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Blues for the red *Oxyagrion*: a redefinition of the genera *Acanthagrion* and *Oxyagrion* (Odonata: Coenagrionidae)

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Abstract

Examination of diagnostic features for all known species of *Acanthagrion* and *Oxyagrion* shows color pattern alone not to be a reliable diagnostic character. Both genera are redefined based on morphological characters, and some color pattern characters which further aid in their diagnoses. A preliminary phylogenetic analysis indicates both genera are monophyletic. They are distinguished from other genera of neotropical coenagrionids by their decumbent cerci with a dorso-basal tubercle in males correlated with the presence of paired mesepisternal fossae in females. *Acanthagrion* and *Oxyagrion* can be unequivocally distinguished from each other by the minimum width of abdomen, shape of distal portion of genital ligula and position of lateral lobes of genital ligula relative to flexure in males, development of mesepisternal carinae and of dark mid-dorsal and humeral stripes in females, and ratio of caudal lamellae to abdominal length in ultimate larval instars. According to our redefinition we transfer *A. ablutum* (a 'blue' species), *A. hermosae* and *A. imeriense* to *Oxyagrion*, and *O. egleri* to *Acanthagrion*. The generic placement of '*A.*' *taxaense* and '*O.*' *pseudocardinale* is deemed doubtful.

Resumen

Examinación de caracteres diagnósticos en todas las especies de *Acanthagrion* y *Oxyagrion* muestra que el patrón de coloración por si mismo no es un carácter diagnóstico confiable. Ambos géneros son redefinidos sobre la base de caracteres morfológicos, y algunos caracteres de coloración que proporcionan caracteres adicionales para sus diagnosis. Un análisis filogenético preliminar indica que ambos géneros son monofiléticos. Se distinguen de otros géneros de coenagrionidos neotropicales por sus cercos decumbentes con un tubérculo dorso-basal en machos correlacionado con la

presencia de fosas mesepisternales pares en hembras. *Acanthagrion* y *Oxyagrion* pueden ser inequívocamente reconocidos por el ancho mínimo del abdomen, forma de la porción distal de la lígula genital y posición de los lóbulos laterales de la ligula genital relativa a la flexura en machos, desarrollo de las carenas mesepisternales y de rayas oscuras medio-dorsales y humerales en hembras, y proporción de laminillas caudales respecto al largo abdominal en últimos estadios larvales. De acuerdo a nuestra redefinición transferimos *A. ablutum* (una especie 'azul'), *A. hermosae* y *A. imeriense* a *Oxyagrion*, y *O. egleri* a *Acanthagrion*. La posición genérica de '*A.*' *taxaense* y '*O.*' *pseudocardinale* es cuestionada como dudosa.

Introduction

Acanthagrion and *Oxyagrion*, two speciose coenagrionid genera from the Neotropical region, were described by Selys in his 'Synopsis des Agrionines' (1876). He provided the following characters for *Acanthagrion* [current vein terminology in square brackets]: inferior sector of triangle [CuP & AA'] originating at the postcostal basal vein [CuP] at least in Hw; 10-14 (occasionally 8) postcubitals [postnodals] in Fw; pterostigma similar in all four wings of both sexes; postocular spots present; labium split at apical ¼ with branches needle-shaped, distant; posterior margin of prothorax ordinarily straight centrally; abdomen slender and long; legs regularly spined (generally 6 beneath posterior tibiae); male coloration bronzy and blue or greenish, with S8 or S9 or S10 blue; margin of S10 more or less prolonged or straight, or forming an emarginated flap; cerci generally lamellar, inclined with a basal internal branch; female vulvar spine generally needle-shaped and coloration nearly similar. *Oxyagrion* was described as follows: inferior sector of triangle [CuP & AA'] originating at the postcostal basal vein [CuP]; 10-14 (occasionally 8) postcubitals [postnodals] in Fw, pterostigma similar in all four wings of both sexes; no postocular spots; labium split at apical ⅓ or ¼, its branches a little distant; posterior margin of prothorax rounded, a little straight; abdomen normal or long; legs regularly spined (5-8 beneath posterior tibiae); male body and pterostigma coloration reddish (S8-9 or S10 often blue); margin of S10 more or less straight or slightly emarginated; cerci ordinarily lamellar, inclined basally with an internal branch; female vulvar spine strong, pointed.

