

# Rediscovery of *Mesagrion leucorrhinum* (Zygoptera: Megapodagrionidae): a "formal" description of female and ultimate stadium of larva with notes on habits

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(Received 6 October 2010; final version received 14 February 2011)

Adult female and ultimate stadium larva of *Mesagrion leucorrhinum* are formally described and illustrated based on material from three locations in Antioquia, Meta and Cundinamarca Departments, Colombia. The species is sexually dimorphic. The  $\circ$  is distinguishable from other related genera by a pair of notches in the prothoracic anterior lobe and shares with *Heteropodagrion* and *Dimeragrion* females a yellowish, scarcely sclerotized region dorsally between the posterior margin of S7 and anterior border of S8. The larva is very similar to *Heteropodagrion*. Differences for separating them are: the pro-, meso- and metathoracic supracoxal processes are less prominent in *Mesagrion*, and the length of the terminal filament of the middle gill is notably longer in *Mesagrion*. The specimens were also compared with other related genera. Observations on habits are added.

La Hembra y la larva en último estadio de *Mesagrion leucorrhinum* son formalmente descritas e ilustradas basadas en material de Colombia de tres localidades en los departamentos de Antioquia, Meta y Cundinamarca. Existe marcado dimorfismo sexual en la especie. La  $\varphi$  es distinguible de otros géneros relacionados por un par de muescas en el lóbulo anterior del protórax, dorsalmente presenta en el borde posterior del S7 y base del S8 una zona escasamente esclerotizada de color amarillo, similar a la que se observa en hembras de *Heteropodagrion* y *Dimeragrion*. La larva es muy similar a la de *Heteropodagrion*. Diferencias para separarlas son: los procesos supracoxales en pro-, meso- y metatórax son menos promientes en *Mesagrion*, y el tamaño del filamento terminal en la branquia media es marcadamente más largo en *Mesagrion*. Los ejemplares fueron comparados con géneros relacionados. Adicionalmente se presentan datos sobre hábitos.

**Keywords:** Odonata; Damselfly; Megapodagrionidae; *Mesagrion*; *Heteropodagrion*; female; larva; Colombia

# Introduction

*Mesagrion* Selys, 1885 is a monotypic genus. Its sole species, *M. leucorrhinum*, was known only from the male until recently. The female was diagnosed and illustrated by Garrison et al. (2010) but not formally described. This genus is endemic to the central-eastern sector of the Colombian

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Andes. In addition to the type locality (Cristalina, eastern slopes of the central Cordillera, Antioquia Department) new findings have been made at other places, namely Alban, Chirajara and Guayabetal (Cundinamarca Department) and Vereda La Victoria (Villavicencio, Meta Department), significantly expanding the known distribution of the species. It has been considered of conservation interest under the standards of International Union for Conservation of Nature (IUCN) (Paulson, 2004) due to advanced habitat deterioration and poor knowledge about its reproductive biology and population ecology. The phylogenetic position of the genus is unknown, but a relationship with *Heteropodagrion* Selys has been proposed based on adult morphology (Garrison & von Ellenrieder, 2005). Behaviorally, *Mesagrion* is one of the few representatives in the family that closes its wings when perched (Donnelly, 1992), a feature shared in the New World only with *Heteropodagrion*, *Paraphlebia* Selys in Hagen, and *Thaumatoneura* McLachlan (Garrison et al., 2010).

#### Material and methods

Terminology follows Westfall and May (1996) for body characters, Riek and Kukalová-Peck (1984) for wing vein nomenclature, and Watson (1956) for larval mandibular formula. All dimensions are given in millimeters and were made with a calibrated ocular micrometer. Illustrations were made with the help of a camera lucida coupled to a Wild M-8 stereoscope and are not to scale. Specimens are deposited at Universidad del Atlántico Región Caribe (UARC), Barranquilla, Atlántico, Colombia and at the Museo del Instituto de Zoología Agrícola MIZA, Maracay, Aragua, Venezuela. Abbreviations: S = abdominal segment (e.g. S7 = abdominal segment 7).

