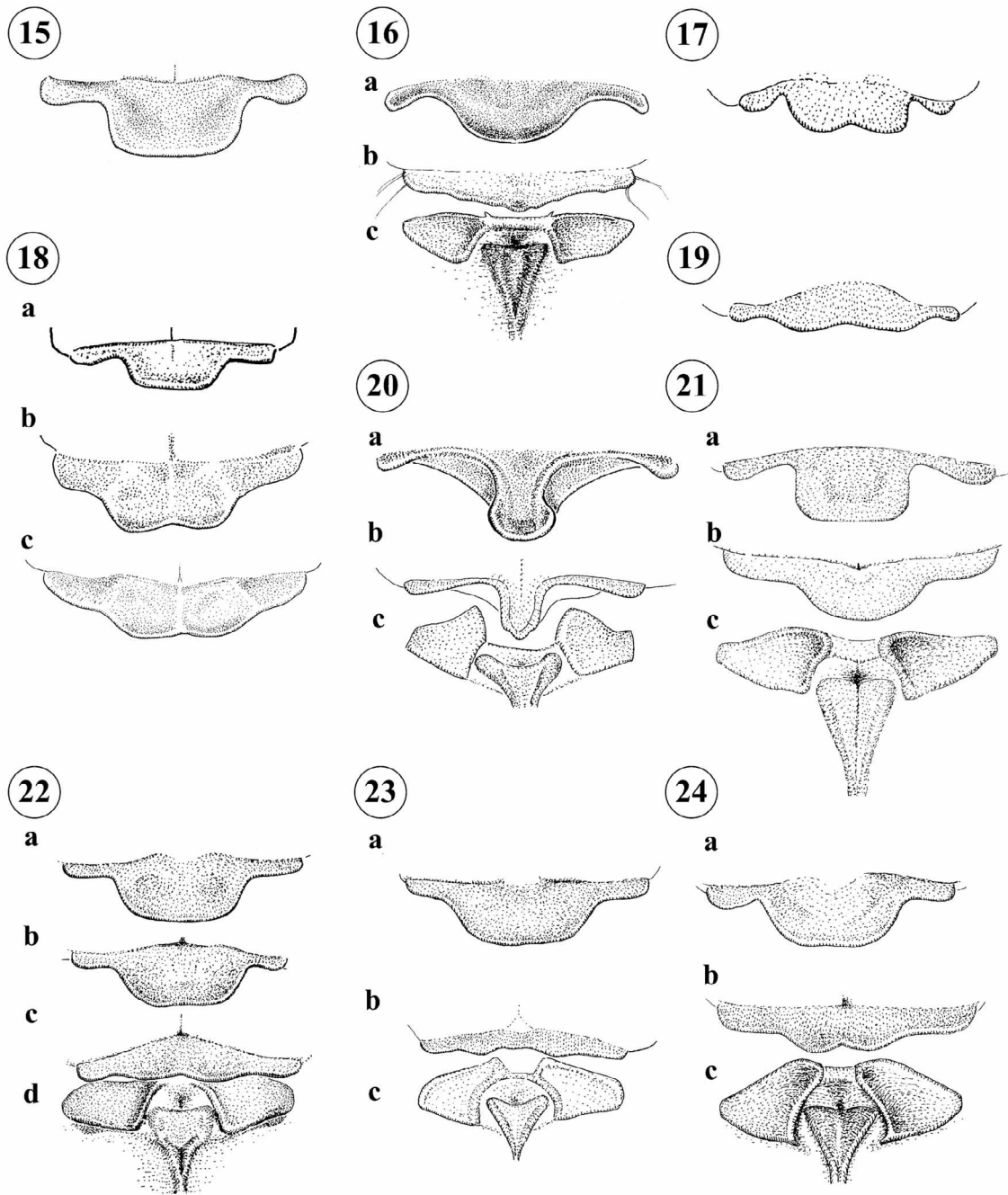
Abdomen (Fig. 4b–e). Black with blue spots on base and distal segments (S6–10 or less), and reddish-orange (on S1–3) on not fully mature specimens (Figs. 108–109); relatively short, with a ratio of 3.39–4.28 to length of head plus thorax, less in *M. ecuatoriale* (4.2 to 4.85). Genital ligula with distal segment lacking inner fold; with paired latero-apical lobes and paired latero-medial lobes (Figs. 38–48); with two ental membranous transverse folds distal to flexure, one between medio-lateral lobes and the second between medio-lateral lobes and flexure, this latter fold projected into a medial membranous process that may be folded and hidden in lateral view; second segment lacking wide latero-apical folds with sclerotized margins (Figs. 38–48). Postero-dorsal margin of male S10 with a 'u'-shaped cleft margined by a pair of tubercles (Figs. 60–70; 71a; 77b–c; 78b–79b; 80–84). Male cercus sometimes with a pale spot on its posterior surface but lacking differentiated scalariform-like cuticle in that area. Male cercus structure complex with four processes that usually can be seen simultaneously only in medio-posterior view (Figs. 70b; 71–76; 77a–79a): a dorsal process that may be apical, long, and hooked (as in *M. demarmelsi*, *M. dunklei*, *M. gaianii*, *M. laterale*, and *M. tamaense*) or sub-

apical and short (as in *M. ecuatoriale*, *M. occultum*, *M. ovigerum*, *M. risi*, and *M. tepuianum*); two ventro-apical processes represented by short lobes each of which may be rounded (as in *M. ecuatoriale*, *M. occultum*, *M. ovigerum*, and *M. risi*) or bluntly pointed (as in *M. demarmelsi*, *M. tepuianum*, *M. dunklei*, *M. gairanii*, *M. laterale*, and *M. tamaense*); and a broadly triangular ventro-basal process that is directed antero-medially and is



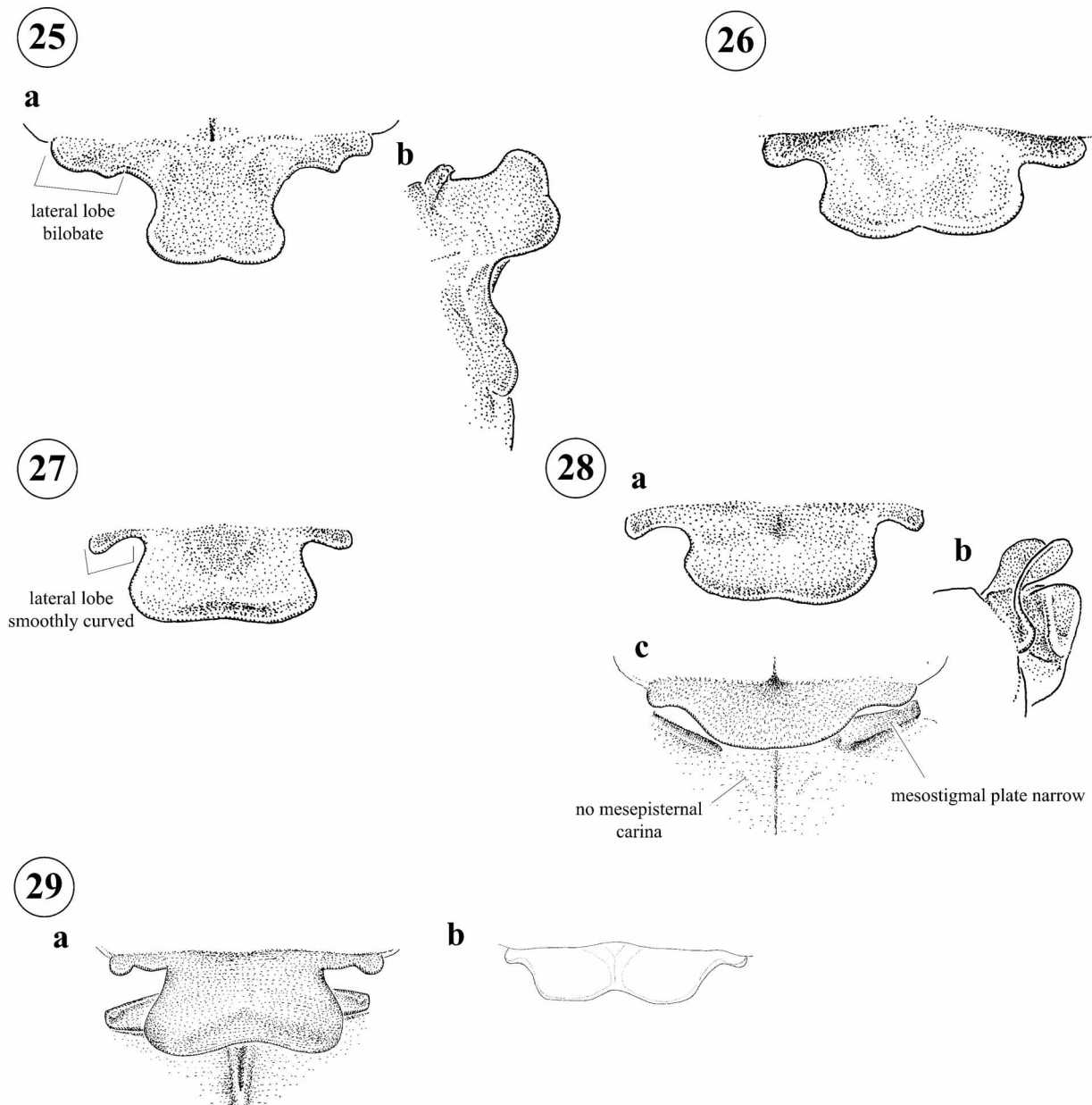
FIGURES 9–14. Male posterior lobe of prothorax, dorsal view (a), female posterior lobe of prothorax, dorsal view (b), female mesostigmal plates, dorsal view (c). (9) *Cyanallagma interruptum*, Argentina, Queñi; (10) *C. ferenigrum*, Brazil, Utiariti, (a) male holotype, (b–c) female paratype; (11) *C. bonariense*, Argentina, Campana; (12) *C. angelae*, Brazil, Salesópolis; (13) *C. nigrinuchale*, (a) male, Brazil, Jacareí, (b–c) female, Argentina, Iguazú; (14) *C. trimaculatum*, Brazil, (a) male lectotype, Santa Cruz, (b–c) female paralectotype, Teresópolis.

visible only in medio-posterior view or in dorso-external view (as in *M. demarmelsi*, Fig. 65b). Male paraproct with a dorsal branch ending on a sclerotized tip (Figs. 60–69; 70a–71a; 72; 76; 77b–c; 78b–79b).



FIGURES 15–24. Posterior lobe of prothorax and mesostigmal plates, dorsal view. (15) *Mesamphiagrion occultum*, posterior lobe of prothorax, male, Colombia, Chingaza; (16) *M. ecuatoriale*, Ecuador, Archidona-Baeza, (a–b) posterior lobe of prothorax, (a) male holotype, (b) female allotype, (c) mesostigmal plates, female allotype; (17) *M. risi*, posterior lobe of prothorax, male, Colombia, Anolaima (modified from De Marmels 1989); (18) *M. ovigerum*, posterior lobe of prothorax, male, Colombia, (a) Bogotá, holotype, (b) Pennsylvania, holotype of *Argia hebdomatica*, (c) Arcabuco; (19) *M. tepuianum*, male holotype, Venezuela, Mt. Duida (modified from De Marmels 1997); (20) *M. demarmelsi*, Colombia, Bogotá, (a–b) posterior lobe of prothorax, (a) male, (b) female, (c) mesostigmal plates, female (b–c, modified from De Marmels 1997); (21) *M. tamaense*, Colombia, La Pica, (a–b) posterior lobe of prothorax, (a) male, (b) female, (c) mesostigmal plates, female; (22) *M. dunklei*, Ecuador, Coyuja, (a–c) posterior lobe of prothorax, (a) male holotype, (b) male paratype, (c) female paratype, (d) mesostigmal plates, female paratype; (23) *M. gaianii*, Venezuela, La Cristalina, paratype, (a–b) posterior lobe of prothorax, (a) male, (b) female, (c) mesostigmal plates, female (b–c modified from De Marmels 1997); (24) *M. laterale*, Colombia, La Pica, (a–b) posterior lobe of prothorax, (a) male, (b) female, (c) mesostigmal plates, female.

Female with vulvar spine on S8; ovipositor slightly shorter to slightly longer than S10, not reaching tips of cerci (Figs. 4c, e).



FIGURES 25–29. Posterior lobe of prothorax. (25) *Oreiallagma prothoracicum*, male paratype, Ecuador, Intaj, (a) dorsal view, (b) medio-dorsal view; (26), *O. oreas*, male holotype, Colombia, Monte Socorro, dorsal view; (27) *O. acutum*, male lectotype, Bolivia, Río Zongo, dorsal view; (28) *O. quadricolor*, Peru, (a–b) posterior lobe of prothorax, male, holotype, Santa Ana, (a) dorsal view, (b) antero-lateral view, (c) female, Morro Leguía, dorsal view; (29) *O. thelktion*, Venezuela, dorsal view, (a) male, Monte Zerpa, (b) female, Guaramacal.

Generic diagnosis. Male cercus of *Mesamphiagrion* is unique among all New World Coenagrionidae by its four processes: one dorsal, two short ventro-apical and one ventro-basal (Figs. 70b; 71–76; 77a–79a). As mentioned under *Cyanallagma*, the combination of a rounded frons, presence of pale postocular spots, a trilobate prothoracic posterior lobe, striped pterothorax and male cerci provided with some kind of processes is shared among New World Coenagrionidae not only with *Cyanallagma* and *Oreiallagma* but also with *Apanisagrion*, *Chrysobasis*, *Hesperagrion*, *Homeoura*, some *Ischnura* species, *Leptobasis*, and *Telagrion*. *Mesamphiagrion* differs from *Cyanallagma* by having the rear of head surrounding occipital foramen pale (Fig. 1b)

and by the male cercus having a dorsal process (Figs. 60–84). It can be distinguished from all remaining mentioned genera except *Hesperagrion* and some *Ischnura* species by its most posterior point of head located at level of postocular lobes (Figs. 3c–e) rather than at level of eyes (as in Fig. 5).

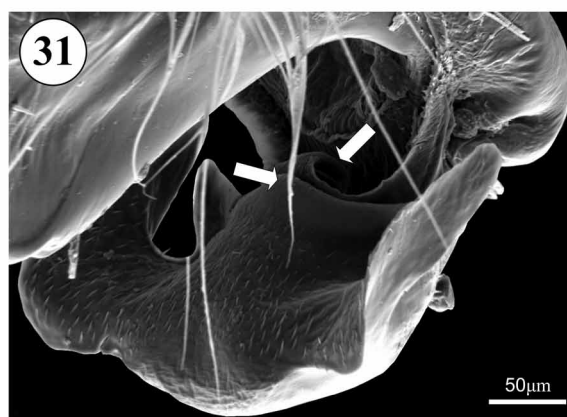
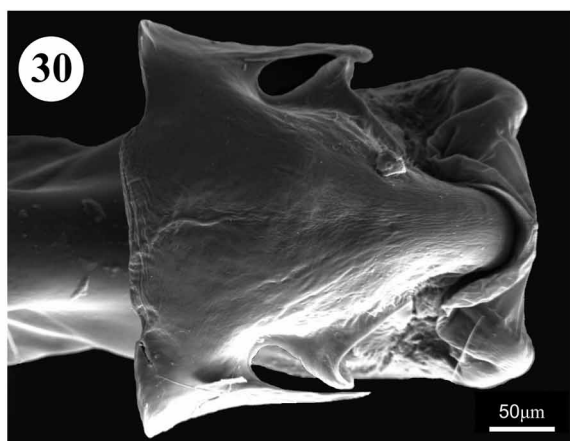
Mesamphiagrion is separated from *Hesperagrion* by the male postero-dorsal margin of S10 with a 'u'-shaped cleft margined by a pair of tubercles (Figs. 60–84), genital ligula lacking a pair of large lateral chitinized spines (Figs. 38–48), and female mesanepisterna with well developed carinae forming distinct ridges (Figs. 16c; 20c; 22d; 23c–24c). *Mesamphiagrion* differs from *Ischnura* by the presence of a ventro-basal process in male cercus (Figs. 60–84), genital ligula distal segment lacking an inner fold, presence of paired latero-apical and latero-medial lobes and distal corners not projected into flagellae (Figs. 38–48), and female mesanepisterna with well developed carinae forming distinct ridges (Figs. 16c; 20c; 22d; 23c–24c).

Distribution. Northwestern South America from Ecuador to Venezuela along the Andes and in the Tepuis, from 650 to 4000 m above sea level (Fig. 103).