Selys (1876) considered these two groups to constitute a natural assemblage, and he separated them only to facilitate determination – blue or green color with postocular spots corresponding for *Acanthagrion*, and dominant red coloration and absence of postocular spots for *Oxyagrion*.

In the ensuing years several new species have been added and some have been transferred to other genera, and the generic limits have become increasingly vague. Kennedy (1920) transferred *A. acutum* Ris, 1918, *A. cheliferum* Selys, 1876, *A. interruptum* Selys, 1876 and *A. laterale* Selys, 1876 to his newly erected genus *Cyanallagma*. Leonard (1977) revised *Acanthagrion*, transferring also *A. ambiguum* Ris, 1904, *A. lindneri* Ris, 1928, *A. nigrinuchale* Selys, 1876 and *A. trimaculatum* Selys, 1876 to *Cyanallagma*, and Costa (1978) revised *Oxyagrion*. Leonard (1977) mentioned the absence of an internal fold (transverse membranous fold proximal to flexure) in the genital ligula, and presence of distinct thoracic pattern and postocular

spots as diagnostic for separating *Acanthagrion* from *Oxyagrion*. Costa (1978) demonstrated that the presence or absence of postocular spots was variable, stated that the only reliable character separating *Oxyagrion* from *Acanthagrion* was their red coloration and that a revision of all *Acanthagrion* species was necessary to redefine the boundaries between these two genera. De Marmels (1984: 24) characterized *Oxyagrion* by red coloration of male, lack of postocular spots, absence of extended black areas on head and mesepisternum and both with frequent presence of stippling, more or less clearly bilobate apex of genital ligula, absence of mesepisternal fossae in females of some species, and exclusively South American distribution, with all centers south of the Amazon. For *Acanthagrion* he mentioned: predominant color blue or green, postocular spots present and well defined, black areas on head and black stripes (brown in females) on mesepisternum with no dark stippling on head and thorax, distal genital ligula segment not bilobate, mesepisternal fossae present in all known females, and distribution from Mexico to Argentina, with most centers in the Amazonian and circum-Amazonian (Andean) region. However, he noted exceptions forming intermediates, such as *A. ablutum* (ill defined pale postocular spots), *A. hermosae* (no pale postocular spots and presence of red), *A. chararum* (ill defined pale postocular spots), *O. cardinale* (blue color and no stippling), *O. fluviatile* (both sexes blue), *O. egleri* (distributed north to the Amazon).

Currently there are 65 species described for these two genera; 42 in *Acanthagrion* and 23 in *Oxyagrion*, and their assignment to either genus seems to be arbitrary in several cases. Not all species included under *Acanthagrion* are blue with pale postocular spots, nor are all those under *Oxyagrion* red lacking pale postocular spots. Genital characters previously proposed do not hold true, since not only *Acanthagrion* (as suggested by Leonard 1977) but also *Oxyagrion* species lack a true internal fold in male genital ligula (De Marmels 1997: 137), and distal apex of male genital ligula is variable (proposed by De Marmels 1984) with bilobate and not bilobate states found in both genera (e.g. Fig. 5; not bilobate in *Oxyagrion haematinum*, *O. simile* and *O. zielmae*, and bilobate in *Acanthagrion adustum, A. chacoense, A. fluviatile, A. indefensum, A. minutum, A. quadratum, A. risi, A. rubrifrons, A. tepuiense* and *A. yungarum*).

Our purpose here is to re-diagnose both genera so that all of their described species can be unequivocally assigned to either one of them.

Material and methods

Examination of specimens

All characters were illustrated with the aid of a camera lucida. Measurements are in mm, and total length and abdominal length do not include appendages. Wing terminology follows Riek & Kukalová-Peck (1984), and genital ligula Kennedy (1916). We examined adults of 77% of all described species and all original descriptions and revisions, and performed a cladistic analysis based on some selected characters of both adults and larvae. Species examined are asterisked in species lists and are deposited in following collections: British Museum of Natural History, London, UK; Fundación Miguel Lillo, Tucumán, Argentina; Departamento Científico Entomología, Museo de

La Plata, Argentina; Florida State Collection of Arthropods, Gainesville, Florida, USA; Museu Nacional Río de Janeiro, Rio de Janeiro, Brazil; N. von Ellenrieder personal collection, Salta, Argentina; R.W. Garrison personal collection, Sacramento, California, USA, University of Michigan, Museum of Zoology; detailed locality information is available from the authors. Larval character states were extracted from larval descriptions referenced in the species lists as [L:]. Based on our redefinitions we transfer some species between these two genera, and deem the status of some others as doubtful; rationale for so doing follows generic diagnoses.