# **Description of female**

#### Material examined

Fifteen φφ: COLOMBIA: Cundinamarca Department, Guayabetal, altitude 1270 m, 1 φ, 10 December 2007, L.A. Pérez, deposited at UARC, Barranquilla, Atlántico, Colombia; 1 φ same locality, but 13 June 2008, L.A. Pérez, deposited at the Museo del Instituto de Zoología Agrícola (MIZA), Maracay, Aragua, Venezuela. 13 φφ same locality, but 7 February 2009, L.A. Pérez, deposited at Universidad del Atlántico Región Caribe (UARC), Barranquilla, Atlántico, Colombia. Overall coloration, morphology and wing venation of female are very similar to male (Ris, 1918, Garrison & von Ellenrieder, 2005) (Figure 1a–c).

## Head (Figure 2a)

Labrum rounded, yellow with black anterior margin, anteclypeus yellow, postclypeus yellow with dark stripe along posterior margin (presumably showing varying degree of color intensity according to individual maturity), genae greyish-brown, antefrons shining black and flat, frontal edge prominent with long hairs on both sides, vertex black, postocular spots absent, occipital border brown with a few long hairs.

#### **Thorax**

Largely black with distinctive yellow stripes on lateral sclerites. Prothorax largely black (Figure 2b), anterior lobe yellow, laterally blackish, with two excisions on anterior margin, middle lobe with reddish dorsolateral spot, propleuron and procoxae dark, posterior lobe yellow with black center. Pterothorax with long hair pencil at external angle of each mesostigmal plate. Middorsal

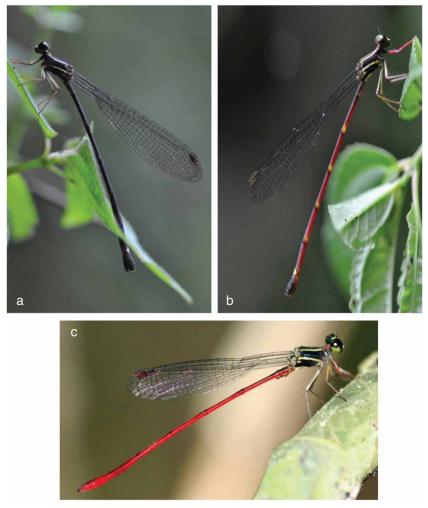


Figure 1. Mesagrion leucorrhinum: (a) female, lateral view, Alban (Cundinamarca), 6 July 2010; (b) immature female, lateral view, Alban (Cundinamarca), 6 July 2010; (c) male, lateral view, Rio Claro (Antioquia), 4 July 2009. All Photos by LP.

carina black, mesepisternum with complete yellow antehumeral stripe, of roughly same width over its entire length, mesinfraepisternum black, mesocoxa black, metepisternum black with complete yellow stripe which is curved towards the metapleural suture. Metinfraepisternum black, metacoxae black. Metepimeron black with yellow spot at metapleural suture; in ventral view metathorax completely yellow. Legs with femora black on dorsal surface, ventral surface reddish, more intense on forelegs, in mature specimens yellowish; inner row of hind femora armed with eight setiform spurs approximately of same size and a little longer than the space between them. Tibiae yellowish, those of hind legs armed with eight setiform spurs (inner row) decreasing distally, but first, second and third spurs of same size. Tarsal claw with inner tooth approximately half size of tip.

## Wings

Wings hyaline, with margins smoky at anal region, venation black, Pt reddish (brownish in immature specimens), of same shape and size in both wings, inferior margin covering less

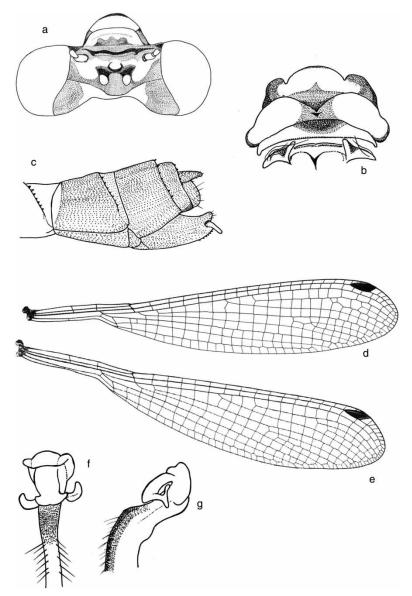


Figure 2. Morphological details of *Mesagrion leucorrhinum*. Female (a) head, dorsal view; (b) prothorax, dorsal view; (c) fore wing; (d) hind wing; (e) distal portion of abdomen, lateral view. Male (f) genital ligula, ventral view; (g) genital ligula, lateral view.