Key to males of *Mesamphiagrion*

1. Medial lobe of posterior prothoracic lobe narrow, strongly projected and dorsally concave (Fig. 20a); Cundinamarca Dept., Colombia (Fig. 103) *M. demarmelsi*
- 1'. Medial lobe of posterior prothoracic lobe relatively broad, as wide as or wider than long and not dorsally concave (Figs. 15; 16a; 17–19; 21a; 22a–b; 23a–24a) 2
- 2.(1'.) Medial lobe of posterior prothoracic lobe bilobate and only slightly projected (Fig. 19); basal segment of genital ligula with long setae along sides (Fig. 44); Tepui region of Amazonas State, Venezuela (Fig. 103) *M. tepuiantum*
- 2'. Medial lobe of posterior prothoracic lobe projected caudally (Figs. 15; 16a; 17–18; 21a; 22a–b; 23a–24a); basal segment of genital ligula lacking long setae along sides (Figs. 38–43; 45–48) 3
- 3(2). Cercus dorsal process short and subapical, inner ventro-apical process rounded (Figs. 60–63) 4
- 3'. Cercus dorsal process long and apical, inner ventro-apical process pointed (Figs. 66–69) 7
- 4.(3.) Cercus dorsal process bluntly rounded, ventro-basal process recurved anteriorly and with pointed tip (Fig. 71); Boyacá and Cundinamarca Depts., Colombia (Fig. 103) *M. ovigerum*
- 4'. Cercus dorsal process hooked, ventro-basal process approximately aligned with anterior margin of cercus, with rounded or pointed tip (Figs. 70; 72; 74) 5
- 5.(4'.) Cercus ventro-basal process with narrow pointed tip (Fig. 72); apex of genital ligula markedly concave (Fig. 41b); Napo Prov., Ecuador (Fig. 103) *M. ecuatoriale*
- 5'. Cercus ventro-basal process with rounded tip (Figs. 70; 74); apex of genital ligula slightly to markedly convex (Figs. 38b; 42b); Cundinamarca Dept., Colombia (Fig. 103) 6
- 6.(5'.) Medial lobe of posterior prothoracic lobe entire and forming an approximate right angle with lateral lobes (Fig. 15) *M. occultum*
- 6'. Medial lobe of posterior prothoracic lobe bilobate and forming an acute angle with lateral lobes (Fig. 17) *M. risi*
- 7.(3'.) S7 tergum entirely black or with a pale blue spot on its distal fifth; cercus inner ventro-apical process located approximately midway between dorsal process and outer ventro-apical process, clearly visible in lateral view (Fig. 66); latero-apical lobe of genital ligula prominent, directed antero-distally and longer than latero-medial lobe (Fig. 45); Boyacá Dept., Colombia and Táchira State, Venezuela (Fig. 103) *M. tamaense*
- 7'. S7 tergum black at basal fifth to basal half (Figs. 4b; 107; 109); cercus inner ventro-apical process at about same level as outer ventro-apical process, barely visible in lateral view (Figs. 67–69); latero-apical lobe of genital ligula less prominent, recurved ventro-posteriorly and subequal in size to latero-

- medial lobe (Figs. 46–48) 8
- 8.(7'.) Anterior half of metepimeron black (Figs. 3d, f; 107); cercus with ventro-apical processes located mid-way between dorsal and ventro-basal processes in postero-medial view (Fig. 77a); Napo Prov., Ecuador (Fig. 103) *M. dunklei*
- 8'. Metepimeron mostly pale (Fig. 2b); cercus with ventro-apical processes located at about the same level as ventro-basal process in postero-medial view (Figs. 78a–79a) 9
- 9.(8'.) Basal third to half of S7 tergum black; cercus ventro-apical processes recessed (Fig. 79a); Mérida, Trujillo, Lara, and Zulia States, Venezuela (Fig. 103) *M. galianii*
- 9'. Basal fifth of S7 tergum black (Fig. 109); cercus ventro-apical processes roundly pointed (Fig. 78a); Mérida and Táchira States, Venezuela and Boyacá, Cundinamarca, Cauca, and Santander Depts., Colombia (Fig. 103) *M. laterale*



FIGURES 30–31. Distal segment of male genital ligula, *Cyanallagma interruptum*, Argentina, Tecka. (30) ectal view; (31) latero-ental view; white arrow on the left points to transverse fold between latero-medial lobes; white arrow on the right points to inner process on second transverse fold.

Key to females of *Mesamphiagrion*

[*M. occultum*, *M. ovigerum*, and *M. tepuianum* unknown]

1. Medial lobe of posterior prothoracic lobe narrow, strongly projected and dorsally concave (Fig. 20b); Cundinamarca Dept., Colombia (Fig. 103) *M. demarmelsi*
- 1'. Medial lobe of posterior prothoracic lobe relatively broad, as wide as or wider than long and not dorsally concave (Figs. 16b; 21b; 22c; 23b–24b) 2
- 2.(1'.) Medial lobe of prothoracic posterior lobe not projected caudally beyond lateral lobes (Figs. 22c; 23b) 3
- 2'. Medial lobe of prothoracic posterior lobe projected caudally beyond lateral lobes (Figs. 16b; 21b; 24b) 4
- 3.(2.) Metepimeron mostly pale (as in Fig. 2b); basal third to half or entire S7 tergum black (Fig. 108); Mérida, Trujillo, Lara, and Zulia States, Venezuela (Fig. 103) *M. galianii*
- 3'. Anterior half of metepimeron black (Fig. 3f); basal fourth of S7 tergum black; Napo Prov., Ecuador (Fig. 103) *M. dunklei*
- 4.(2'.) Medial lobe of prothoracic posterior lobe projected posteriorly only slightly beyond lateral lobes for a distance much shorter than lateral lobes' length (Fig. 16b); Napo Prov., Ecuador (Fig. 103) *M. ecuatoriale*
- 4'. Medial lobe of prothoracic posterior lobe projected posteriorly beyond lateral lobes for a distance

- about as long as lateral lobes' length (Figs. 21b; 24b) 5
- 5.(4'.) Medial lobe of prothoracic posterior lobe broadly rectangular and slightly bilobate (as in Fig. 17); Cundinamarca Dept., Colombia (Fig. 103) *M. risi*
- 5'. Medial lobe of prothoracic posterior lobe semicircular, entire or slightly bilobate (Figs. 21b; 24b) ... 6
- 6.(5'.) Each mesostigmal plate about as wide as 0.70 its length or wider (Fig. 24c); tergum of S7 usually black on its basal fifth to half, but entirely black in some specimens; Mérida and Táchira States, Venezuela, and Boyacá, Cundinamarca, Cauca, and Santander Depts., Colombia (Fig. 103) *M. laterale*
- 6'. Each mesostigmal plate about as wide as 0.66 its length or narrower (Fig. 21c); tergum of S7 entirely black or with a pale blue spot only on its distal fifth; Boyacá Dept., Colombia and Táchira State, Venezuela (Fig. 103) *M. tamaense*

***Mesamphiagrion dunklei* sp. nov.**

Figures 3d–f; 4b–c; 7a; 22; 46; 67; 77; 83; 103; 107

Cyanallagma laterale; Dunkle 1981: 5 (mention from Ecuador).

Daigle 1996: 12 (mention from Ecuador).

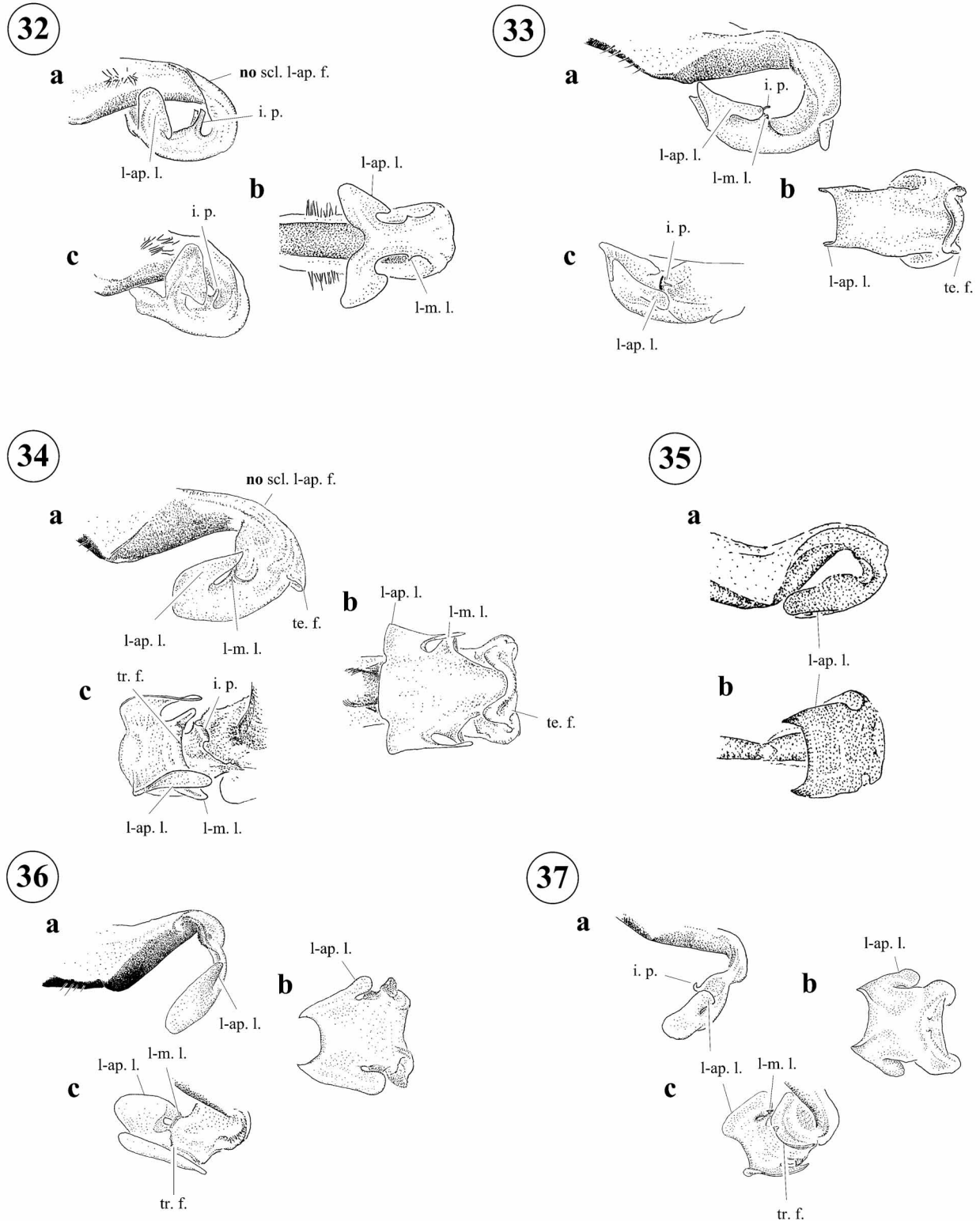
Etymology: Named *dunklei* in honor of our good friend and colleague Sidney W. Dunkle, who collected the type series, in recognition of his valuable contributions to New World odonatology.

Type specimens: Holotype (♂). Ecuador. Napo Prov.: 13 km E of Coyuja on road to Chaco, marsh, 17.viii.1980, S.W. Dunkle leg.. **Allotype** (♀). Same data. Both in FSCA. **Paratypes** (30 ♂, 10 ♀). Same data 1 ♂, 1 ♀ (FSCA); same data 18 ♂, 4 ♀ (SWD); same data 2 ♂, 1 ♀ (MLP); same data 3 ♂, 2 ♀ (RWG); same data 3 ♂, 1 ♀ (DRP); Baeza, 10.6 km S on Hwy 45 near Bermojo, 1710 m, seepage marsh, 24.vii.1996, B. Mauffray leg., 1 ♂ (FSCA); seep and marsh along Archidona-Baeza road, 00°36'12"S, 77°50'36"W, 2100 m, 19.xi.1997, T.W. Donnelly leg., 1 ♂ (TWD); Baeza/Tena Rd., 26.7 km N of Narupa junction, 2240 m, seep, 19.xi.1997, K.J. Tennessen leg., 1 ♂ (FSCA).

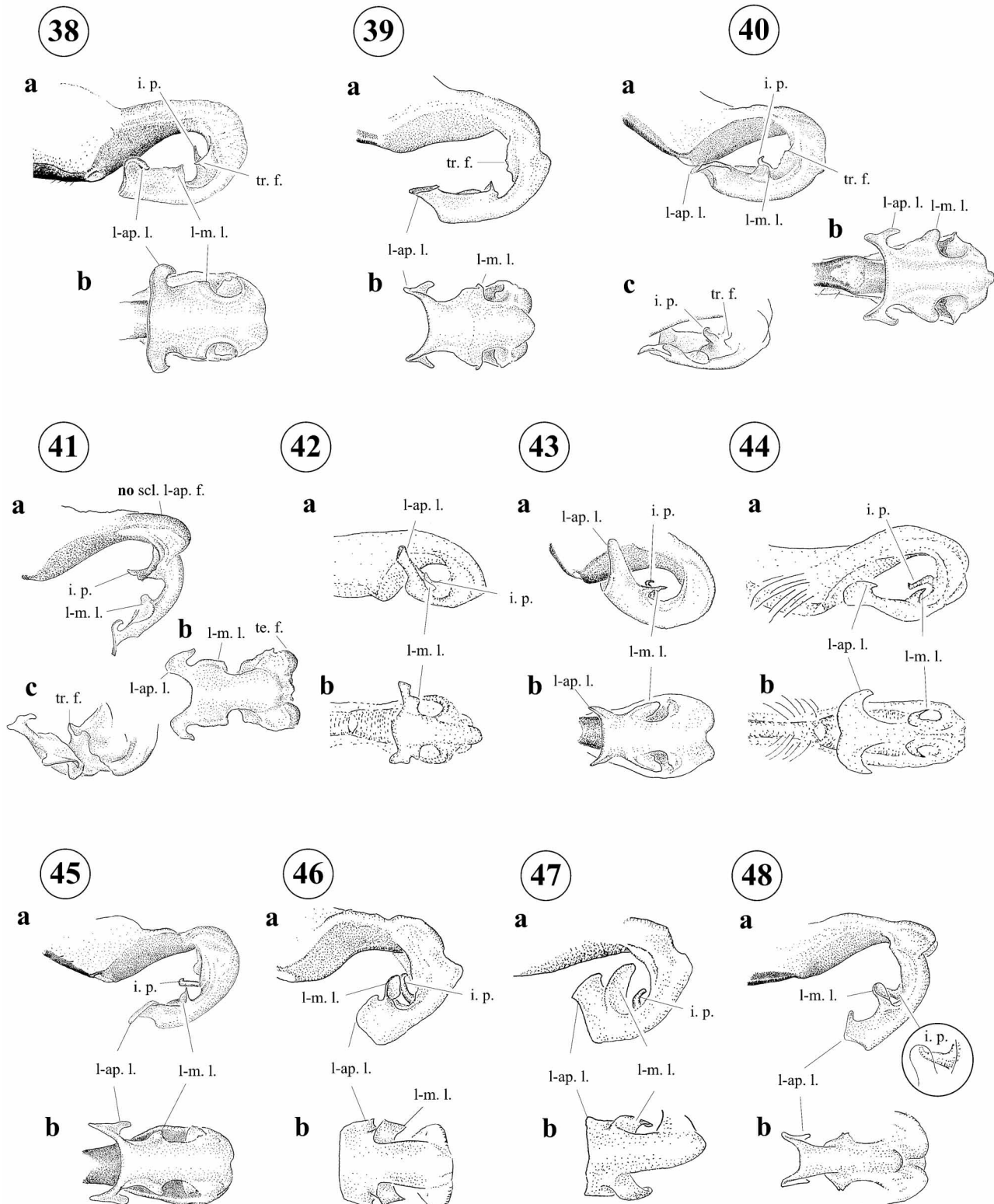
Description. Male holotype

Head (as in Fig. 3d). Labium pale yellow; labrum, base of mandibles, anterior surface of genae and anteclypeus light blue, with a medial black spot on posterior margin of labrum and two short black stripes on anteclypeus; postclypeus, dorsal surface of genae, frons, antennae and top of head black, with a pair of pale blue postocular spots; rear of head ventrally brown, pale yellow along medial third and turning dark brown to black along dorsal margin. Frons in profile rounded.