For the cladistic analysis we analyzed 16 characters of generic diagnostic value for 62 ingroup species and *Argia translata* Hagen in Selys, 1865 as outgroup, using the command mhennig*; bb* in Hennig86 (version 1.5). Character matrix is shown in Table 1. Species with high number of unknown states (43% or more) were excluded from the analysis (*A. latapistylum, A. taxaense* and *O. pseudocardinale*).

Characters

1 — Pale postocular spots: (0) present (Figs 8a-c); (1) absent
2 — Female mesepisternal fossae: (0) absent (Figs 6a, c, f); (1) present (Figs 6b, d, e, g, h)
3 — Well defined female mesepisternal carinae between mesostigmal plates and medio-dorsal carina: (0) present (Figs 6a-d); (1) absent (Figs 6e-h)
4 — Well defined dark (usually black, sometimes reddish brown) mid-dorsal stripe in males: (0) present (Figs 9a, b); (1) absent (as in Fig. 9c)
5 — Well defined dark (usually black, sometimes reddish brown) mid-dorsal stripe in females: (0) present (as in Figs 9a, b); (1) absent (Fig. 9c)
6 — Well defined dark (usually black, sometimes reddish brown) humeral stripe: (0) present (Figs 9a, b); (1) absent (Fig. 9c)
7 — CuP: (0) reaching CuP & AA' (Fig. 1a); (1) reaching hind margin of wing (Fig. 1b)
8 — Flexure of male genital ligula: (0) shorter; ligula distal segment considerably longer than flexure height in lateral view (Figs 5a, g-l); (1) longer; ligula C-shaped, distal segment about as long as flexure height in lateral view (Figs 5b-f)
9 — Lateral lobes of male genital ligula: (0) absent (Fig. 5a); (1) distal to flexure, on distal portion of ligula (Figs 5g-l); (2) at level of flexure, on posterior surface of ligula (Figs 5b-f)
10 — Male abdomen: (0) robust (Figs 4a-e; 0.4-0.65 minimum width at S3); (1) slender (Figs 4f-j; 0.25-0.35 minimum width at S3)
11 — Dorsum of S3-6: (0) entirely or mostly black (Figs 4f-i); (1) lacking black or with black limited to posterior ring, band or spot covering less than ⅓ of segment length (Figs 4a-d)
12 — Female vulvar spine on sternum S8: (0) absent (Fig. 7a); (1) present (Fig. 7b)
13 — Male cerci: (0) not slanting from base (Figs 2a, d); (1) slanting from base (Figs 2b-d, 3a-d)
14 — Dorso-basal tubercle on male cerci: (0) absent (Figs 2a, d); (1) present (Figs 2b, c)
15 — Larval caudal lamellae: (0) foliate, with width/length ratio 0.20 or more (Fig. 10a); (1): markedly lanceolate, with width/length ratio 0.18 or less (Fig. 10b)
16 — Larval caudal lamellae length/abdomen length: (0): less than 0.92 (Fig. 10a); (1): more than 1.00 (Fig. 10b)

Table 1. Matrix of 16 characters and 63 species. Species with identical coding coalesced. Question marks refer to unknown character states. All characters are listed and defined in the text.