than two cells, proximal margin very oblique. Petiolation reaching level of arculus, no supplementary sectors between RP2 and IR2. Fw (Figure 2c) 27–31 mm, usually with two complete antenodals, occasionally one incomplete supernumerary Ax, 18–22 postnodals, IR2 arising beyond first Px, RP2 arising between sixth and eighth Px; RP3 arising at or immediately beyond subnodus, CuP close to level of first primary Ax, CuA arising between second Ax and nodus. Hw (Figure 2d) 28–31.5mm, two complete antenodal crossveins, 17–20 Px, RP2 arising between fifth and sixth Px, RP3 arising right before subnodus. IR2 arising at first postnodal.

#### Abdomen

In immature specimens abdominal segments scarlet red with distal yellow rings and narrow yellow mid-dorsal line; mature specimens with greyish-brown abdomen. In dorsal view, between end of S7 and anterior margin of S8, a distinctive yellowish, scarcely sclerotized region. No vulvar spine on S8, basal plate large. Posterior gonapophyses slightly surpassing tips of cerci (Figure 2e).

# Diagnostic remarks

We observed that young females of M. leucorrhinum are identical to males in coloration in life, with striking red color and yellow distal rings on abdominal segments, and red fore legs. The red abdomen and the yellowish portion between S7 and S8 are very distinctive, and together with the black and yellow color pattern of labrum and clypeus easily distinguish the species in its natural environment. A pair of notches in the prothoracic anterior lobe distinguishes female M. leucorrhinum from similar species, such as H. superbum.

#### Additional notes on males

Male genital ligula with inner fold vestigial (Figure 2f, g), shaft of genital ligula sclerotized to middle region, with 6-7 setae on each side. Apical segment membranous, tip convex, notched and expanded, in lateral view with bilobulated trumpet-shaped extensions, closely apressed to middle region of ligula.

## **Description of larva**

#### Material examined

1 ♂ ultimate stadium exuviae, 1 ♂, 4 ♀ ultimate stadium larvae, COLOMBIA: Cundinamarca Department, Guayabetal, altitude 1270 m, 1 g, 10 December 2007, L. A. Pérez. Other material considered: 13 specimens of early stadia, same data, preserved in ethanol.

Larva yellow-ochraceous with irregular, dark spots on thorax and abdomen (Figure 3a).

## Head

Head slightly wider than meso- and metathorax, antenna curved with seven segments, the two basal segments dorsally darker and with abundant hairs. Labium short, almost square (Figure 3c), base of prementum at rest located between first pair of coxae, in dorsal view with slightly curved row of very small transverse ridges on each side. Middle lobe slightly convex, with blunt denticles (Figure 3d), median cleft shallow, in dorsal view palpal lobe without setae or spines, in ventral view with long and thin hairs; three palpal hooks, the medial one longest, basal hook shortest; mandibles with incisor and molar teeth; formula:  $L1 + 2345 \ O \ a \ (m^{1,2,3,4,5}) \ b \ b' \ (1 < 3 < 2 <$ 4 < 5)/R1 + 2345 y a b (1 < 3 < 2 < 4 < 5) in both mandibles a > b (Figure 3e–g); molars number vary between five and seven (two specimens with seven molars, one with six molars and one with five molars), posterior margin of compound eye with sinuosity, frons flat.

# Thorax

Prothorax laterally black, flat sides forming a prominent keel, armed anterolaterally with two small but distinct supracoxal processes, of which the posterior process is larger. Mesothorax pale with