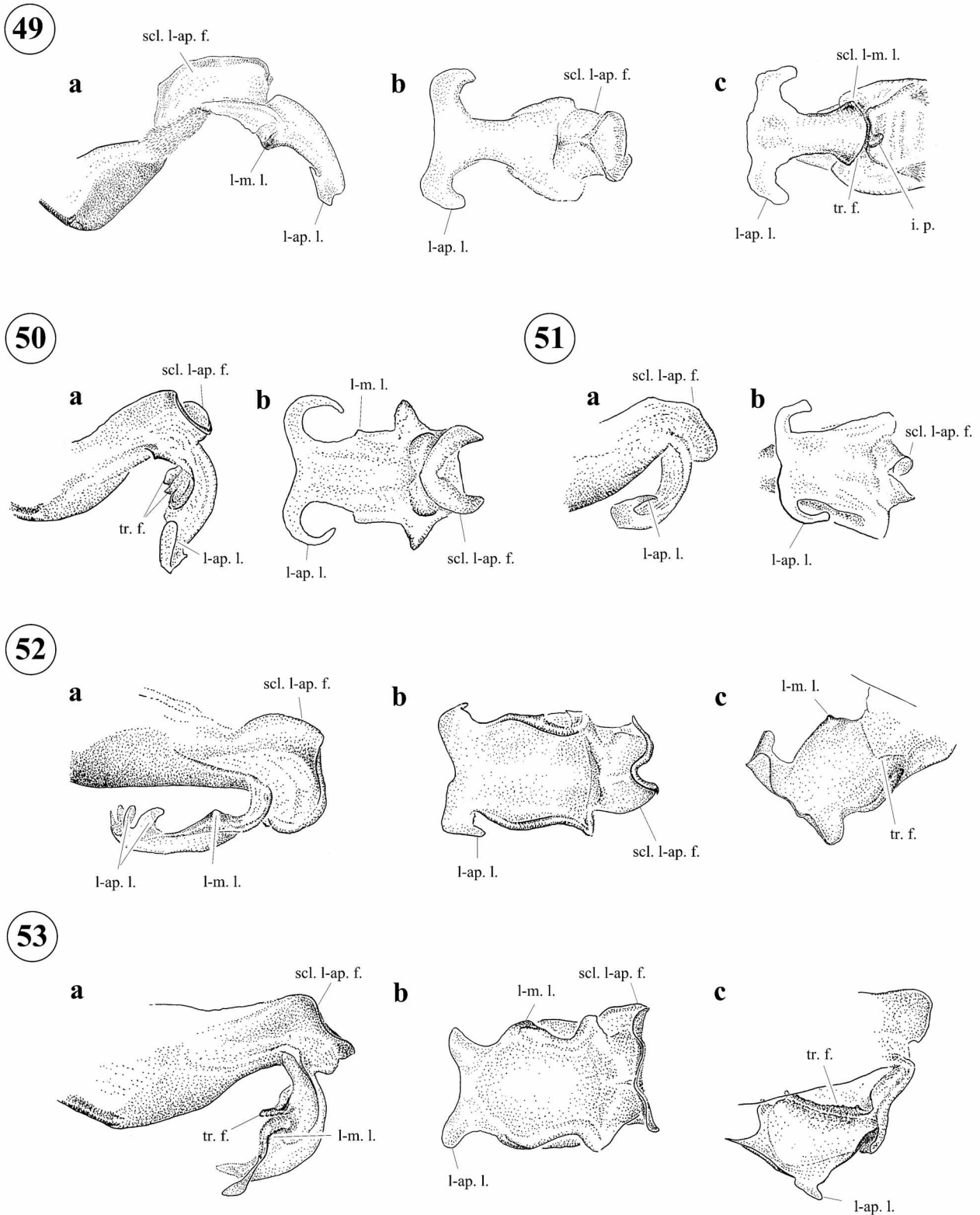
Thorax. Prothorax black; medial lobe of posterior prothoracic lobe developed into caudally projected squarish plate with smoothly rounded margins and dorsal surface slightly concave (Fig. 22a). Mesepisternal plates approximately flat and triangular. Pterothorax black with almost linear longitudinal pale blue antehumeral stripe along distal 7/8 of mesepisternum; wide pale blue lateral stripe on mesepimeron and metepisternum (as in Fig. 3d), and ventral half of metepimeron pale blue (Fig. 3f). Venter of thorax brown, except for anterior margin and central spot pale yellow, with a postero-medial low rounded tubercle (Fig. 3f). Legs black with a bluish yellow spot on coxae and on base of flexor surface of femora (as in Fig. 3d) and basal two thirds of tarsi and pretarsal claws reddish brown; 8 metafemoral spurs on right and 7 on left femur, longer than width of femur on distal half (as in Fig. 3d); metatibial spurs about as long as intervening spaces (as in Fig. 3d); pretarsal claw with well developed supplementary tooth. Wings (as in Fig. 7a) hyaline; pt dark reddish brown, covering one cell, with anterior (costal) margin slightly longer than posterior margin; CuP reaching CuPAA slightly distal to confluence of CuPAA with hind margin of wing, petiolation ending slightly distal to midpoint between Ax 1 and Ax 2; Px 12 in right FW, 13 in left FW, 11 in HW; RP₂ branching between Px 5 and 6 but closer to 6 in right FW, slightly proximal to Px 6 in left FW, between Px 5 and 4 but closer to 5 in right HW, at Px 4 in left HW.



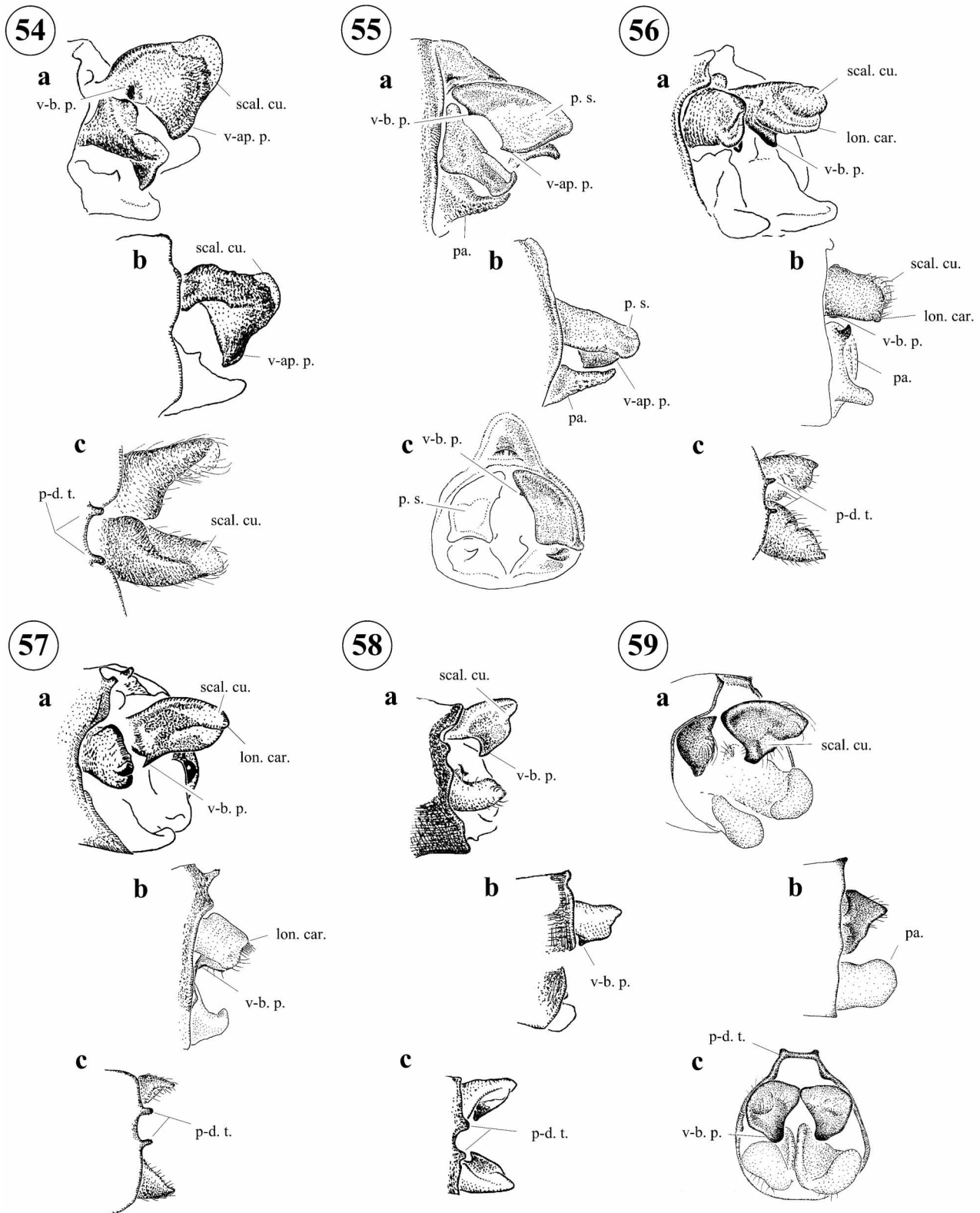
FIGURES 32–37. Distal segment of male genital ligula, (a) lateral view, (b) ectal view, (c) latero-ental view. (32) *Cyanallagma ferenigrum*, holotype, Brazil, Utiariti; (33) *C. bonariense*, Argentina, Berisso; (34) *C. interruptum*, Argentina, Tecka; (35) *C. trimaculatum*, lectotype, Brazil, Santa Cruz; (36) *C. angelae*, paratype, Brazil, Salesópolis; (37) *C. nigrinuchale*, Brazil, Lagoa dos Cordois. i. p.: inner process; l-ap. l.: latero-apical lobe; l-m. l.: latero-medial lobe; te. f.: terminal fold; tr. f.: transverse fold; scl. l-ap. f.: sclerotized latero-apical fold.



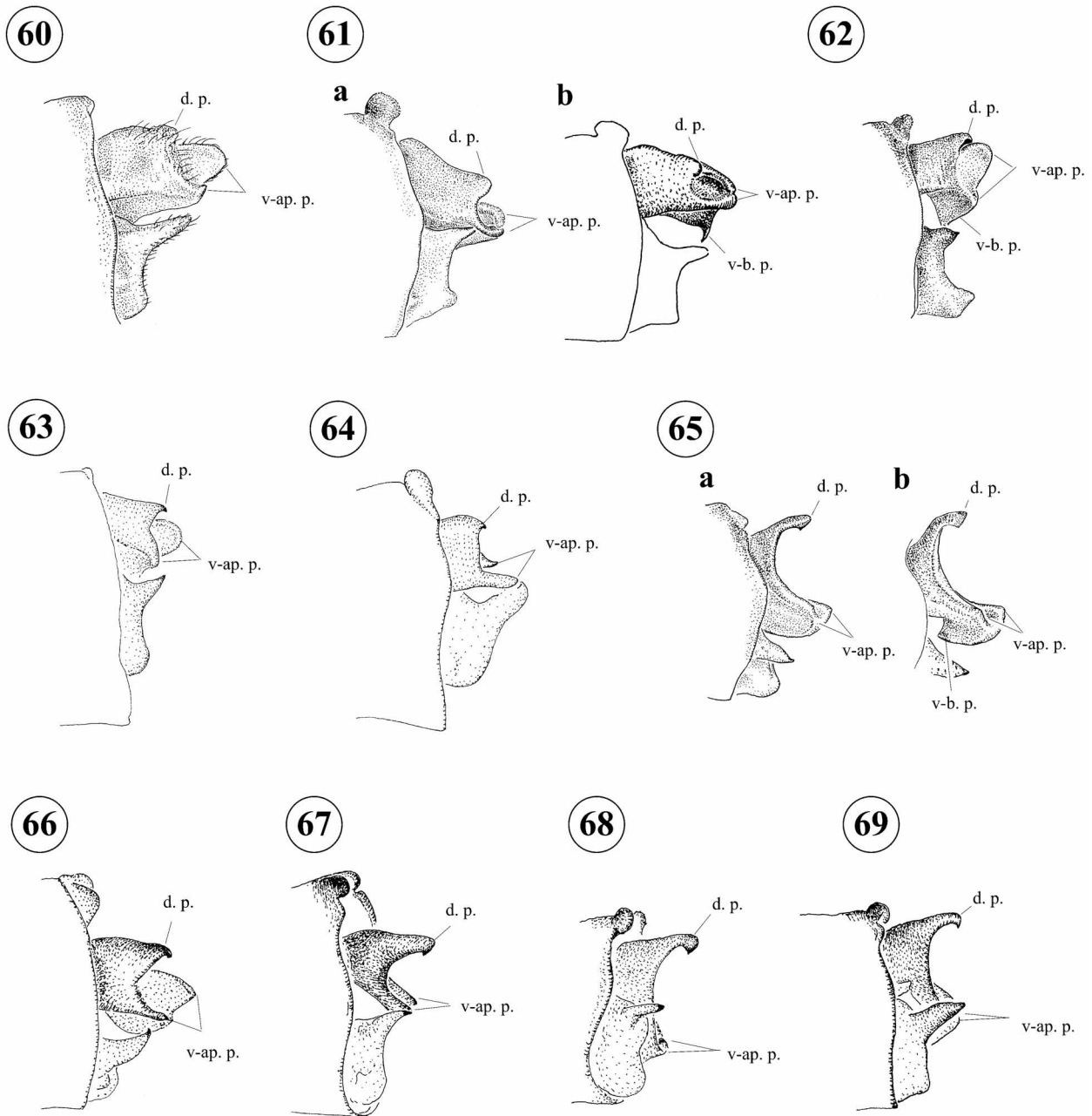
FIGURES 38–48. Distal segment of male genital ligula, (a) lateral view, (b) ectal view, (c) latero-ental view. (38) *Mesophiagrium occultum*, Colombia, Chingaza; (39) *M. ovigerum*, Colombia, Pennsylvania, holotype of *Argia hebdomatica*; (40) *M. ovigerum*, Colombia, Arcabuco; (41) *M. ecuatoriale*, holotype, Ecuador, Archidona-Baeza; (42) *M. risi*, Colombia, Anolaima (modified from De Marmels 1990); (43) *M. demarmelsi*, Colombia, Bogotá; (44) *M. tepuianum*, paratype, Venezuela, Mt. Duida (modified from De Marmels 1997); (45) *M. tamaense*, Colombia, La Pica; (46) *M. dunklei*, Ecuador, Coyoja; (47) *M. laterale*, Colombia, La Pica; (48) *M. galianii*, paratype, Venezuela, La Cristalina. i. p.: inner process; l-ap. l.: latero-apical lobe; l-m. l.: latero-medial lobe; te. f.: terminal fold; tr. f.: transverse fold; scl. l-ap. f.: sclerotized latero-apical fold.



FIGURES 49–53. Distal segment of male genital ligula, (a) lateral view, (b) ectal view, (c) ental view. (49) *Oreiallagma thelakterion*, paratype, Venezuela, Monte Zerpa; (50) *O. quadricolor*, holotype, Peru, Santa Ana; (51) *O. acutum*, lectotype, Bolivia, Río Zongo; (52) *O. oreas*, holotype, Colombia, Monte Socorro; (53) *O. prothoracicum*, paratype, Ecuador, Intaj. i. p.: inner process; l-ap. l.: latero-apical lobe; l-m. l.: latero-medial lobe; te. f.: terminal fold; tr. f.: transverse fold; scl. l-ap. f.: sclerotized latero-apical fold.

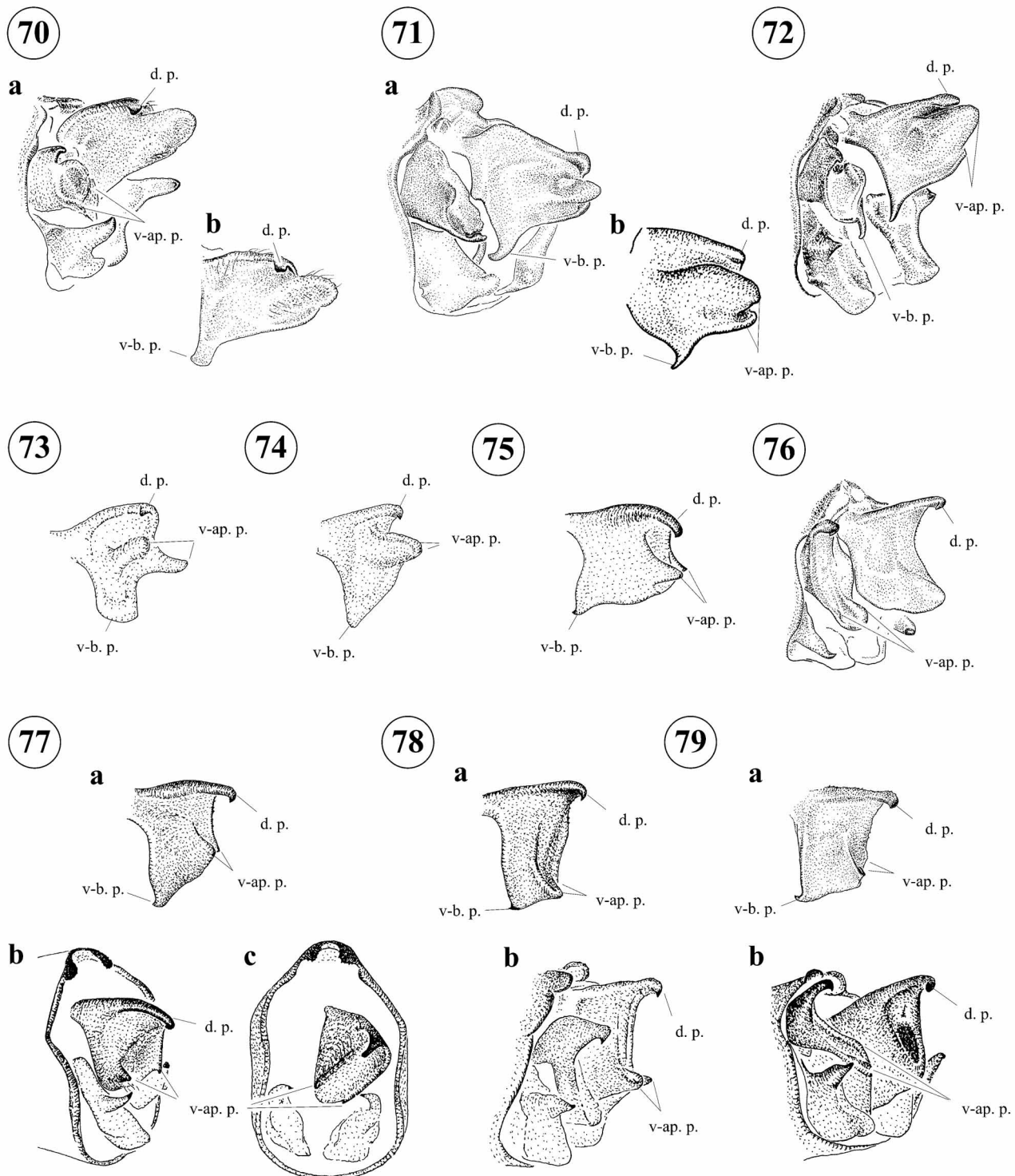


FIGURES 54–59. Male caudal appendages, (a) medio-dorsal view, (b) lateral view, (c) posterior view (54, 56–58), dorsal view (55, 59). (54) *Cyanallagma interruptum*, Argentina, Nahuel Huapi; (55) *C. ferenigrum*, holotype, Brazil, Utiariti; (56) *C. bonariense*, Argentina, Berisso; (57) *C. angelae*, paratype, Brazil, Salesópolis; (58) *C. nigrinuchale*, male, Brazil, Lagoa dos Cordois; (59) *C. trimaculatum*, lectotype, Brazil, Santa Cruz. lon. car.: longitudinal carina; pa.: paraproct; p-d. t.: postero-dorsal tubercle; p. s.: pale spot; v. ap. p.: ventro-apical process; v-b. p.: ventro-basal process; scal. cu.: scalariform-like cuticle.