Taxa / Characters:	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Outgroup																
Argia translata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthagrion																
adustum	0	1	1	0	0	0	1	0	1	1	0	1	1	1	1	1
(identical coding: *aepiolum*; *apicale*; *ascendens*; *vidua*)																
hildegarda	0	0	1	0	0	0	1	0	1	1	0	1	1	1	1	1
chararum	0	0	1	0	?	0	1	0	1	1	0	1	1	1	?	?
fluviatile	0	0	1	0	0	0	1	0	1	1	0	1	1	1	1	?
abunae	0	1	1	0	0	0	1	0	1	1	0	1	1	1	?	?
(identical coding: *chacoense*; *cuyabae*; *gracile*; *kennedii*; *lancea*; *obsoletum*; *peruvianum*; *phallicorne*; *quadratum*; *speculum*; *temporale*; *tepuiense*; *trilobatum*; *truncatum*; *virides-cens*; *yungarum*)																
longispinosum	0	1	1	0	0	0	1	0	1	1	0	0	1	1	?	?
(identical coding: *rubrifrons*)																
indefensum	0	1	?	0	?	0	1	0	1	1	0	1	1	1	1	1
(identical coding: *egleri*; *hartei*; *inexpectum*; *williamsoni*)																
minutum	0	1	?	0	?	0	0	0	1	1	0	1	1	1	1	1
dichrostigma	0	1	1	0	0	0	1	0	1	?	0	1	1	1	?	?
amazonicum	0	1	1	0	0	0	?	0	1	?	0	1	1	1	?	?
(identical coding: *jessei*; *peruanum*)																
floridense	0	?	?	0	?	0	1	0	1	1	0	?	1	1	?	?
Oxyagrion																
ablutum	0	1	0	0	1	1	1	1	2	0	0	1	1	1	0	0
basale	0	1	0	0	1	1	1	1	2	0	1	1	1	1	0	?
brevistigma	1	1	0	1	1	1	1	1	2	0	1	1	1	1	?	?
(identical coding: *tennesseni*)																
bruchi	1	1	0	1	1	1	1	1	2	0	0	1	1	1	0	0
chapadense	1	1	1	0	1	1	1	1	2	0	1	1	1	1	0	?
evanescens	1	1	0	1	1	1	1	1	2	0	1	0	1	1	0	0
fernandoi	1	1	?	0	?	1	?	1	2	0	1	1	1	1	?	?
haematinum	1	1	0	1	1	1	1	1	2	0	1	1	1	1	0	?
hermosae	1	1	?	0	?	1	?	1	2	?	0	1	1	1	?	?
hempeli	1	0	0	0	1	1	1	1	2	0	1	1	1	0	1	0
imeriense	0	1	0	0	?	0	1	1	2	0	1	1	1	1	0	0
impunctatum	0	1	0	1	1	1	1	1	2	0	1	1	1	1	0	?
(identical coding: *santosi*)																
machadoi	0	1	0	0	1	1	1	1	2	0	1	1	1	1	?	?
microstigma	1	0	0	1	1	1	1	1	2	0	1	1	0	0	1	0
miniopsis	1	1	0	1	1	1	?	1	2	?	1	1	1	1	?	?
pavidum	1	1	0	1	1	1	1	1	2	0	1	1	1	1	1	?
rubidum	1	1	1	1	1	1	1	1	2	0	1	1	1	1	0	0
simile	1	1	0	1	1	1	?	1	2	?	1	1	1	1	0	0
sulinum	1	1	0	0	1	1	1	1	2	0	0	1	1	1	0	?
sulmatogrossense	0	1	0	1	1	1	?	1	2	?	1	1	1	1	?	?
terminale	1	1	0	1	1	1	1	1	2	0	1	1	1	1	0	0
zielma	0	1	?	1	?	1	?	1	2	?	1	1	1	1	?	?

Results

Our preliminary phylogenetic analysis is designed only to test the monophyly of *Acanthagrion* and *Oxyagrion* and by no means attempts to solve infrageneric relationships among their species. Due to the numerous question marks for states of unknown females and larvae or doubtful states in male descriptions, our analysis resulted in a large number of most parsimonious trees (1,506; length 31, ci 54, ri 93), and because of the exclusion of characters of specific diagnostic value the strict consensus tree (length 54, ci 31, ri 81; Fig. 11) shows an unsolved basal polytomy for both genera. It indicates that both genera are monophyletic and that characters states unequivocally defining them are found in male genital ligula shape and position of the lateral projections of the accessory transverse lobes, and minimum male abdominal width. Though variable, color pattern is also valuable with certain restrictions.

Based on our redefinitions we transfer *O. egleri* back to *Acanthagrion*, and *A. ablutum*, *A. hermosae* and *A. imeriense* to *Oxyagrion*. We believe *A. latapistylum* most likely belongs to *Acanthagrion*, but its status requires confirmation pending examination of the types, and that '*Acanthagrion*' *taxaense* and '*Oxyagrion*' *pseudocardinale* likely do not belong to these genera, and we consider that their generic placement is currently uncertain pending examination of their types.