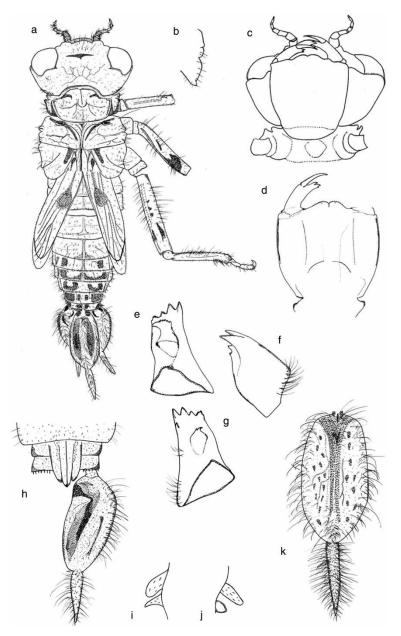


Figure 3. Final stadium larva of *Mesagrion leucorrhinum*. (a) Habitus; (b) lateral margin of meso- and metathorax; (c) head, ventral view; (d) labium and left labial palp, dorsal view; (e) left mandible, medial view; (f) left mandible, posterior (ventral) view; (g) right mandible, medial view; (h) distal segments of female abdomen showing gonapophyses and left gill, ventral view; (i) male cerci, mediodorsal view; (j) male cerci, lateral view; (k) median gill, dorsal view.

low, rounded lateral process in the middle region. Metathorax pale with prominent laterodistal processes (Figure 3b). Diverging wing pads extending to end of S9 with pattern of dark spots at base, legs short, hind femur extending backwards parallel to abdomen to posterior margin of S7. Femur and tibia laterally thickened with distinguishable carinal margins, armed with hairs and spines.

#### Abdomen

Short, S1–8 with prominent lateral keels and long hairs, S9 and S10 constricted and narrow. Female gonapophyses with rounded tips, surpassing posterior margin of S10, without hairs or spines (Figure 3h). Male gonapophyses not obvious in last stadium, cercus kidney-shaped with dorsal margin beset with small setae, paraproct ventrally flat and lobed (Figures 3i, j). Caudal gills not petiolated, without dorsal keels, tracheation not evident; epiproct with well developed lateral keels; lateral and middle gills with articulated terminal filament and with dense hair cover (Figure 3k), terminal filament in middle gill approximately twice the size of lateral ones.

#### Discussion

Reviewing descriptions of other Megapodagrionidae larvae, the species most closely resembling M. leucorrhinum is Heteropodagrion sanguinipes (Tennessen, 2010). Characters shared between these two genera are: presence of a slightly curved row of very small transverse ridges on each side of prementum, and presence of pro-, meso- and metathoracic processes (more prominent in Heteropodagrion). Superficial similarities with the larva of Sciotropis cyclanthorum (Rácenis, 1959) described by De Marmels (2004) may be noted. The most noticeable differences between other related genera are presented in Table 1.

The classification based on gill morphology by Kalkman, Choong, Orr and Schütte (2010) and redefined by Tenessen (2010) is here reviewed. Reexamining larvae of Sciotropis, Heteropodagrion and Dimeragrion and comparing them with descriptions of all neotropical species known to date, it becomes evident that the terminal filament of the middle gill can have two patterns: one group, consisting of Dimeragrion, Heteragrion, Oxistigma and Philogenia, has unarticulated terminal filaments; a second group, which includes Heteropodagrion, Hypolestes, Paraphlebia, Mesagrion, Thaumatoneura and Sciotropis, has articulated terminal filaments, each with a constriction at its base. Sciotropis, exceptionally, lacks a terminal filament on the middle gill, a condition it shares with some genera of the old world, namely *Caledopteryx* (Lieftinck, 1976). Finally, a third group consisting of Teinopodagrion and probably Megapodagrion lacks terminal filament on all gills.

In his description of tha larva of *Thaumatoneura*, Calvert (1915) refers to gill regeneration as a reason for the variability in the size of the filaments. However that is not the case for Mesagrion and Heteropodagrion. After examination of 19 and 15 specimens respectively, we found that proportion of filament length is absolutely stable, even in different stadia. This observation confirms the informative value to this character for separating larvae of *Heteropodagrion* and *Mesagrion*, with the terminal filaments in *Heteropodagrion* shorter than in *Mesagrion*. To corroborate this we measured and compared head width with the total length of terminal filaments, as these structures have proportional growth (Velasquez et al., 2009); see Table 2.

After verifying the mandibular formula in *Heteropodagrion sanguinipes* larvae, we compared results with Mesagrion leucorrhinum and concluded that both genera share the same number of incisors, while the number of molars varying individually between 5 and 7. Hence, this character is uninformative for separating the two genera.