FIGURES 60–69. Male caudal appendages, lateral view, (61a; 65a) lateral view, (61b; 65b) latero-posterior view with cercus rotated dorso-externally. (60) *Mesamphiagrion occultum*, Colombia, Chingaza; (61) *M. ovigerum*, Colombia (a) Arcabuco, (b), holotype, Bogotá; (62) *M. ecuatoriale*, holotype, Ecuador, Archidona-Baeza; (63) *M. risi*, holotype, Colombia, Pacho (modified from De Marmels 1989); (64) *M. tepuianum*, paratype, Venezuela, Mt. Duida (modified from De Marmels 1997); (65) *M. demarmelsi*, Colombia, Bogotá; (66) *M. tamaense*, Venezuela, El Tamá; (67) *M. dunklei*, paratype, Ecuador, Coyuja; (68) *M. laterale*, Colombia, La Pica; (69) *M. gairanii*, paratype, Venezuela, La Cristalina. d. p.: dorsal process; v. ap. p.: ventro-apical process; v-b. p.: ventro-basal process.

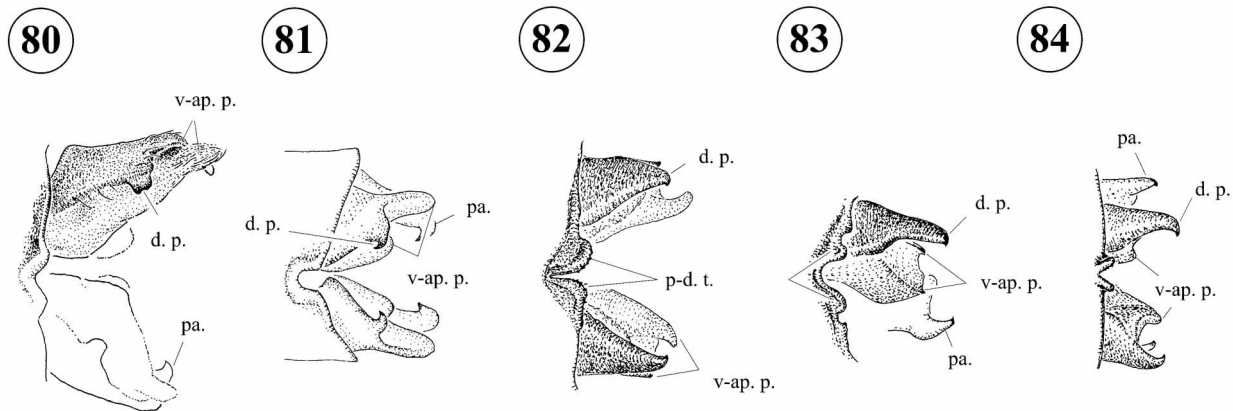
Abdomen (as in Fig. 4b). Dorsum of S1–6 and S10 black, of S7 pale blue except basal fourth black, of S8–9 pale blue; S1–2 with an antero-lateral pale blue spot, S3 pale blue to yellow and S4–10 pale yellow along ventral margin. Genital ligula (as in Fig. 46) with an inner medial process on ental membranous transverse fold basal to latero-medial lobes, a pair of broad latero-apical lobes and a pair of narrower rectangular latero-medial lobes, which are oriented transversely and located close to the latero-apical lobes (distance between them less than width of lobe). Cercus (as in Figs. 67; 77; 83) shorter than S10, with a dorsal process



FIGURES 70–79. Male caudal appendages, medio-dorsal view (70a–71a; 72; 76; 77b–79b), posterior view (77c), medial view of male cercus (70b–71b; 73–75; 77a–79a). (70) *Mesamphiagrion occultum*, Colombia, Chingaza; (71) *M. ovigerum*, Colombia (a) Arcabuco, (b), holotype, Bogotá; (72) *M. ecuatoriale*, holotype, Ecuador, Archidona-Baeza; (73) *M. tepuiantum*, paratype, Venezuela, Mt. Duida (modified from De Marmels 1997); (74) *M. risi*, holotype, Colombia, Pacho (modified from De Marmels 1989); (75) *M. tamaense*, Venezuela, El Tamá; (76) *M. demarmelsi*, Colombia, Bogotá; (77) *M. dunklei*, paratype, Ecuador, Coyuja; (78) *M. laterale*, Colombia, La Pica; (79) *M. gaianii*, paratype, Venezuela, La Cristalina. d. p.: dorsal process; v. ap. p.: ventro-apical process; v-b. p.: ventro-basal process.

ending on an apical tooth directed ventro-posteriorly, a ventro-basal process and two pointed ventro-apical processes, inner slightly larger than outer, and in ental view, ventro-apical processes situated about midway

between ventro-basal and dorsal processes (as in Fig. 77); color of outer surface black. Paraproct pale blue, with medially directed branch black (as in Fig. 68).



FIGURES 80–84. Male caudal appendages, dorsal view. (80) *Mesamphiagrion occultum*, Colombia, Chingaza; (81) *M. tepuiantum*, paratype, Venezuela, Mt. Duida (modified from De Marmels 1997); (82) *M. tamaense*, Venezuela, El Tamá; (83) *M. dunklei*, paratype, Ecuador, Coyuja; (84) *M. laterale*, Colombia, La Pica. d. p.: dorsal process; pa.: paraproct; p-d. t.: postero-dorsal tubercle; v. ap. p.: ventro-apical process; v-b. p.: ventro-basal process.

Dimensions. Total length 29.5 mm; abdomen length 23.5 mm; FW 19.9 mm; HW 18.7 mm.

Female allotype

Head (as in Fig. 3e). As in holotype.

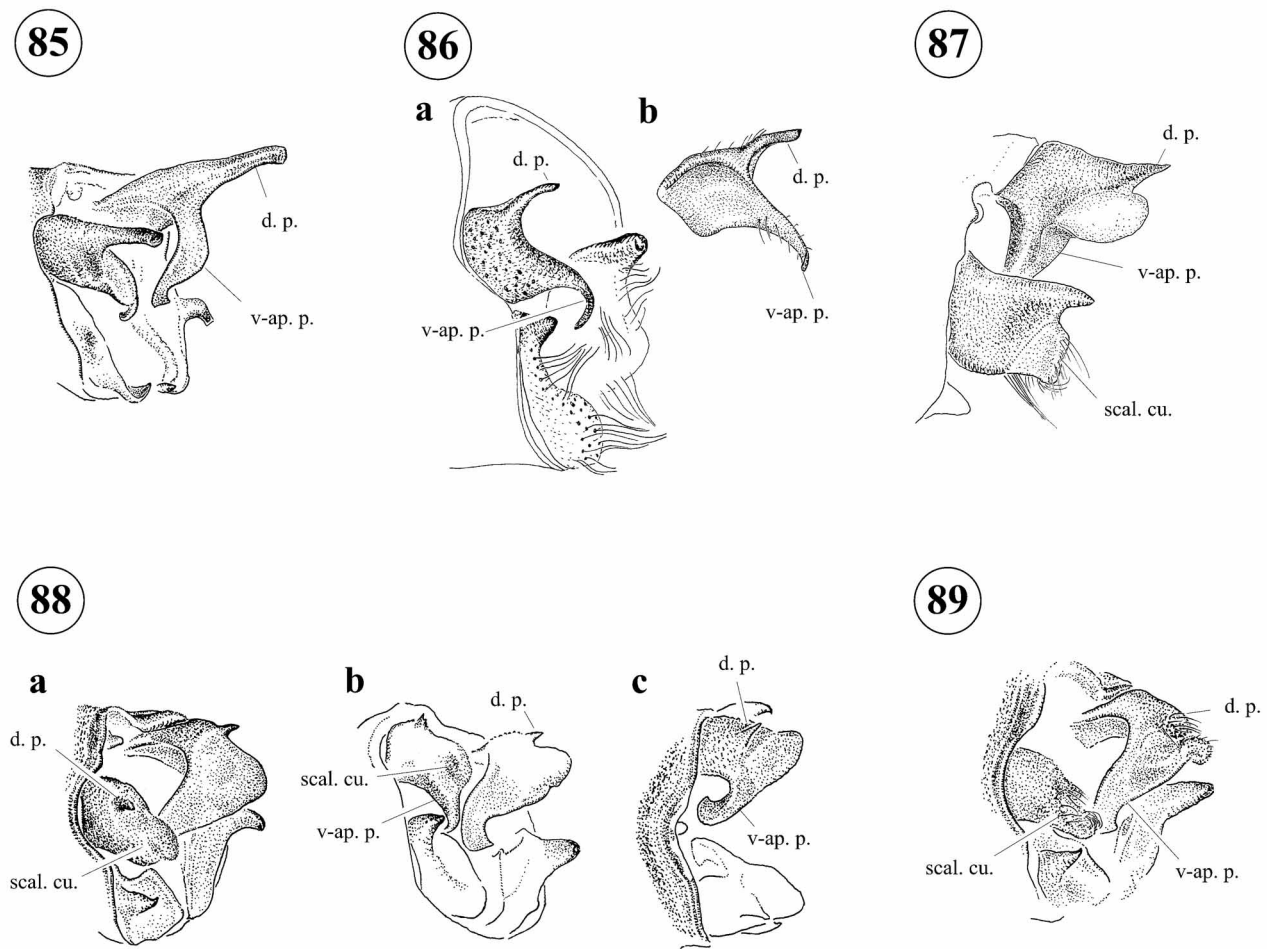
Thorax. Color pattern as in holotype but reddish brown areas present on prothorax, and black less extensive along pale yellow ventral margin of pterothorax (as in Fig. 3e). Venter of thorax, coxae, trochanters, and flexor surface of femora and tibiae pale yellow, remainder of legs pale brown. Projection of medial lobe of posterior prothoracic lobe shorter than in male holotype, and slightly bilobate (as in Fig. 22c). Mesepisternal plates wider than in male holotype (as in Fig. 22d). Metafemoral spurs 8 on right femur and 6 on left femur. Wings as holotype but Px 13 in right FW, 14 in left FW, 12 in right HW, 11 in left HW; RP₂ branching slightly proximal to Px 7 in FW, slightly proximal to Px 5 in HW.

Abdomen. Color pattern as in holotype, except dorsum of S1–2 and basal 4/5 of S3 red, S10 pale blue and distal fifth of S7 black; latero-ventral margins of terga pale yellow from S1–10 (as in Fig. 4c). Cercus shorter than S10, conical and pale brown; paraprocts pale yellow. Vulvar spine on S8 well developed. Sub-basal plate of ovipositor small and triangular; outer valve of ovipositor with a single row of teeth; tip of ovipositor (excluding stylus; styli missing) extending beyond posterodorsal margin of S10 but not reaching tip of cercus (as in Fig. 4c).

Dimensions. Total length 33.7 mm; abdomen length 27.2 mm; FW 22.7 mm; HW 21.2 mm.

Variation in paratypes. Color apparently darkens progressively with age. Freshly emerged teneral specimens, three males and three females with wrinkled opaque wings and tegument not fully hardened, differ from holotype by pale areas of head pale yellow, postocular spots confluent with each other and with pale back of the head. Dark colors of thorax are absent in one female; in others, they are restricted to dark brown spots on the prothorax and on the medio-dorsal area between antehumeral stripes and the dark brown humeral stripe. The remainder of thorax is pale yellow to pale brown and the pt is pale brown. Dorsum of S1–2 and basal 4/5 of S3 are reddish orange; cerci and paraprocts are pale yellow. In three males and one female, dorsum of S1–2 and basal 4/5 of S3 are reddish orange, and in another four males and one female this area is red (Fig. 4b–c). The pale blue postocular spots are defined and the dark areas of the thorax are as in holotype but are dark brown; the legs and cerci are brown, and pt is reddish brown. Three males and three females are colored like the allotype with the dorsum of S1–2 and basal 4/5 of S3 dark reddish brown, and 16 males and one female are

like holotype with the dorsum of S1–3 black (Fig. 107). Some males have a pale blue spot on the posterior surface of the male cercus, delimited by dorsal and ventro-apical processes.



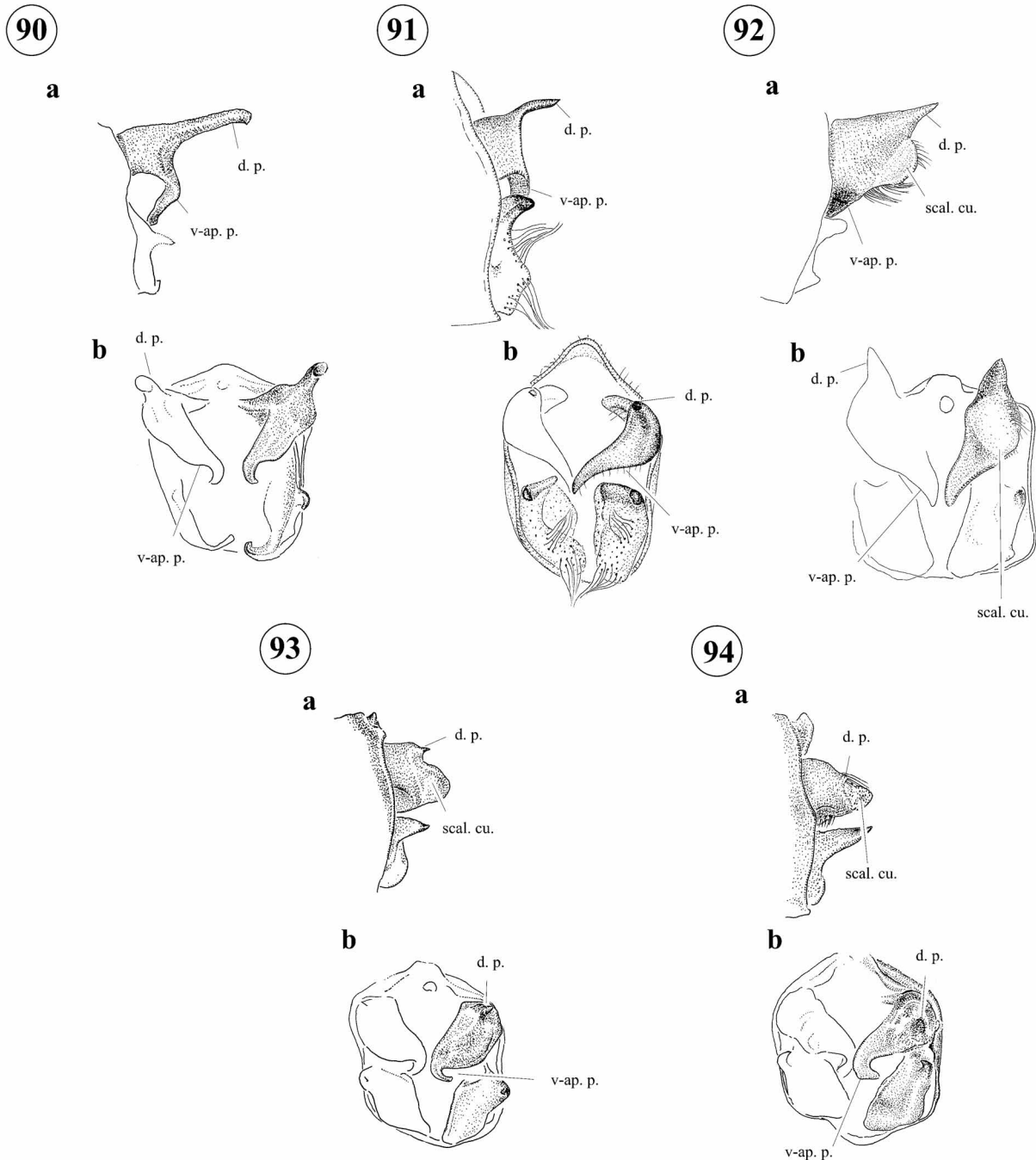
FIGURES 85–89. Male caudal appendages, medio-dorsal view, (86b) medial view of cercus, (88b) medio-ventral view, (88c) dorsal view. (85) *Oreiallagma acutum*, lectotype, Bolivia, Río Zongo; (86) *O. thelakterion*, paratype, Venezuela, Monte Zerpa; (87) *O. prothoracicum*, holotype, Ecuador, Intaj; (88) *O. quadricolor*, holotype, Peru, Santa Ana; (89) *O. oreas*, holotype, Colombia, Monte Socorro. d. p.: dorsal process; v. ap. p.: ventro-apical process; v-b. p.: ventro-basal process; scal. cu.: scalariform-like cuticle.