Acanthagrion Selys, 1876: 304 [60 reprint]

Type species: *Agrion gracile* Rambur, 1842 [Kirby 1890 by subsequent designation].

Diagnosis

Color pattern usually including dark black and pale light blue areas on head, thorax and abdomen. However, dark areas can be reddish brown in teneral specimens (observed in *A. cuyabae, A. gracile, A. hildegarda, A. lancea* and *A. longispinosum*), and in mature specimens of *A. fluviatile* and *A. rubrifons*, and pale areas are yellow to orange on head and thorax of *A. adustum, A. apicale, A. ascendens, A. kennedii, A. obsoletum* and *A. rubrifrons*. Head with rounded frons and postocular pale spots (Fig. 8a), which have irregular margins and are stippled with brown in *A. chararum*, *A. egleri* and *A. fluviatile* (Fig. 8b). Posterior prothoracic lobe straight or moder-

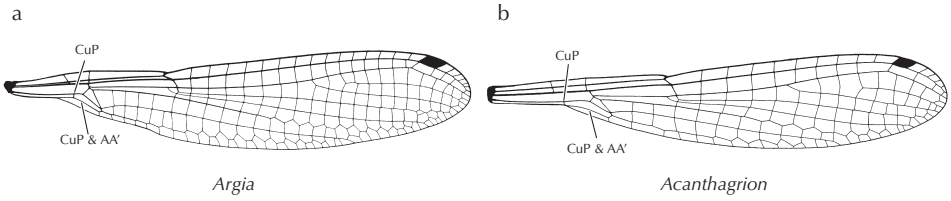


Figure 1: Fore wing — (a) *Argia translata* (AR, Jujuy, Arroyo Zanjón Seco); (b) *Acanthagrion peruvianum* (AR, Salta, Arroyo Yacuy).

ately bi- or trilobate (Fig. 6f); pterothorax with dark mid-dorsal and humeral stripes (Fig. 9a), though narrow and accompanied by brown spots in *A. egleri* (Fig. 9b), and several species also with a dark stripe over metepisternal-metepimeral sutures (*A. adustum, A. apicale, A. ascendens, A. kennedii, A. hartei, A. longispinosum, A. minutum, A. obsoletum, A. phallicorne* and *A. trilobatum*). CuP reaching hind margin of wing (Fig. 1b), except in *A. minutum*. Abdomen extensively dark dorsally (Figs 4f-j) with only apical segments (S7 or S8 to S9 or S10) dorsally pale (light blue, and red only in *A. egleri*). Female vulvar spine of sternum S8 present (as in Fig. 7b), except in *A. longispinosum*, *A. rubrifrons* and some *A. aepiolum* and *A. gracile*. Male abdomen slender with minimum width (at S3) of 0.25-0.35 mm in lateral view (Fig. 4f). Male cerci decumbent from their bases (Figs 2b, 3a, b), with a dorso-basal tubercle (Fig. 2b), correlated with presence of paired mesepisternal fossae in female (Figs 6g, h); only females of *A. chararum*, *A. fluviatile* and *A. hildegarda* lack fossae on mesepisterna (Fig. 6f). Female lacking well defined mesepisternal carinae between mesostigmal plates and medial carina (Figs 6f-h). Length of male genital ligula distal to flexure considerably longer than flexure surface and lateral lobes of distal segment located distal to flexure (Figs 5g-l).

Larvae: Caudal lamellae markedly lanceolate (Fig. 10b), with width/length ratio 0.18 or less, and longer than abdomen (1.02 or more; Fig. 10b) in all known larvae (20% of the species).

Distribution: South-central United States (Texas) to Central Argentina.

Habitat: Slow backwaters of streams and rivers, weedy ponds, and temporary pools.

Species included

A. abunae Leonard, 1977*
A. adustum Williamson, 1916 — [L: Geijskes 1943]*
A. aepiolum Tennessen, 2004— [L: Lozano et al. 2007]*
A. amazonicum Sjöstedt, 1918
A. apicale Selys, 1876 — [L: De Marmels 1992]*
  syn. *apicale descendens* Fraser, 1946
A. ascendens Calvert, 1909 — [L: Geijskes 1941]*
  syn. *luteum* Rácenis, 1958
A. chacoense Calvert, 1909
A. chararum Calvert, 1909*
A. cuyabae Calvert, 1909*
  syn. *cuyabae fimense* Calvert, 1909
  syn. *cuyabae freirense* Calvert, 1909
  syn. *leonardi* Jurzitza, 1980
A. dichrostigma De Marmels, 1985
A. egleri Santos, 1961*
A. floridense Fraser, 1946*
A. fluviatile (De Marmels, 1984) — [L: De Marmels 1990]*
A. gracile (Rambur, 1842)*
  syn. *gracile* var. *cuneatum* Selys, 1876
  syn. *gracile* var. *maculae* Sjöstedt, 1918