Other genera, such as Argiolestes (Lieftinck, 1956), share morphological aspects of the labial palps and prementum with Mesagrion (three palpal hooks, the middle one longest) and absence of premental setae. However, differences in details of gill morphology (saccoid in Mesagrion and fan-like in Argiolestes) (Kalkman et al., 2010) suggest no close relation. The subquadrate shape of prementum and its short length are similar to Caledopteryx sarasini larvae (Lieftinck, 1976).

Table 1. Morphological features in Megapodagrionids larvae known to date, comparisons and differences between Tennessen's and Kalkman's classification systems and their contribution.

		Tennessen, 2010		Kalkman et al. 2010			This contribution		
						Long	Palpal	Gills	Thoracic
Taxa	References	Group 1	Group 2	Baloon	Fan	legged	teeth	filaments	processes
Dimeragrion percubitale	Demarmels, 1999	*			*		3	Not Articulate	Absent
Heteragrion albifrons	Novelo- Gutierrez, 1987	*		*			3	Not Articulate	Absent
Heteragrion alienum	Novelo- Gutierrez, 1987	*		*			3	Not Articulate	Absent
Heteragrion aurantiacum	Santos, 1968	*		*			3	Not Articulate	Absent
Heteragrion bariai	Demarmels, 2004	*		*			3	Not Articulate	Absent
Heteragrion breweri	Demarmels, 2004	*		*			3	Not Articulate	Absent
Heteragrion chlorotaeniatum	Demarmels, 2004	*		*			3	Not Articulate	Absent
Heteragrion consors	Costa & Santos, 1999	*		*			3	Not Articulate	Absent
Heteragrion erythrogastrum	Ramirez, 1992	*		*			3	Not Articulate	Absent
Heteragrion mitratum mitratum	Demarmels, 2004	*		*			3	Not Articulate	Absent
Heteragrion tricelulare	Novelo- Gutierrez, 1987	*		*			3	Not Articulate	Absent
Heteropodagrion sanguinipes	Tenessen, 2010	*		*			3	Articulate	Present
Hypolestes clara	Needham, 1941; Westfall, 1996	*		*			3	Articulate	Present
Hypolestes trinitatis	Alayo- Soto, 1985	*		*			3	Articulate	Absent
Mesagrion leucorrhinum	This study	*		*			3	Articulate	Present
Oxistigma caerulans	Demarmels, 1987	*		*			3	Not Articulate	Absent
Oxistigma petiolatum	Geijskes, 1943	*		*			3	Not Articulate	Absent
Paraphlebia zoe	Novelo- Gutierrez, 2008	*		*			3	Articulate	Absent
Philogenia carrillica	Ramirez & Novelo- Gutierrez, 1994	*		*			3	Not Articulate	Absent
Philogenia cassandra	Demarmels, 1982	*		*			3	Not Articulate	Absent
Philogenia mangosisa	Bybee & Tenessen, 2008	*		*			3	Not Articulate	Absent
Philogenia peacocki	Ramirez & Novelo- Gutierrez, 1994	*		*			3	Not Articulate	Absent
Philogenia terraba	Ramirez & Novelo- Gutierrez, 1994	*		*			3	Not Articulate	Absent
Sciotropis cyclanthorum	Demarmels, 2004	*		*			3	Articulate, middle gill	Present/
• •								without filament	Prominent
Teinopodagrion caquetanum	Pérez- Gutierrez, 2007		*			*	3	Without filament	Absent
Teinopodagrion decipiens	Von Ellenrieder, 2006		*			*	3	Without filament	Absent
Teinopodagrion meridionale	Von Ellenrieder, 2006		*			*	3	Without filament	Absent
Teinopodagrion oscillans	Demarmels, 2001		*			*	3	Without filament	Absent
Teinopodagrion vallenatum	Pérez- Gutierrez, 2007		*			*	3	Without filament	Absent
Thaumatoneura inopinata	Needham 1911; Calvert, 1915	*		*			2	Articulate	Present

Cmaning	Hood width	Length of terminal	1137/171 *	C4- 4:
Species	Head width	filament in middle gill	HW/FL*	Stadium
H. superbum	3.41	0.86	397	Ultimate
	3.37	0.93	3.62	Ultimate
	3.41	0.89	3.83	Ultimate
	3.41	0.93	3.67	Ultimate
	3.37	1.03	3.27	Ultimate
	1.72	0.52	3.31	Early
	3.31	0.86	3.84	Ultimate
	3.31	0.86	3.84	Ultimate
	2.31	0.72	3.21	Early
M. leucorrhinum	3.24	1.27	2.55	Ultimate
	3.17	1.27	2.50	Ultimate
	3.21	1.24	2.59	Ultimate
	3.24	1.31	2.47	Ultimate

Table 2. Measures of head width and length of terminal filament in middle gill of larvae of Heteropodagrion superbum and Mesagrion leucorrhinum.