Male paratypes have 12–13 Px in FW, in HW 10–13; RP₂ branching between Px 5–7 in FW, between Px 4–5 in HW. Female paratypes Px in FW 12–15, in HW 10–12; RP₂ branching between Px 6–7 in FW, between Px 4–5 in HW.

Dimensions. Total length males 28.0–31.3 mm [mean 30.2 mm; SD 1.08; n = 10]; total length females 29.4–34.6 mm [mean 31.9 mm; SD 1.67; n = 10]; abdomen length males 22–25.5 mm [mean 24.2 mm; SD 1.08; n = 10]; abdomen length females 23.2–27.8 mm [mean 25.6 mm; SD 1.62; n = 10]; FW males 19.4–21.6 mm [mean 20.2 mm; SD 0.5; n = 10]; FW females 20.2–22.7 mm [mean 25.6 mm; SD 1.5; n = 10]; HW males 18.4–19.3 mm [mean 18.8 mm; SD 0.3; n = 10]; HW females 19.3–21.2 mm [mean 20.2 mm; SD 0.7; n = 10].

Diagnosis. This species is most similar to *M. laterale* and *M. gairanii* in genital ligula morphology and shares the following features with them: latero-apical and latero-medial lobes almost contiguous (Fig. 46a; shared with *M. laterale*, Fig. 47a), latero-apical lobe broad, and latero-medial lobe twisted basally so that it is oriented transversely (Fig. 46b). The medial lobe of posterior prothoracic lobe in *M. dunklei* is roundly squarish and slightly constricted at its base in the male (Figs. 22a–b; similar to *M. gairanii*, Fig. 23a, and *M. laterale*, Fig. 24a) and in the female, each half is bilobate (Fig. 22c; also similar to *M. gairanii*, Fig. 23b, and *M. lat-*

erale, Fig. 24b). However, this species differs from both by the shape of the male cercus in postero-medial view. The ventro-apical processes are located about midway between dorsal and ventro-basal processes (Fig. 77a); in *M. laterale* and *M. gaianii*, they are at about the same level as the ventro-basal process (Figs. 78a–79a). In *M. laterale* and *M. gaianii*, the metepimeron is mostly pale (Figs. 2b; 108–109) whereas in *M. dunklei* it is about half black (Figs. 3d, f; Fig. 107). The dorsum of S7 is blue with the anterior fourth and lateral surfaces black, S8–9 are blue with lateral surfaces black and S10 black dorsally in the male (Figs. 4b; 107). It is blue in the female (Fig. 4c). In the female of *M. gaianii* (Fig. 108) and in some *M. laterale*, the dorsum of S7 is entirely black.



FIGURES 90–94. Male caudal appendages, (a) lateral view, (b) posterior view. (90) *Oreiallagma acutum*, lectotype, Bolivia, Río Zongo; (91) *O. thelcterion*, paratype, Venezuela, Monte Zerpa; (92) *O. prothoracicum*, holotype, Ecuador, Intaj; (93) *O. quadricolor*, holotype, Peru, Santa Ana; (94) *O. oreas*, holotype, Colombia, Monte Socorro. d. p.: dorsal process; v. ap. p.: ventro-apical process; v-b. p.: ventro-basal process; scal. cu.: scalariform-like cuticle.

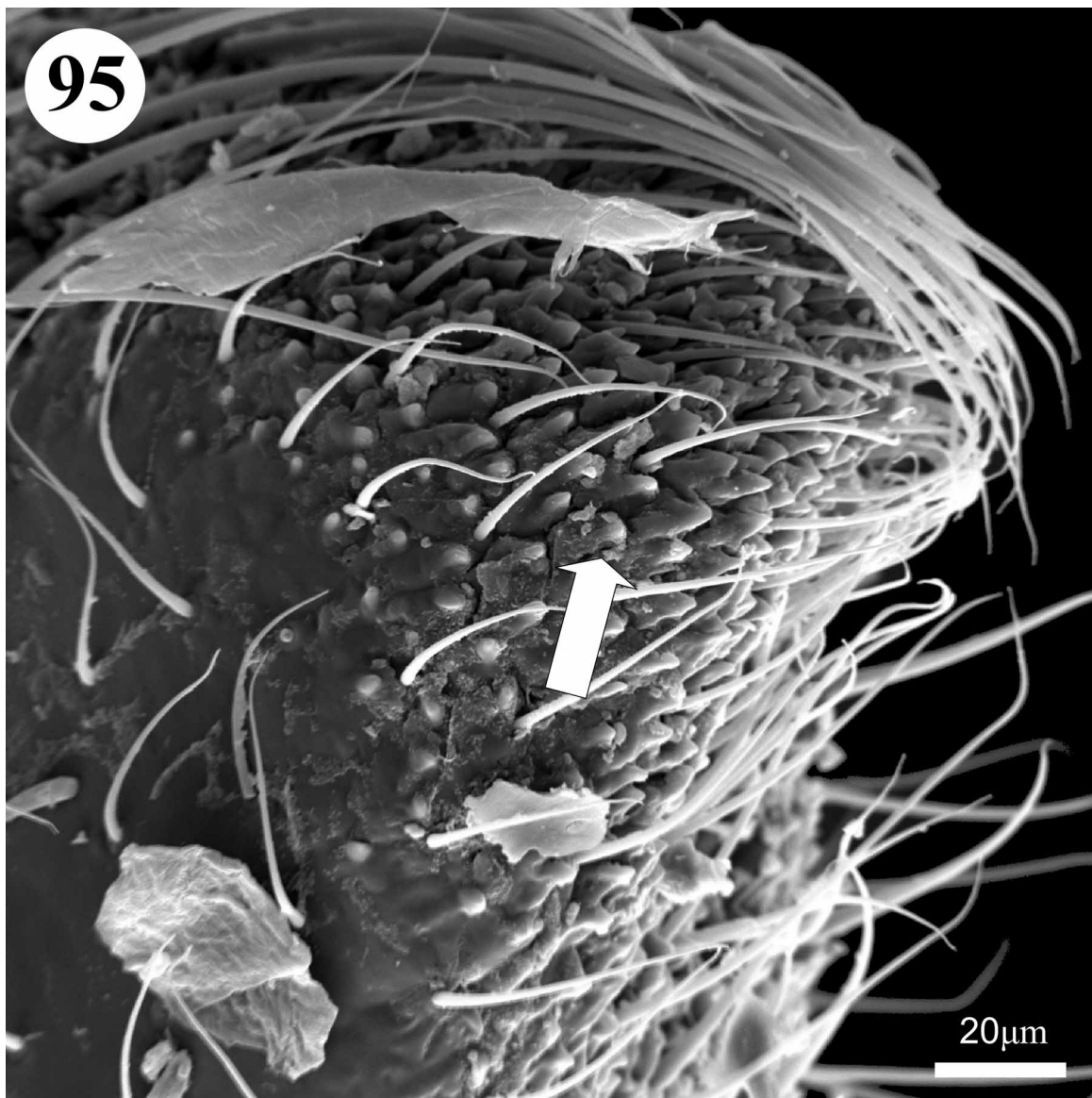


FIGURE 95. Distal end of male cercus, *Cyanallagma interruptum*, Argentina, Nahuel Huapi; white arrow points to scalariform-like cuticle.

Biology. Adults collected at a marsh. Breeding habitat and larva are unknown.

Distribution. Ecuador (Napó Dept.), from 1710 to 2240 m above sea level (Fig. 103).

***Mesamphiagrion ecuatoriale* sp. nov.**

Figures 3c; 4d–e; 7b; 16; 41; 62; 72; 103

Etymology: Named *ecuatoriale* in reference to its distribution.

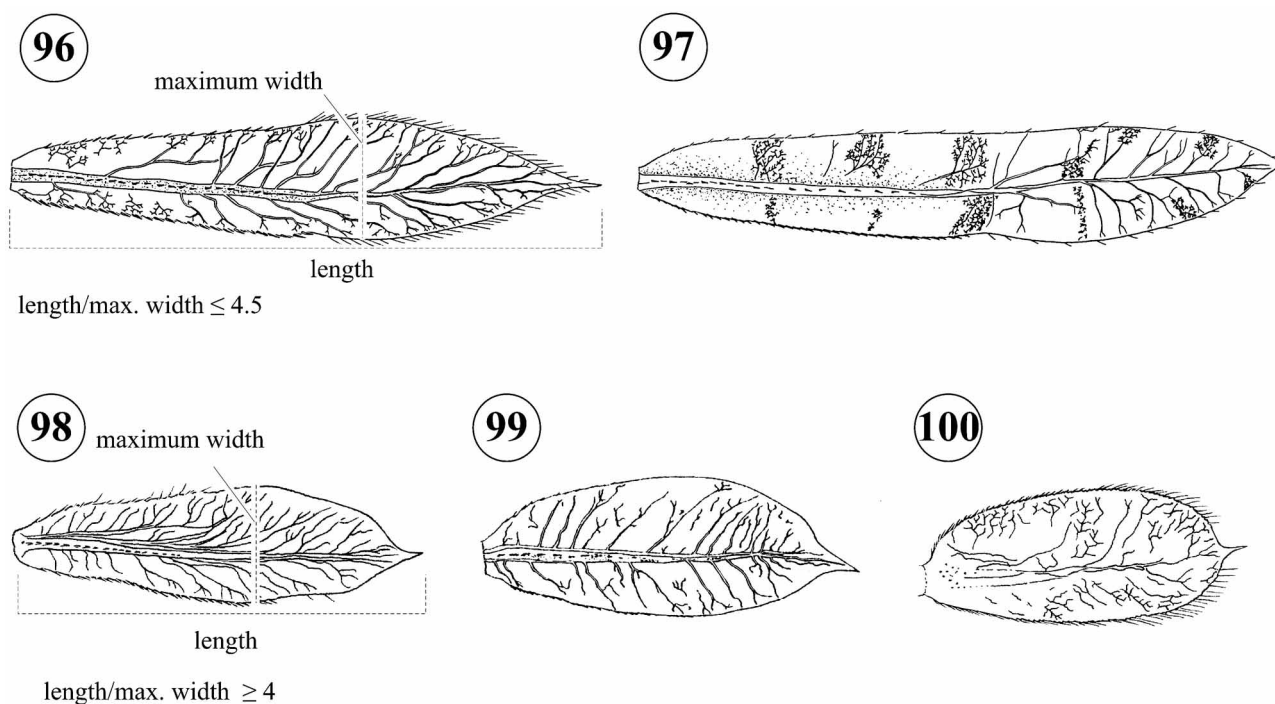
Type specimens: Holotype (♂). Ecuador. Napó Prov.: seep and marsh along Archidona-Baeza road, 00°36'12"S, 77°50'36"W, 2100 m, 19.xi.1997, T.W. Donnelly leg. **Allotype** (♀). Same data. Both in FSCA.

Paratypes (3 ♂, 1 ♀). same data 2 ♂, 1 ♀ (TWD); same data 1 ♂ (RWG).

Description. Male holotype

Head (Fig. 3c). Labium pale yellow; labrum, base of mandibles, anterior surface of genae, anteclypeus, and antefrons light blue, with a black medial spot and a marginal spot on each side along posterior margin of

labrum; postclypeus, postfrons, antennae, and top of head black, with a pair of large pale blue postocular spots; rear of head pale yellow. Frons in profile rounded.



FIGURES 96–99. Larval lateral caudal lamella, lateral view. (96) *Cyanallagma interruptum*, Chile, Chagres; (97) *C. bonariense*, Argentina, Sauce Grande; (98) *Mesamphiagrion laterale*, Venezuela, Road to Las Copas; (99) *M. gaianii*, Venezuela, Laguna Negra; (100) (99) *M. tamaense*, Venezuela, Las Copas (Figs. 96–97 from Bulla 1973; Fig. 99 from De Marmels 1997; Figs. 98, 100 from De Marmels 2007).

Thorax. Prothorax black except for medial portion of anterior lobe, a latero-dorsal oval spot on each side of middle lobe and lateral margin of middle lobe pale blue; medial lobe of posterior prothoracic lobe developed into caudally projected squarish plate separated from lateral lobes by an obtuse angle, with smoothly rounded margins and slightly concave dorsal surface (Fig. 16a). Mesepisternal plates approximately flat and triangular. Pterothorax largely pale blue becoming pale bluish-yellow latero-ventrally, with a mid-dorsal black stripe narrower than antehumeral pale blue area, a narrow black stripe along humeral suture and a reddish brown oval spot at posterior end of second lateral suture (Fig. 3c). Venter of thorax bluish yellow. Legs black except pale blue coxae, trochanters and a spot along basal third to half of flexor surface of femora, and pale brown basal 3/4 of pretarsi; 8 metafemoral spurs on left femur (right femur missing), longer than width of femur on distal half; metatibial spurs slightly longer than intervening spaces; pretarsal claw with well developed supplementary tooth. Wings (Fig. 7b) hyaline; pt dark reddish brown, covering one cell, with anterior (costal) margin slightly longer than posterior margin; CuP reaching CuPAA slightly distal to confluence of CuPAA with hind margin of wing, petiolation ending approximately at midpoint between Ax 1 and Ax 2; Px 14 in FW, 12 in right HW, 13 in left HW; RP₂ branching slightly proximal to Px 7 in FW, slightly proximal to Px 6 in HW.

Abdomen (Fig. 4d). Dorsum of S1–6 and S10 black, of S7 pale blue except basal eighth black, of S8–9 pale blue; sides of S1–2 and base of S3 pale bluish yellow, most of S3 and S4–7 pale yellow. Genital ligula (Fig. 41) with apex concave, an inner medial process on ental membranous transverse fold basal to latero-medial lobes, a pair of latero-apical lobes of narrow base directed anteriorly and a pair of latero-medial lobes of broader base. Cercus (Figs. 62, 72) shorter than S10, with a short subapical hooked dorsal process, a pointed ventro-basal process, and two blunt ventro-apical processes; color of outer surface black. Paraproct

pale blue, with medially directed branch and tip of ventral branch black (Fig. 62).

Dimensions. Total length 38.5 mm; abdomen length 31.5 mm; FW 24.0 mm; HW 23.0 mm.

101

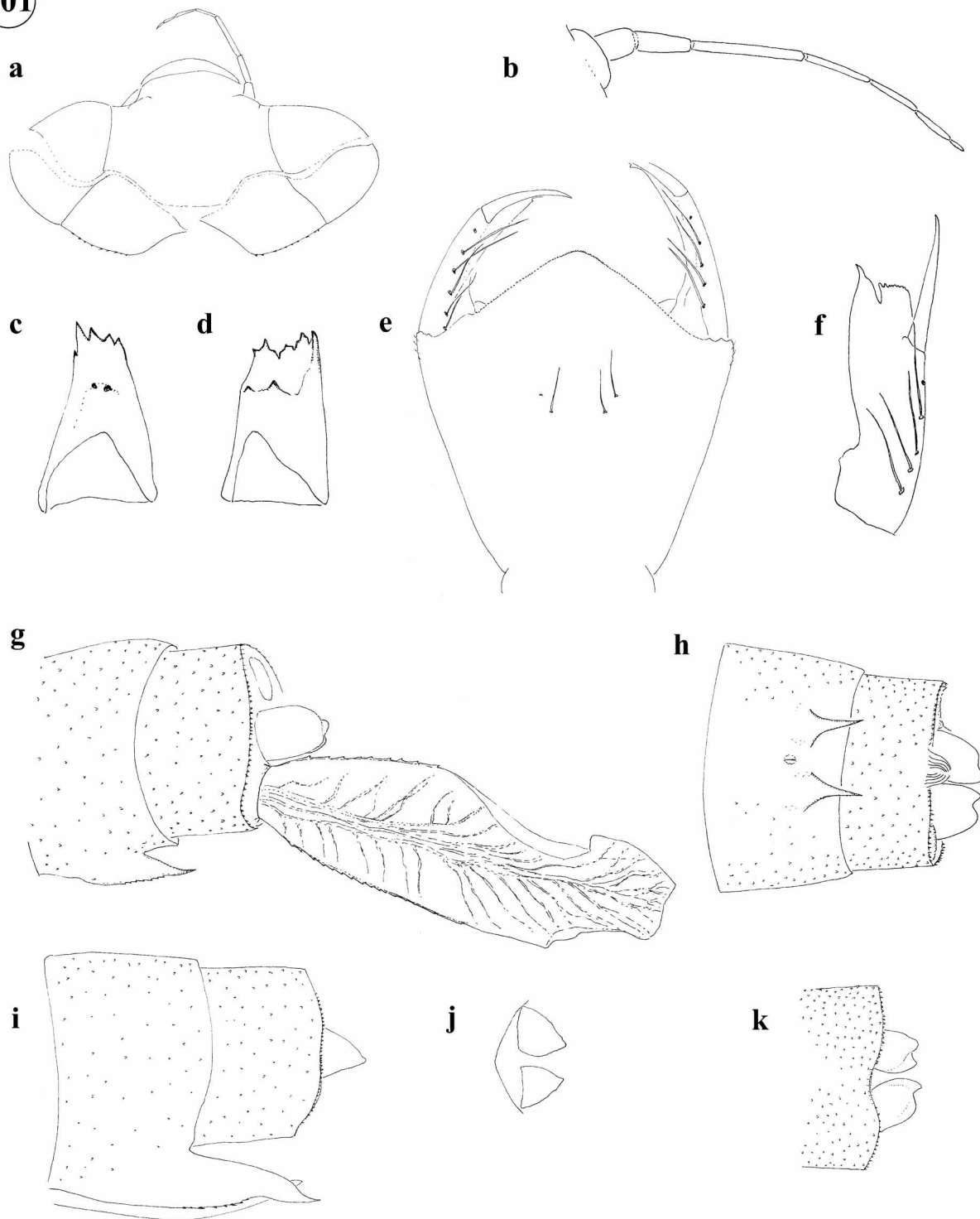


FIGURE 101. *Oreiallagma quadricolor* (Peru, Morro Leguía). Last larval stadium, (a) head, dorsal view; (b) antenna, lateral view; (c) right mandible, ental view; (d) left mandible, ental view; (e) prementum, ental view; (f) premental palp, ental view; (g) male S9–10, lateral view; (h) male S9–10, ventral view; (i) female S9–10, lateral view; (j) female cerci, dorsal view; (k) male S10, dorsal view.

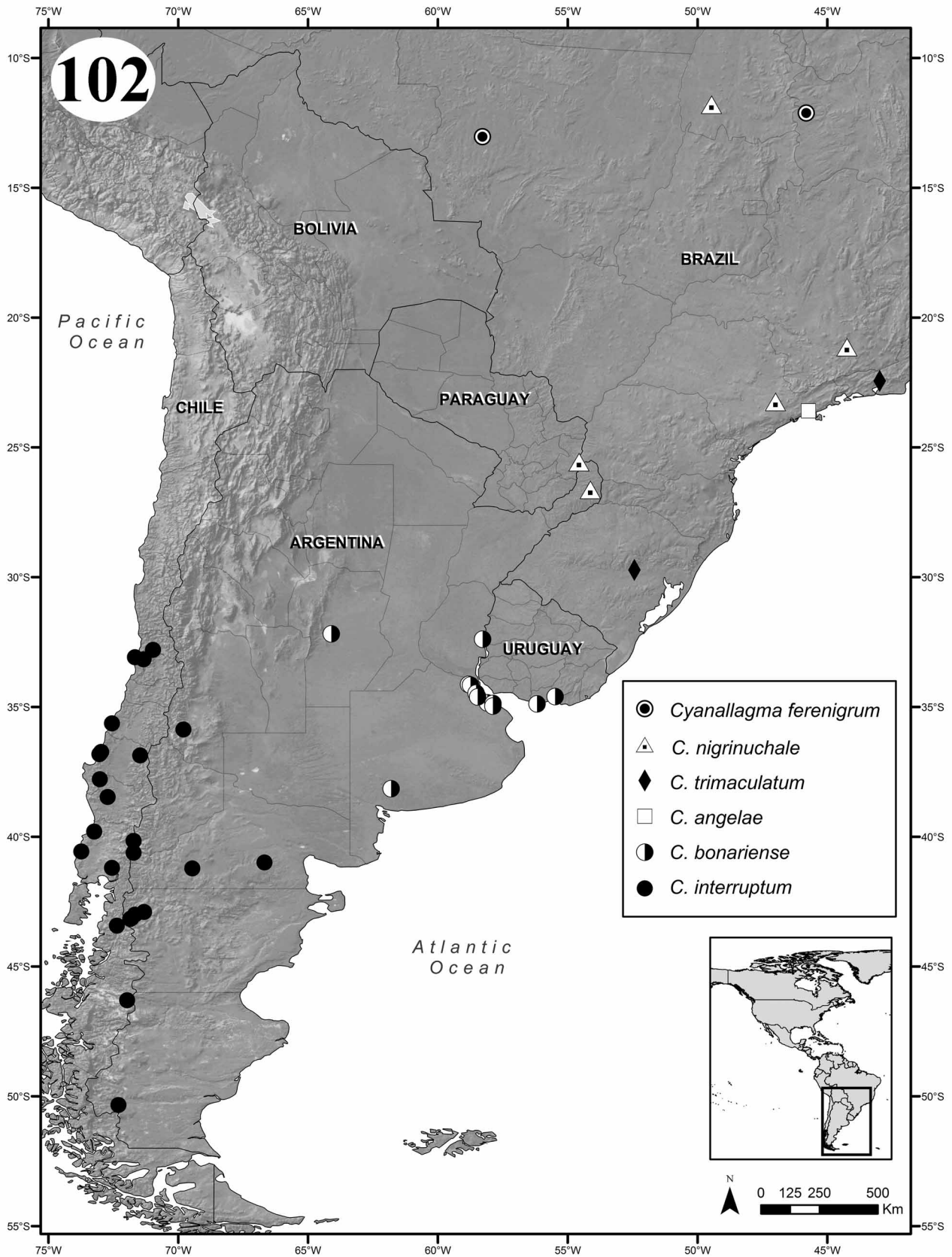


FIGURE 102. Distribution of species of *Cyanallagma* in South America.

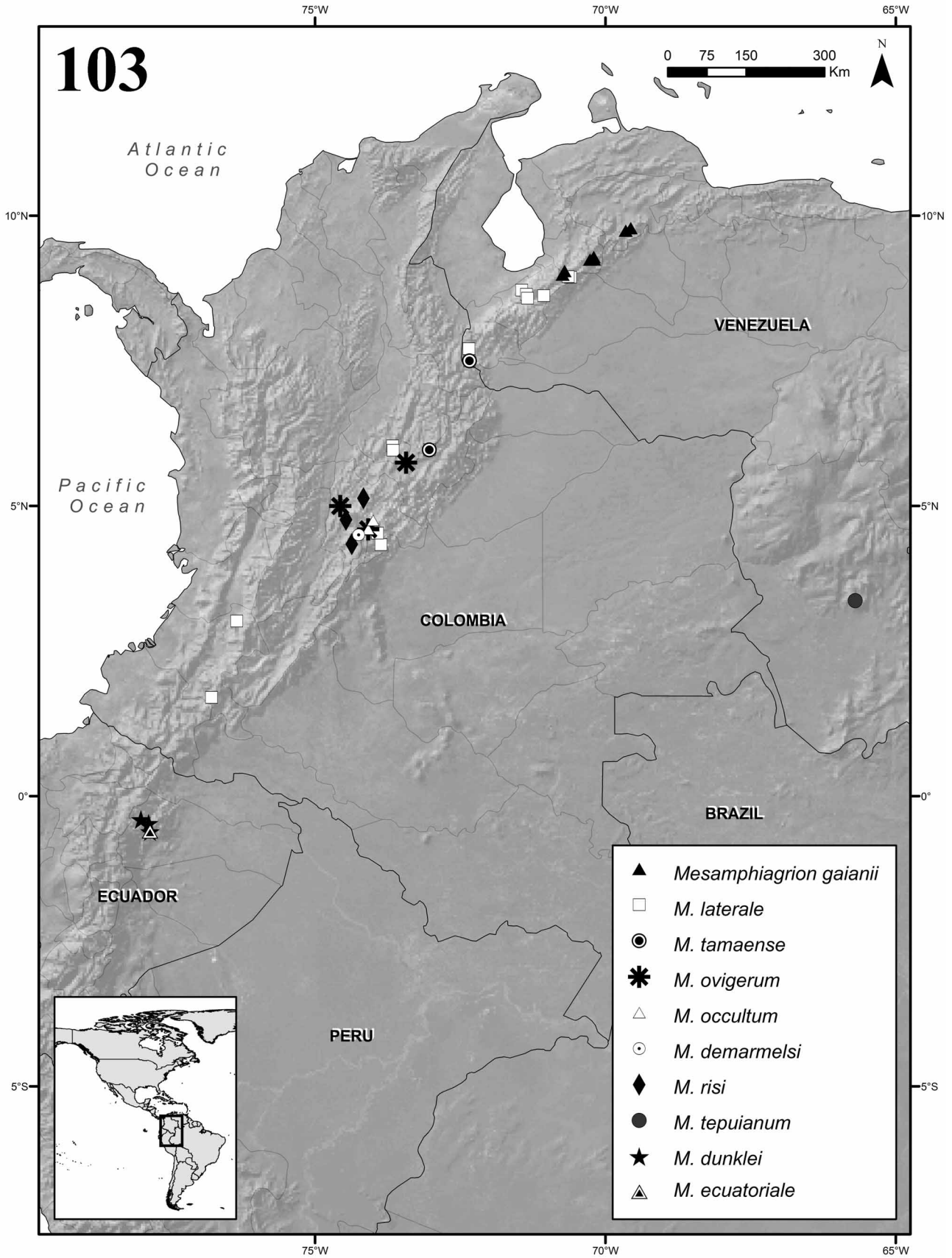


FIGURE 103. Distribution of species of *Mesamphiagrion* in South America.

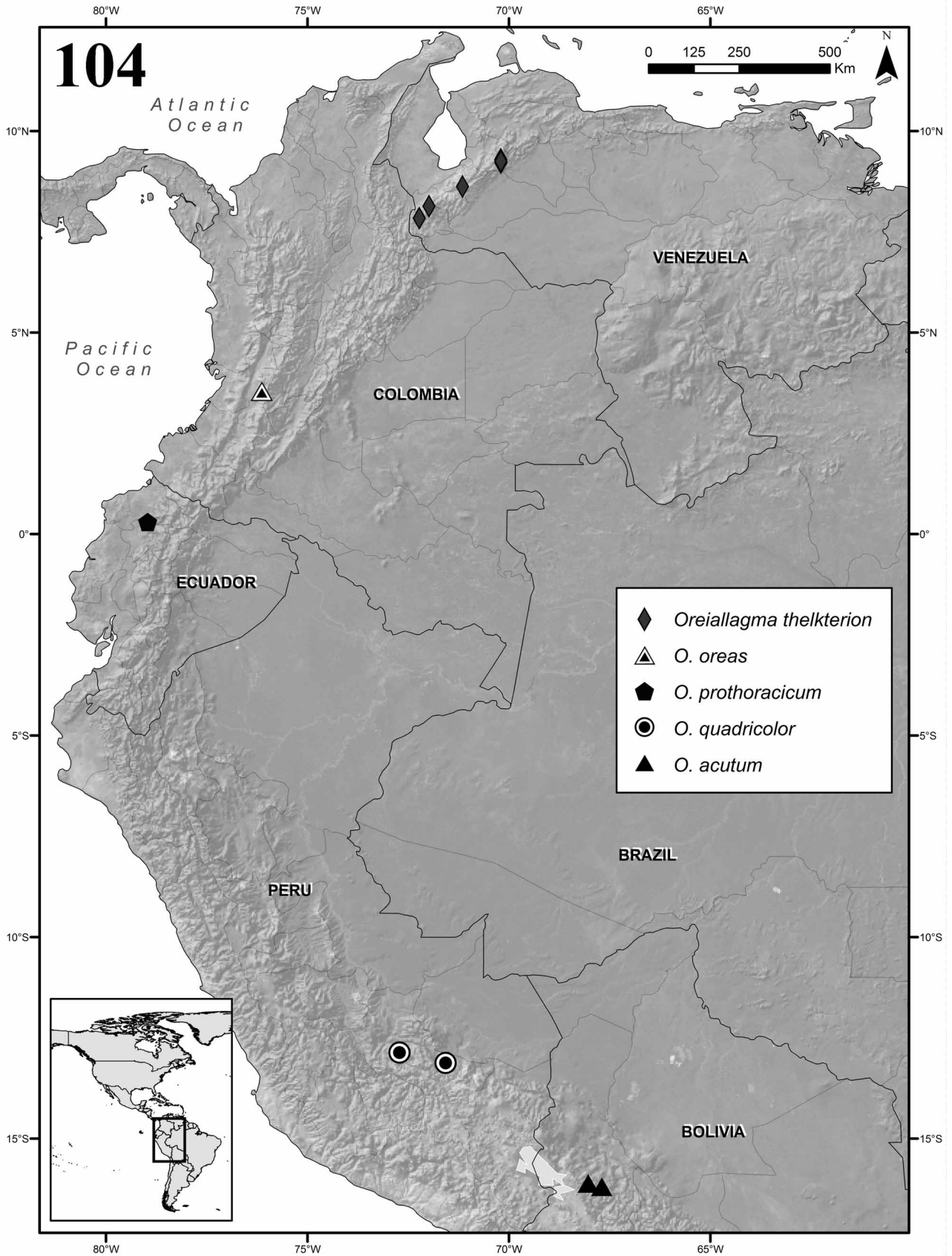


FIGURE 104. Distribution of species of *Oreiallagma* in South America.

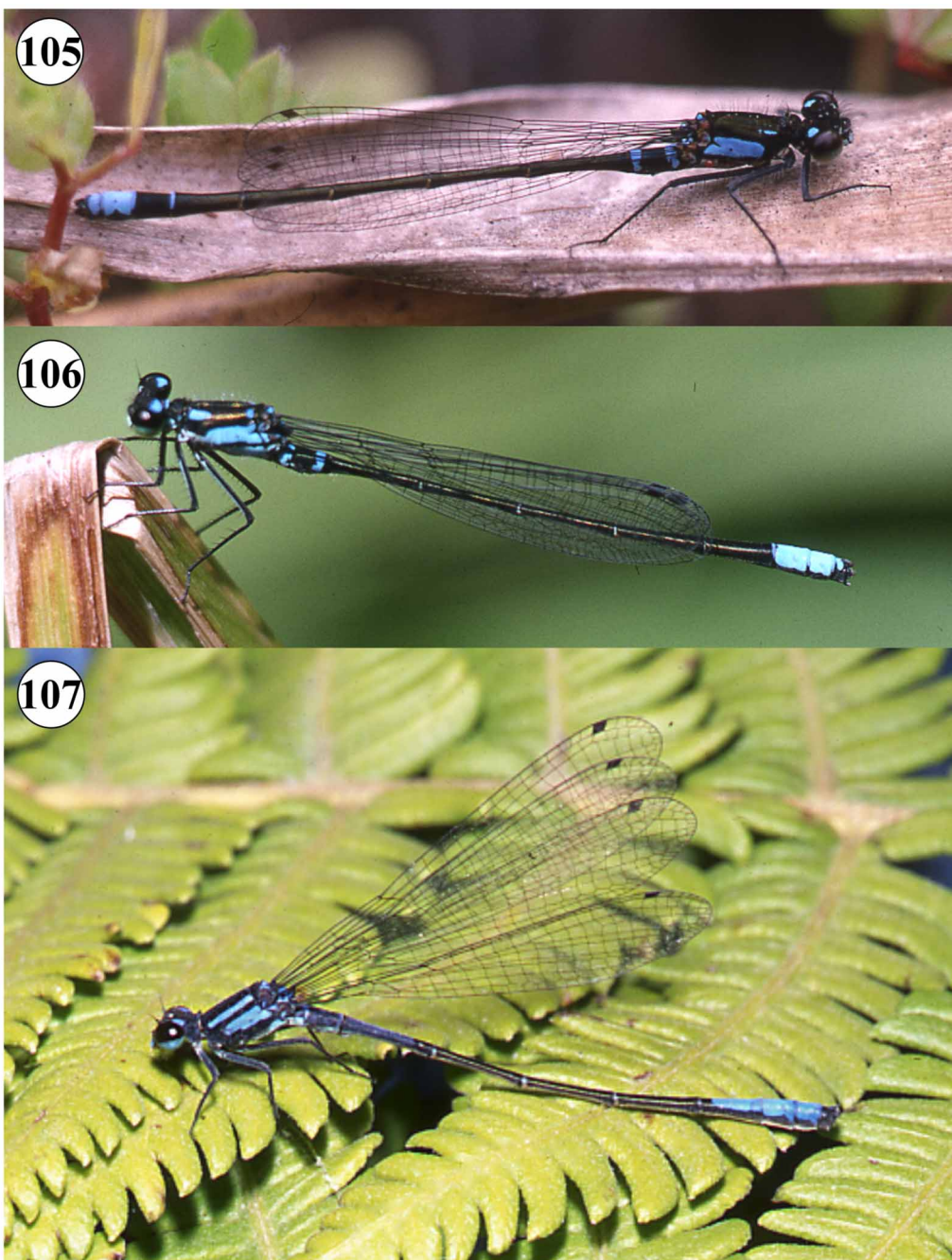


FIGURE 105. Mature adult male of *Cyanallagma interruptum* (Chile, X Región, marsh 5 km W of Puerto Ramirez by route 231, 18.i.1995). Photographed by R.W. Garrison.

FIGURE 106. Mature adult male of *Cyanallagma bonariense* (Argentina, Buenos Aires Province, Sierra de la Ventana, Arroyo del Loro, 29.i.1995). Photographed by R.W. Garrison.

FIGURE 107. Mature adult male of *Mesamphiagrion dunklei* (Ecuador, Napo Province, Baeza, 1710 m, seepage marsh, 24.vii.1996, B. Mauffray leg.). Photographed by S.W. Dunkle.

Female allotype

Head. As in holotype but base of mandibles, anterior surface of genae, anteclypeus, and antefrons pale bluish yellow; postclypeus with a pair of transversely elongate oval yellow spots, and anterior portion of postfrons pale yellow.

Thorax. As in holotype but mid-dorsal black stripe margined by reddish brown, and faint reddish brown narrow stripe along humeral suture. Legs yellow, except distal portion of femora, tibiae, tarsi and tip of pre-

tarsi reddish brown. Medial portion of posterior lobe of prothorax only slightly projected caudally at mid-line (Fig. 16b). Mesepisternal plates wider than in male holotype (Fig. 16c). Wings as holotype but pt pale reddish brown; 13 Px in left FW, 13 in right HW, 12 in left HW.