Note: \*Ratio of head width to middle filament length.

## Habitat notes

At localities where *Mesagrion leucorrhinum* occurs, a close relationship with small waterfalls of forest streams between 500 and 1300 m was observed.

In their habitat individuals can be numerous, without evidencing competition behavior for space. Flight is smooth, females and males are active without disturbing or aggressive behavior. It is still necessary to clarify the details of reproductive biology, but we presume that oviposition takes place on the rock surfaces washed by waterfalls (splash zone). Larvae are camouflaged through their color which is similar to the rock colors, moss and detritus on which they were found. When disturbed, they move rapidly with lateral wave movements, like Plecoptera larvae.

## Acknowledgements

We wish to express our warm thanks to Prof. Dr Jürg De Marmels for the critical reading and suggestions for improving this manuscript, to Natalia von Ellenrieder and an anonymous referee for the critical revision of a former draft.

## References

- Alayo Soto, R. (1985). Descripción de la náyade de Hypolestes trinitatis Gundlach (Odonata: Hypolestidae). Ciencias Biológicas, 14, 111–113.
- Bybee, S.M., & Tenessen, K.J. (2008). Description of the female and nymph of *Philogenia mangosisa* from southern Ecuador (Odonata: Megapodagrionidae). 2ootaxa, 1787, 63-68.
- Costa, J.M., & Santos, T.C. (1999). Odonata da Marambaia (Ilha e Restinga), Rio de Janeiro, Brasil. Resultado das expedições do Museu Nacional pelo convênio entre a Universidade Federal Rural do Rio de Janeiro e a Marinha do Brasil, com a descrição de Heteragrion consors Hagen in Selys, 1862 (Zygoptera: Megapodagrionidae). Contrib.Avuls. sobre Hist. Nat. Bras; Sér. Zool., 5, 1-7. Seropédica.
- De Marmels, J. (1982). Dos náyades nuevas de la familia Megapodagrionidae (Odonata, Zygoptera). Boletin de Entomologia Venezolana (Nueva serie), 2, 89–93.
- De Marmels, J. (1987). On the Type specimens of some neotropical Megapodagrionidae, with a description of Heteragrion pemon spec. nov. and Oxystigma caerulans spec. nov. from Venezuela (Zygoptera). Odonatologica, 16, 225-238, figs 1-51.
- De Marmels, J. (1999). A new species of Dimeragrion Calvert 1913 from Pantepui, Venezuela (Odonata: Megapodagrionidae). Boletin de Entomología Venezolana (Nueva serie), 14, 27–36.
- De Marmels, J. (2004). Heteragrion makiritare sp. nov., with descriptions of hitherto unknown females and larvae of other species from Venezuela (Odonata: Megapodagrionidae, Lestidae). International Journal of Odonatology, 7, 439-458.

- Donnelly, T.W. (1992). The Odonata of central Panama and their position in the neotropical odonate fauna, with a checklist, and descriptions of new species. In D. Quintero & A. Aiello (Eds.) *Insects of Panama and Mesoamerica: selected studies* (pp. 52–90). Oxford: Oxford University Press.
- Dos Santos, N.D. (1968). Contribuição ao conhecimento da fauna do Estado da Guanabara. 65. Descrição da ninfa de "Heteragrion aurantiacum" Selys, 1862 e notas sobre o imago (Odonata, Megapodagriidae). Atas de Sociedade de Biologia do Rio de Janeiro, 12, 13–15.
- Garrison, R.W., & von Ellenrieder, N. (2005). Neuragrion mysticum (Odonata: Megapodagrionidae) demystified. Canadian Entomologist, 137, 169–163.
- Garrison R.W., von Ellenrieder, N. & Louton, J.A. (2010) Damselfly Genera of the New World. An Illustrated and Annoated Key to the Zygoptera. Baltimore (MD): John Hopkins University Press, 490 pp.
- Geijskes, D.C. (1943). Notes on Odonata of Surinam. IV. Nine new or little known Zygopterous nymphs from inland waters. Annals of the Entomological Society of America 36: 165–184.
- Kalkman, V.J., Choong, Ch.Y., Orr, A.G. & Schütte, K. (2010). Remarks on the taxonomy of Megapodagrionidae with emphasis on the larval gills (Odonata). *International Journal of Odonatology*, 13, 119–135.
- Lieftinck, M.A. (1956). Revision of the genus *Argiolestes* Selys (Odonata) in New Guinea and the Moluccas, with notes on the larval forms of the family Megapodagrionidae. *Nova Guinea* (*N.S.*), 7, 59–121.
- Lieftinck, M.A. (1976). The dragonflies (Odonata) of New Caledonia and the Loyalty Islands. Part. 2. Immature stages. *Cahiers O.R.S.T.O.M. Série Hidrobiologique 10*, 165–200.
- Needham, J.G. (1941). Life history notes on some West Indian coenagrionine dragonflies (Odonata). *Journal of Agriculture of the University of Puerto Rico*, 25, 1–18.
- Novelo-Gutierrez, R. (1987). Las náyades de *Heteragrion albifrons*, H. alienumy H. tricellulare (Odonata: Megapodagrionidae); su descripción y hábitos. Folia Entomológica Mexicana, 73, 11–22.
- Novelo-Gutierrez, R. (2008). Description of the larva of *Paraphlebia zoe*, 1861. (Odonata: Megapodagrionidae). *Zootaxa*, 1876, 29–34.
- Paulson, D.R. (2004). Critical species of Odonata in the neotropics. IUCN Regional Report. Guardians of the watershed. Global status of dragonflies: critical species, threat and conservation. *International Journal of Odonatology*, 7, 163–188.
- Rácenis, J. (1959). Notes taxonómicas sobre la familia Megapodagrionidae (Odonata: Zygoptera) con la sinopsis de las especies venezolanas. *Acta Biologica Venezuelica* 20(30): 335–367.
- Ramírez-Ulate, A. (1992). Description and natural history of Costa Rican dragonfly larvae. 1. *Heteragrion erythrogastrum* Selys, 1886 (Zygopetra: Megapodagrionidae). *Odonatologica*, 21, 361–365.
- Ramírez-Ulate, A. & Novelo-Gutiérrez, R. (1994). Megapodagrionidae (Odonata: Zygoptera) de México y Centroamerica I. Las náyades de *Philogenia carrilica, P. peacocki y P. terraba. Acta Zoologica Mexicana (Nueva serie), 63,* 61–73.
- Riek, R.F., & Kukalová-Peck, J. (1984). A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta:Odonatoidea) and basic character states in pterygote wings. Canadian Journal of Zoology, 62, 1150–1166.
- Ris, F. (1918). Libellen (Odonata) aus der Region der amerikanischen Kordilleren von Costa rica bis Catamarca. *Archiv fuer Naturgeschichte A, 9*, 1–197.
- Selys-Longchamps, E. (1885). Programme d'une revision des Agrionines. Comptes Rendus de la Societe Entomologique de Belgique, 29: cxli-cxlvi (1–8 separate).
- Tennessen, K. (2010). The madicolous nymph of *Heteropodagrion sanguinipes* Selys (Odonata: Megapodagrionidae). *Zootaxa*, 2531, 29–38.
- Velásquez, N., Bautista, K., Guevara, M., Ramírez, D., Realpe, E. & Pérez-Gutiérrez, L.A. (2009). Larval development and growth ratio of *Ischnura cruzi* (Zygoptera: Coenagrionidae), with description of last larval instar. *Odonatologica*, 38, 29–38.
- von Ellenrieder, N. (2006). The larvae of *Teinopodagrion decipiens* De Marmels and *T. meridionale* De Marmels (Zygoptera: Megapodagrionidae). *Odonatologica*, 35, 281–287.
- Watson, M.C. (1956). The utilization of mandibular armature in taxonomic studies of anisopterous nymphs. *Transactions of the American Entomological Society*, 81, 155–202.
- Westfall, M.J. & May, M.L. (1996). Damselflies of North America. Gainesville: Scientific Publishers.