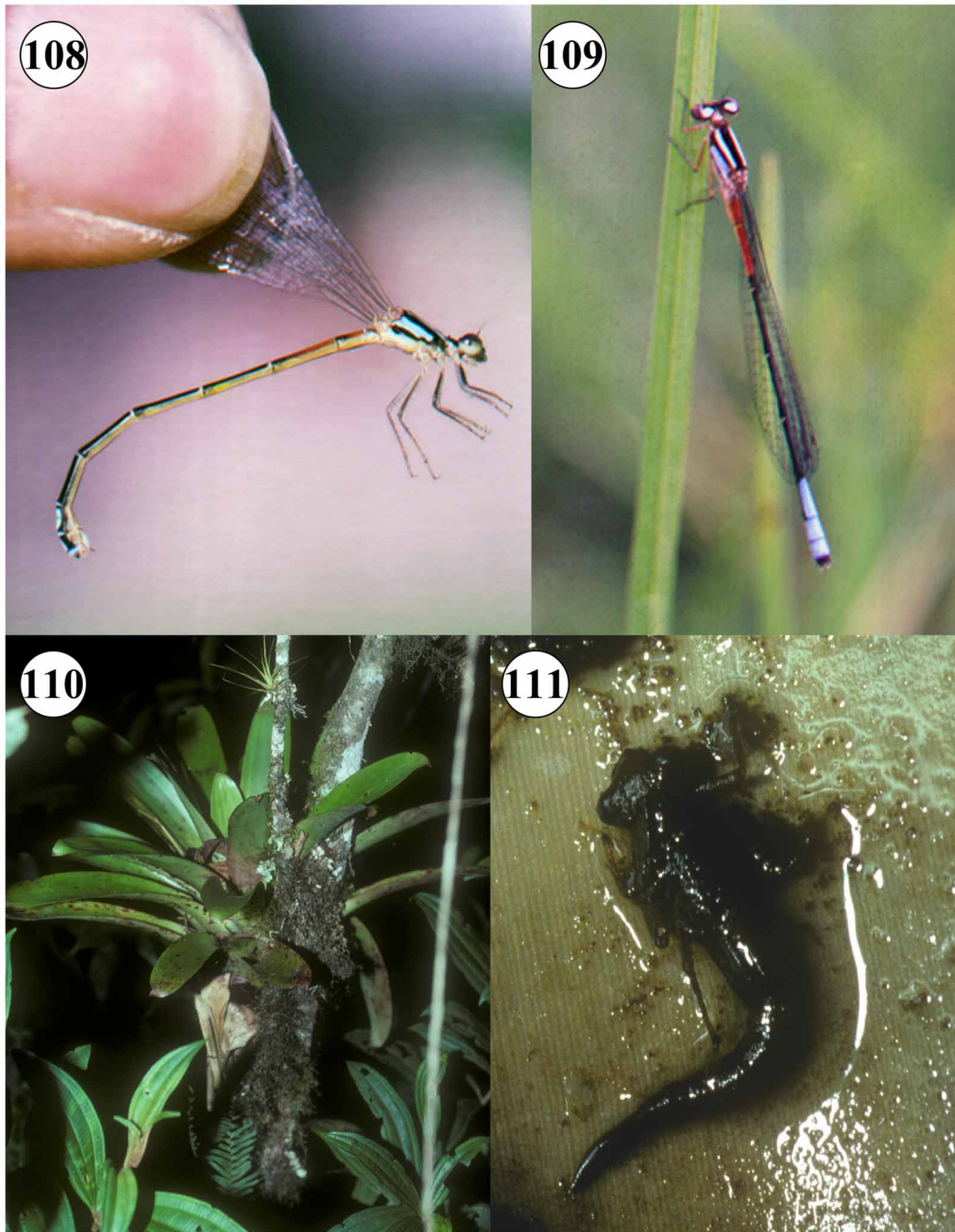


FIGURE 108. Juvenile adult female of *Mesamphiagrion gaianii* (Venezuela, Trujillo State, 9 km East of Mosquey, Laguna Negra, 16/22.x.1991). Photographed by J. De Marmels.

FIGURE 109. Juvenile adult male of *Mesamphiagrion laterale* (Venezuela, Mérida State, road to La Culata, 2646 m, 04.vii.1991). Photographed by J. De Marmels.

FIGURE 110. Bromeliad inhabited by larvae of *Oreiallagma quadricolor* (Peru, Cusco Department, Morro Leguía, km 135, road between Paucartambo and Atalaya, 2250 m, 21.vi.1993). Photographed by J.A. Louton.

FIGURE 111. Larva of *Oreiallagma quadricolor*. Photographed by J.A. Louton.

Abdomen. Color pattern as in holotype, except dorsum of S1–7 black, of S8 pale blue at distal third, of S9 pale blue at distal half, of S10 entirely pale blue; latero-ventral margins of terga pale yellow from S1–10 (Fig.

4e). Cercus shorter than S10, conical and brown; paraprocts pale yellow. Vulvar spine on S8 well developed. Sub-basal plate of ovipositor broadly rounded; outer valve of ovipositor with a single row of teeth; tip of ovipositor (excluding stylus) extending beyond posterodorsal margin of S10 but not reaching tip of cercus (Fig. 4e).

Dimensions. Total length 38.0 mm; abdomen length 31.0 mm; FW 25.5 mm; HW 24.5 mm.

Variation in paratypes. Paratype males are similar to holotype but the anteclypeus in three has a pair of transverse oval black spots, and outer surfaces of cercus delimited between dorsal, inner ventro-apical process, and outer ventro-apical processes are pale blue. One male has basal sixth of S7 black. Female as in allotype.

Male paratypes Px in FW 13–16, in HW 12–13; RP₂ branching between Px 7–8 in FW, between Px 5–6 or slightly proximal to 6 in HW. Female Px in FW 15–14, in HW 14–13; RP₂ branching slightly proximal to Px 7 in FW, between Px 5–6 in HW.

Dimensions. Total length males 35.5–38 mm [mean 36.8 mm; SD 1.26; n = 3]; total length female 39.0 mm; abdomen length males 29.0–31.5 mm [mean 30.3 mm; SD 1.26; n = 3]; abdomen length female 31.5 mm; FW males 23.0–24.5 mm [mean 23.6 mm; SD 0.76; n = 3]; FW female 26.5 mm; HW males 22.0–23.5 mm [mean 22.7 mm; SD 0.76; n = 3]; HW female 25.5 mm.

Diagnosis. Male of *M. equatoriale* shares only with *M. occultum*, *M. ovigerum*, and *M. risi* the short subapical dorsal process of cercus but differs from them by the ventrally pointed ventro-basal process of the cercus (Fig. 72) that is rectangular in *M. occultum* (Fig. 70b), narrowly spatulate and curved anteriorly in *M. ovigerum* (Fig. 71), and broadly triangular in *M. risi* (Fig. 74). Absence of metapleural dark stripe (Fig. 3c) is shared only by males (female is unknown) of *M. occultum*, *M. ovigerum*, and *M. tepuianum*. *Mesamphiagrion equatoriale* differs from *M. tepuianum* in following characters (contrasting character states for *M. tepuianum* in parentheses): medial lobe of posterior prothoracic lobe projected caudally into a semicircular lobe (Fig. 16a; bilobate and only slightly projected, Fig. 19); basal segment of genital ligula lacking long setae along sides (Fig. 41a; with long setae along sides, Fig. 44); and acutely pointed ventro-basal process of cercus in medio-dorsal view (Fig. 72; broadly rectangular ventro-basal process, Fig. 73).

Female of *M. equatoriale* differs from other known females of *Mesamphiagrion* by medial lobe of posterior prothoracic lobe only slightly projected medially beyond lateral lobes (Fig. 16b), whereas the same is well-developed and posteriorly projected in *M. demarmelsi* and *M. tamaense* (Figs. 20b–21b), and bilobate in *M. dunklei*, *M. gaianii*, and *M. laterale* (Figs. 22c, 23b–24b).

Biology. Adults collected at seeps and marsh. Breeding habitat and larva unknown.

Distribution. Ecuador (Napo Dept.), at 2100 m above sea level (Fig. 103).

***Oreiallagma* gen. nov.**

Figures 5; 8; 25–29; 49–53; 85–94; 101; 104; 110–111

Type species: *Cyanallagma thelakterion* De Marmels 1997 by present designation.

Other species included: *O. acutum* (Ris 1918) **comb. nov.**, *O. oreas* (Ris 1918) **comb. nov.**, *O. prothoracicum* (Kimmins 1945) **comb. nov.**, and *O. quadricolor* (Ris 1918) **comb. nov.**

Etymology: From 'oreios' (Greek): of or from the mountains, and 'allagma' (Greek): a neuter noun used for many damselfly names, allusion that was originally chosen by Charpentier (1840) to denote the possibility of mistaking coenagrionid genera with blue and black males with those of the genus *Enallagma* (Fliedner 2006). The name refers to the habitat of these species, which inhabit the Andean mountain range.

Generic characterization. Head. Color of dorsum dark brown to black with pale blue to olive postocular spots (Fig. 5), no pale postocular bar, rear of head pale. Frons rounded, occipital lobes not protruding posteriorly so that most posterior point of head is at eyes (Fig. 5).

Thorax. Medial lobe of posterior lobe of prothorax developed into caudally projected foliate plate (Figs. 25–29). Female mesostigmal plates rectangular and narrow with ratio of maximum width/length of less than 0.5 (Fig. 28c). Pterothorax with dark mid-dorsal and humeral stripes, sometimes with a dark stripe over metapleural suture (absent in *O. acutum*, *O. prothoracicum*, and *O. quadricolor*); with pale blue antehumeral stripe usually complete but interrupted distally in *O. acutum* and *O. thelakterion* (Fig. 5). Legs long with femur 1 always longer than distance between eyes at level of antennifer (Fig. 5; ratio = 1.08), tibial spurs shorter than or as long as distance between them, pretarsal claw with well developed supplementary tooth. Wings in most examined specimens smoky especially along costal area; CuP reaching CuPAA, proximal to hind margin of wing for a distance as long as CuP or shorter; vein descending from quadrangle not forming a straight line to wing margin (Fig. 8).

Abdomen. Color reddish-orange, black, and blue (Fig. 5); relatively long with a ratio of 4.4–6.5 to head plus thorax length. Genital ligula distal segment with one (*O. oreas* and *O. prothoracicum*) or two (*O. acutum*, *O. quadricolor*, and *O. thelakterion*) ental transverse folds and usually lacking inner process (inner process observed only in *O. thelakterion*, Fig. 49c), always with paired latero-apical lobes and usually with a pair of small accessory latero-medial lobes (absent in *O. acutum*; Fig. 51); second segment with unique wide paired latero-apical folds with sclerotized margins (Figs. 49–53). Postero-dorsal margin of male S10 recessed in dorsal view, with very slight (*O. quadricolor*, *O. thelakterion*; Figs. 86; 88) to more pronounced (*O. acutum*, *O. oreas*, *O. prothoracicum*; Figs. 85; 87; 89) 'v'-shaped cleft lacking a lateral pair of tubercles. Male cercus with a long blade-like ventral process bent medio-anteriorly each of which converges with the one on opposite cercus before finally diverging at tip (Figs. 85–94), and a dorsal process directed posteriorly of variable length: very short and subapical in *O. oreas* and *O. quadricolor* (Figs. 93a–94a), long and apical in *O. prothoracicum*, *O. thelakterion*, and *O. acutum* (Figs. 90a–92a). Patch of differentiated scalariform-like cuticle on posterior surface of male cercus present (*O. oreas*, *O. quadricolor*, and *O. prothoracicum*) or absent (*O. thelakterion* and *O. acutum*). Male paraproct with a dorsal branch ending on a sclerotized tip or ridge (Figs. 90–94). Female (known only for *O. thelakterion* and incompletely for *O. quadricolor*) with vulvar spine on S8; ovipositor not reaching tips of cerci.

Generic diagnosis. *Oreiallagma* is unique among all genera of New World Coenagrionidae by the presence of a pair of wide latero-apical folds with sclerotized margins on second segment of genital ligula (Figs. 49–53), and by the forked male cercus combining a dorsal process and a long blade-like ventral process bent medio-anteriorly (Figs. 85–94). *Oreiallagma* differs from *Cyanallagma* by having the rear of head surrounding occipital foramen pale (as in Fig. 1b) and by the male cercus having a dorsal process (Figs. 85–94). *Oreiallagma* differs from *Mesamphiagrion* by having a forked male cercus combining a dorsal process and a long blade-like ventral process bent medio-anteriorly (Figs. 85–94). Further differences are given in Table 2. As mentioned under the previous two genera, the combination of a rounded frons, presence of pale postocular spots, a trilobate prothoracic posterior lobe, striped pterothorax, and male cerci provided with some kind of processes is shared among New World Coenagrionidae not only with *Cyanallagma* and *Mesamphiagrion* but also with *Apanisagrion*, *Chrysobasis*, *Hesperagrion*, *Homeoura*, some *Ischnura* species, *Leptobasis*, and *Telagrion*. *Oreiallagma* differs from all except *Chrysobasis*, *Leptobasis*, and *Telagrion* by its long abdomen in relation to length of head plus thorax with a ratio of over 4.4 versus less than 4.4. It differs from *Chrysobasis*, *Leptobasis*, and *Telagrion* by the presence of well developed supplementary teeth on pretarsal claws (vestigial or forming a right angular notch in the other three genera) and by female ovipositor not surpassing tip of cerci (extending beyond tip of cerci in other genera).

Remarks. Specimens are rare in collections, females are known for only two species, and all but two (*O. quadricolor* and *O. thelakterion*) have not been collected since their original descriptions. Species vary considerably in total length; their ranges from longest to shortest are: *O. prothoracicum* (= 55 mm), *O. oreas* and *O. thelakterion* (44–46 mm), *O. quadricolor* (40 mm), and *O. acutum* (37 mm). If breeding biology for the genus mirrors that for *O. quadricolor* (within bromeliads in high elevation forest areas), we suspect future collecting

in these forest zones will yield more specimens, and intraspecific adult size variation will be considerable due to differences in space and food availability within phytotelmata habitats.

Distribution. Narrow mountainous corridor in Andes from Venezuela to Bolivia, from 800 to 2300 m above sea level (Fig. 104).

Key to males of *Oreiallagma*

1. Medial lobe of posterior prothoracic lobe heart-shaped, markedly constricted at base and with a moderate medial concavity on posterior margin, and lateral lobes bilobate (Figs. 25; 29a) 2
- 1'. Medial lobe of posterior prothoracic lobe sub-quadrate, slightly constricted at base and with a shallow medial concavity on posterior margin, and lateral lobes not bilobate (Figs. 26-27; 28a) 3
2. (1.) Dorsal process of male cercus digitiform (Figs. 86; 91); distal segment of genital ligula wider at apex than at base, with latero-apical lobes recurved and directed basally (Fig. 49b), and with two ental membranous transverse folds, the one basal to the latero-medial lobes with a medial inner process (Fig. 49c); Trujillo, Mérida, and Táchira States, Venezuela (Fig. 104) *O. thelkerion*
- 2'. Dorsal process of male cercus approximately triangular (Figs. 87; 92); distal segment of male genital ligula as wide at apex as at base, with latero-apical lobes directed distally and not recurved (Fig. 53b), and with one sclerotized transverse fold basal to latero-medial lobes (Figs. 53a, c); Imbabura Prov., Ecuador (Fig. 104) *O. prothoracicum*
3. (1'.) Dorsal process of male cercus longer than ventral process (Figs. 85; 90); La Paz Dept., Bolivia (Fig. 104) *O. acutum*
- 3'. Dorsal process of male cercus much shorter than ventral process (Figs. 88–89; 93–94) 4
4. (3'.) Dorsal process of male cercus represented by a blunt setose tubercle (Figs. 89; 94); distal segment of genital ligula with two pairs of contiguous latero-apical lobes (Fig. 52a); Valle del Cauca Dept., Colombia (Fig. 104) *O. oreas*
- 4'. Dorsal process of male cercus represented by a pointed tooth (Figs. 88; 93); distal segment of genital ligula with one pair of latero-apical lobes (Fig. 50a); Cusco Dept., Peru (Fig. 104) *O. quadricolor*

Key to known females of *Oreiallagma*

[*O. acutum*, *O. oreas*, and *O. prothoracicum* unknown]

1. Posterior margin of medial lobe of posterior prothoracic lobe smoothly rounded (Fig. 28c); Cusco Dept., Peru (Fig. 104) *O. quadricolor*
- 1'. Posterior margin of medial lobe of posterior prothoracic lobe medially concave (Fig. 29b); Trujillo, Mérida, and Táchira States, Venezuela (Fig. 104) *O. thelkerion*

Oreiallagma acutum (Ris 1918) comb. nov.

Figures 27; 51; 85; 90; 104

Acanthagrion acutum Ris 1918: 120–122, figs. 61–62 [mislabelled as 59] (description of male, illustration of S10 and wings).

Cyanallagma acutum Kennedy 1920: 87 (inclusion in *Cyanallagma*).

Davies & Tobin 1984: 66 (synonymic list).

De Marmels 1989: 246–247, figs. 1–7 (notes on male and illustrations of head, posterior lobe of prothorax, S7–10, genital ligula, and S10).

Garrison 1991: 11 (synonymic list).

Bridges 1994: VII.3 (synonymic list).

Steinmann 1997: 247 (synonymic list as *Cyanallagma acuta*).

De Marmels 1997: 138, fig. 82 (key to northern *Cyanallagma* species, map, comparison with *C. thelakterion*).

Tsuda 2000: 31 (synonymic list).

Types: Ris (1918) described this species based on nine males (three from Río Zongo, six from Coroico) but did not designate a holotype. We examined a male syntype labeled "Río Zongo, 800 m./ BOLIVIA. [La Paz Dept.] 1913 (2), A.H. Fassl", which also has a red label "Lecto-[in ink by an unknown hand]/Para-/typoid [printed]" affixed to the envelope. De Marmels (1989) stated that he examined two paralectotypes from Coroico. In order to clarify application of the name, we designate the specimen we examined as **lectotype** (Senckenberg Register No. 10196) that served as basis for our Figures 27; 51; 85; 90. In FNS.

Characterization. Medial lobe of posterior lobe of prothorax slightly constricted at base, subquadrate, with shallow medial concavity on posterior margin (Fig. 27; as in *O. oreas* and *O. quadricolor*). Distal segment of genital ligula (Fig. 51) approximately as wide at apex as at base with a pair of latero-apical lobes recurved and directed basally, no accessory latero-medial lobes (unique), and two ental membranous transverse folds (as in *O. quadricolor* and *O. thelakterion*). Dorsal process of male cercus approximately as long as ventral process (Figs. 85; 90; unique). Dorsum of S1–7 black, of S8–9 blue, sides of S3–7 reddish-orange, of S8 with a black stripe along anterior 2/3, S9 entirely blue and S10 entirely black. Female unknown.

Diagnosis. Species unique by cercus morphology: the long, digit-like dorsal process (Fig. 85) is shared only with *O. thelakterion* (Fig. 86) but is more robust and as long as or longer than ventral process (Figs. 85; 90); in *O. thelakterion*, dorsal process is more acuminate and shorter than ventral process (Fig. 86). In *O. prothoracicum* (Figs. 87; 92) and *O. quadricolor* (Figs. 88a; 93), dorsal process is small and acute, and in *O. oreas* it is represented by a blunt setose tubercle (Figs. 89; 94).

Biology. Unknown; see remarks under generic account.

Distribution. Bolivia (La Paz Department), from 800 to 1400 m above sea level (Fig. 104).

Oreiallagma oreas (Ris 1918) comb. nov.

Figures 26; 52; 89; 94; 104

Telagrion oreas Ris 1918: 136, 138–139, fig. 78 (diagnosis from *T. quadricolor*, description of male, illustration of S10).

Kimmins 1945: 189 (comparison with *T. prothoracicum*).

St. Quentin 1960: 48 (key for males).

Santos 1965: 9 (possible placement in *Leptagrion*).

Davies & Tobin 1984: 94 (synonymic list).

Garrison 1991: 13 (synonymic list).

Bridges 1994: VII.174 (synonymic list).

Steinmann 1997: 358 (synonymic list).

Tsuda 2000: 50 (synonymic list).

Lencioni 2004: 92 (mention).

Types: ♂ **holotype** in FNS (examined) with following data: "Monte Socorro 2300 m/ [Valle del Cauca Dept.] Colombia, W. Cordill./ vii. 09 [A.H.] Fassl"; (Senckenberg Register No. 10764).

Characterization. Medial lobe of posterior lobe of prothorax is slightly constricted at base, subquadrate, with shallow medial concavity on posterior margin (Fig. 26; as in *O. acutum* and *O. quadricolor*). Distal segment of genital ligula (Fig. 52) approximately as wide at apex as at base with two contiguous pairs of latero-apical lobes (unique) recurved and directed basally, small accessory latero-medial lobes and one (as in *O. prothoracicum*) ental membranous faint transverse fold (Fig. 52c). Dorsal process of male cercus much shorter than ventral process, represented by a blunt setose tubercle (Figs. 89; 94; unique). Dorsum of S1 dark brown, posteriorly with a transverse oval greenish blue spot; of S2 orange becoming diffuse brown anteriorly; of S3–

5 pale orange-red; of S6 orange antero-laterally, black dorso-posteriorly; of S7 black with a narrow reddish lateral margin over the anterior three fourths; of S8–9 blue, laterally reddish, both colors separated through a black longitudinal stripe; of S10 black. Female unknown.

Diagnosis. This species, known only from the mature holotype male, is unique in that the dorsal process of the cercus is represented by a blunt setose tubercle (Figs. 89; 94). In all other species the dorsal process is either long and digit-like (*O. acutum*, Figs. 85; 90; *O. thelakterion*, Figs. 86; 91) or acute if small (*O. prothoracicum*, Figs. 87; 92; *O. quadricolor*, Figs. 88a; 93). The distal segment of the genital ligula (Fig. 52a) is uniquely armed with a pair of small contiguous latero-apical lobes (a single long latero-apical recurved lobe in *O. thelakterion*, Fig. 49b; *O. quadricolor*, Fig. 50b; and *O. acutum*, Fig. 51b; and a single small latero-apical lobe in *O. prothoracicum*, Fig. 53b).

Biology. Unknown; see remarks under generic account.

Distribution. Colombia (Valle del Cauca Department) at 2300 m above sea level (Fig. 104). Following information about this locality is provided by Ris (1918): ".....Santa Margarita ('situated deep in the high mountain forest at 2200 m is the last house Santa Margarita, on upper bank of Rio Cali, the estate of a Colombian general'); out from here the gold mine Monte Socorro is reachable with effort."

***Oreiallagma prothoracicum* (Kimmins 1945) comb. nov.**

Figures 8b; 25; 53; 87; 92; 104

Telagrion prothoracicum Kimmins 1945: 187–189, figs. 1A–C (description of male, illustration of S10, and posterior lobe of prothorax).

St. Quentin 1960: 48 (in key for males).

Kimmins 1970: 190 (type catalog BMNH).

Leptagrion prothoracicum Santos 1965: 9 (transfer to *Leptagrion*).

Davies & Tobin 1984: 82 (synonymic list).

Garrison 1991: 13 (synonymic list).

Bridges 1994: VII.191 (synonymic list).

Steinmann 1997: 310 (synonymic list).

Tsuda 2000: 38 (synonymic list).

Costa & Garrison 2001: 384 (mention).

Types: ♂ **holotype** in BMNH (examined) with following data: "Intaj [Imbabura Prov.]/Ecuador [in ink]"; 3 ♂ **paratypes** in BMNH (examined).

Characterization. Medial lobe of posterior lobe of prothorax heart-shaped, markedly constricted at base, with moderate medial concavity on posterior margin, and each lateral lobe bilobate (Fig. 25; as in *O. thelakterion*). Distal segment of genital ligula (Fig. 53) approximately as wide at apex as at base, with a pair of latero-apical lobes each of which are not recurved and are directed distally (unique), a pair of small accessory latero-medial lobes (as in *O. quadricolor*), and one ental sclerotized transverse fold (unique, Fig. 53c; one non-sclerotized fold in *O. oreas*, Fig. 52c). Dorsal process of male cercus shorter than ventral process, approximately triangular and directed postero-dorsally in lateral view (unique; Figs. 87; 92). Dorsum of S1 orange yellow; of S2–5 orange yellow with posterior black margin; of S6 brown; of S7 black; of S8 blue with lateral black longitudinal stripe on anterior 2/3; of S9 blue; of S10 black. Female unknown.

Diagnosis. This species, the largest of the genus, is unique by cercus morphology: the dorsal process is small, acute, and apical (Figs. 87; 92); in *O. quadricolor* the dorsal process is also short and acute, but it is sub-apical (Figs. 88a; 93). The short latero-apical lobe of distal segment of genital ligula (Fig. 53b) is shared only with *O. oreas* (Fig. 52b), but in the latter species there is a pair of contiguous latero-apical lobes on each side (Fig. 52a). Medial lobe of posterior lobe of prothorax is constricted basally and each lateral lobe is bilobate (Fig. 25); *O. thelakterion* (Fig. 29) is the only other species with bilobate lateral lobes, but its medial lobe is broader than in *O. prothoracicum*.

Biology. Unknown; see remarks under generic account.

Distribution. Ecuador (Imbabura province), at 2000 m above sea level (Fig. 104).

***Oreiallagma quadricolor* (Ris 1918) comb. nov.**

Figures 28; 50; 88; 93; 101; 104; 110

Telagrion quadricolor Ris 1918: 136-137, fig. 77 (diagnosis from *T. oreas*, description of male, illustration of S10).

Schmidt 1942: 240 (mention from Peru).

Kimmins 1945: 189 (comparison with *T. prothoracicum*).

Rácenis 1959b: 472 (mention from Peru).

St. Quentin 1960: 48 (key for males).

Santos 1965: 9 (possible placement in *Leptagrion*).

Davies & Tobin 1984: 94 (synonymic list).

Garrison 1991: 14 (synonymic list).

Bridges 1994: VII.196 (synonymic list).

Steinmann 1997: 358 (synonymic list).

Tsuda 2000: 50 (synonymic list).

Lencioni 2004: 92 (mention).

Types: ♂ **holotype** in FNS (examined) with following data: "S[an]ta. Ana b[ei] Cuzco/ [Cusco Dept.] PERU—2300 m./p. [A.H.] Fassl 1911"; (Senckenberg Register No. 10763).

Other specimens examined: PERU. Cusco Dept.: Quebrada Morro Leguía, km 135, road between Paucartambo and Atalaya, 2250 m, collected from water held in bromeliad bracteae, 21.vi.1993, J.A. Louton & R.W. Garrison leg., 1 ♂ adult and its larval exuviae (emerged 23.vii.1993, *ex* bromeliad B-7), 1 ♀ partially out of exuviae, died while emerging (RWG).

Characterization. Medial lobe of male posterior lobe of prothorax slightly constricted at base, subquadrate, with shallow medial concavity on posterior margin (Fig. 28a; as in *O. acutum* and *O. oreas*); of female not constricted at base, smoothly rounded lacking medial concavity on posterior margin (Fig. 28c). Distal segment of genital ligula (Fig. 50) approximately as wide at apex as at base, with a pair of latero-apical lobes recurved and directed basally, a pair of small accessory latero-medial lobes, and two ental membranous transverse folds (as in *O. acutum* and *O. thelakterion*). Dorsal process of male cercus much shorter than ventral process represented by a pointed tooth (Figs. 88; 93; unique). Male dorsum of S1 anteriorly dull reddish, posteriorly blackish; of S2 dull reddish, darker anteriorly; of S3–5 orange-red, gradually turning yellow toward lateral margins, terminal dorsal blackish spot of about 1/6 of segment length; of S6 orange-red with black posterior spot to entirely black; of S7 black, laterally pale orange; of S8 entirely blue or with two longitudinal wide black stripes along two thirds of its length, sides on anterior 2/3 dull orange, of posterior 1/3 blue; of S9 blue; of S10 black.

Diagnosis. This species is unique by cercus morphology (Figs. 88; 93), which is similar to *O. oreas* (Figs. 89; 94) and is diagnosed under that species.

Description of last stadium larva. Head (Fig. 101a). Pale brown with pale ocellar rounded spots on dorsum; trapezoidal, *ca.* 1.8 times as wide as long, with posterior margin concave. Antenna 7-segmented with third antennomere the longest (Fig. 101b). Prementum (Fig. 101e) 0.72–0.83 times as wide as long, with 2 setae on each side and with 3–4 short latero-apical setae; ligula bluntly triangular and finely crenulated along entire margin. Labial palp (Fig. 101f) with 5–6 setae along inner margin and with 6 small distal teeth (2–3 larger medial and 3–4 smaller outer ones) in addition to inner tooth. Articulation of pre- and postmentum midway between bases of coxae 1 and 2. Mandibles (Figs. 101c–d) with following formula: L 1'1234 a b, R 1234 y a b.

Thorax. Wing pads reaching mid-length of abdominal S4 (male) to posterior margin of S5 (female). Legs pale brown except distal end of tibiae and distal tarsi darker brown.

Abdomen. Pale brown with a narrow medio-longitudinal pale line along S2–9. Male cerci bilobate (Figs. 101h, k); female cerci conical with an apical blunt point (Figs. 101i–j). Male and female gonapophyses acutely pointed (Figs. 101g–i) with a medio-longitudinal row of setae, female gonapophyses extending to posterior margin of S10 (Fig. 101i). Lateral caudal lamella broadly lanceolate, pale, with faint and scarcely branched tracheae (Fig. 101g), about as long as 0.30 times abdomen length.

Dimensions (measurements of male followed by those for female in parentheses when available). Total length without appendages: 13.00 mm; prementum length: 2.65 mm (3.25 mm); prementum maximum width: 2.20 mm (2.35 mm); femur I: 2.00 mm (2.10 mm); femur II: 2.90 mm (3.00 mm); femur III: 3.60 mm (3.80 mm); tibia I: 2.50 mm (2.60 mm); tibia II: 2.90 mm (3.00 mm); tibia III: 3.50 mm (3.70 mm); inner wing pads: 4.30 mm (5.30 mm); external wing pads: 4.70 mm (5.10 mm); abdomen length without appendages: 8.50 mm; lateral caudal lamellae: 2.50 mm.

Diagnosis. The last larval stadium of *Oreiallagma quadricolor* is similar to known species of *Mesamphiagrion* and *Cyanallagma*. The ultimate stadium larvae of *M. gaianii* (De Marmels 1997), *M. laterale* and *M. tamaense* (De Marmels 2007), *C. bonariense* and *C. interruptum* (Bulla 1973) have been described to date. *Oreiallagma quadricolor* differs from all of them by (alternative states in parentheses): head more elongated transversely, *ca.* 1.80 times as wide as long (versus *ca.* 1.50–1.60), with occipital lobes less prominent (more prominent); two premental setae on each side (three to five); and dorso-posterior margin of S10 smoothly rounded (with a marked 'u' cleft). The left mandible lacks a 'y' tooth (with an accessory 'y' tooth at the base of outer most incisor in *M. laterale*, only species for which mandibles have been described), and front femur is longer than distance between compound eyes (shorter in *M. gaianii*, only species for which head and legs were illustrated).

Remarks. Caution should be exercised in applying differences we note here based on only two specimens. Whether differences we ascribe here between the larva of *Oreiallagma quadricolor*, *Cyanallagma*, and *Mesamphiagrion* are of generic value will be determined only when more larvae become known. As stated above, we suspect all species of *Oreiallagma* breed in phytotelmata and their relatively long abdomen is an adaptation for oviposition in deep containers (as for species of Pseudostigmatidae, *Bromeliagrion* De Marmels 2005, *Diceratobasis* Kennedy 1920, and *Leptagrion*).

Biology. Larvae found in water-filled bromeliad reservoirs (Figs. 110–111).

Distribution. Peru (Cusco Dept.), from 2250 to 2300 m above sea level (Fig. 104).

Oreiallagma thelktion (De Marmels 1997) comb. nov.

Figures 5; 8a; 29; 49; 86; 91; 104

Cyanallagma thelktion De Marmels 1997: 138–139, 152–156, figs. 7, 13, 19, 31, 38, 43, 49, 63, 64, 70, 82; in key for northern *Cyanallagma* species, description of male and female, illustrations of male S10, genital ligula, posterior lobe of prothorax of male and female, pterothorax, FW pt, male S6–10 and female S8–10, map).

Tsuda 2000: 31 (synonymic list).

Types: ♂ holotype in MIZA (not examined); 4 ♂ paratypes, 1 ♀ paratype (MIZA); 1 ♂ paratype (RWG) (examined).

Specimens examined.: VENEZUELA. Mérida State: Monte Zerpa, Santa Rosa Experimental Station, 29.iii.1992, C. Chaboo leg., 1 ♂ **paratype** (RWG).

Characterization. Medial lobe of male posterior lobe of prothorax heart-shaped, markedly constricted at base, with a moderate medial concavity on posterior margin, and with each lateral lobe bilobate (Fig. 29a; as in *O. prothoracicum*); of female not constricted at base and with moderate medial concavity on posterior margin (Fig. 29b). Distal segment of genital ligula (Fig. 49) wider at apex than at base (unique), with a pair of latero-apical lobes recurved and directed basally, a small sclerotized latero-medial lobe, and two ental

membranous transverse folds, one connecting latero-medial lobes and the second basal to them (as in *O. acutum* and *O. quadricolor*), the latter medially projected into an inner process (unique; Fig. 49c). Dorsal process of male cercus shorter than ventral process, digitiform, and pointed (Figs. 86; 91; unique). Male dorsum of S1–3 reddish orange to dark brown; of S4 reddish orange to black; of S5–7 and S10 black; of S8–9 blue (Fig. 5). Female dorsum of S2–3 orange; of S4–7 and S10 successively darker brown; of S8 black with posterior blue spot; of S9 blue with anterior black spot.

Diagnosis. This species, unique by cercus morphology, is diagnosed under *O. acutum*.

Biology. Adults collected in the neighborhood of ponds rich in riparian vegetation in Trujillo State (De Marmels 1997) and within cloud forest away from water in Táchira state (De Marmels *pers. comm.*); larva unknown, although we suspect that like *O. quadricolor* it will be found to breed in phytotelmata.

Distribution. Venezuela (Trujillo, Mérida, and Táchira States), from 1650 to 2050 m above sea level (Fig. 104).

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