A. hartei Muzón & Lozano, 2005*
A. hildegarda Gloger, 1967 — [L: Muzón et al. 2001]*
A. indefensum Williamson, 1916 — [L: Geijskes 1943]*
A. inexpectum Leonard, 1977*
A. jessei Leonard, 1977
A. kennedii Williamson, 1916*
A. lancea Selys, 1876*
A. latapistylum Calvert, 1899
A. longispinosum Leonard, 1977*
A. minutum Leonard, 1977*
A. obsoletum (Förster, 1914)*
  syn. *leonora* Gloger, 1967
  syn. *luna* Ris, 1916
A. peruanum Schmidt, 1942
  syn. *deceptum* Leonard, 1977
A. peruvianum Leonard, 1977*
A. phallicorne Leonard, 1977*
A. quadratum Selys, 1876 — [L: Westfall & May 1996]*
A. rubrifrons Leonard, 1977*
A. speculum Garrison, 1985*
? *A. taxaense* Santos, 1965
A. temporale Selys, 1876*
A. tepuiense De Marmels, 1985*
A. trilobatum Leonard, 1977*
A. truncatum Selys, 1876*
A. vidua Selys, 1876 — [L: De Marmels 2007]*
  syn. *risi* Leonard, 1977
A. viridescens Leonard, 1977*
A. williamsoni Leonard, 1977*
A. yungarum Ris, 1918*

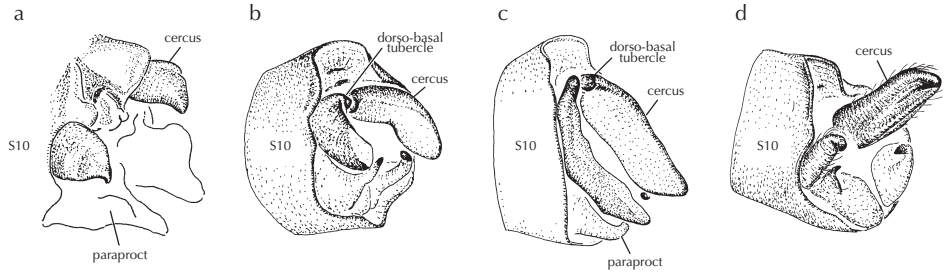


Figure 2: Male S10 in medio-dorsal view — (a) *Argia translata* (USA, Arizona, Maricopa; by RWG); (b) *Acanthagrion hildegarda* (AR, Buenos Aires, Arroyo N Matilde); (c) *Oxyagrion ablutum* (AR, Salta, Río La Caldera); (d) *O. microstigma* (BR, São Paulo, Vassununga).

Acanthagrion egleri Santos, 1961
(Figs 4f-j, 8b, 9b)

Acanthagrion egleri Santos, 1961: 1, figs 1-7 (description of male; illustrations of male S10 and genital ligula, prothorax, pterostigma); — Costa (1978: 40; mention of red color).
Oxyagrion egleri (Santos) — De Marmels (1984: 25; transfer to *Oxyagrion* based on Costa's 1978 comment).

Although this is the only species so far known for any of these two genera with apical portion of wings amber, and it is an 'atypical' *Acanthagrion* due to its red S8-10 and stippled pale postocular spots and thoracic dorsum (Figs 8b, 9b), we believe it belongs in *Acanthagrion* because of the structure of its genital ligula, with its portion distal to flexure considerably longer than flexure and lateral lobes situated distal to flexure (Fig. 5k) and its slender abdomen (minimum width 0.27 mm; Fig. 4f). Morphology of male cerci, high S10, simplified ligula structure, long wing petiolation (beyond CuP juncture) and high number of postnodals (13 in FW) would indicate a relationship with Leonard's (1977: 66) '*yungarum*' group. Female and larvae are still unknown.

Acanthagrion latapistylum Calvert, 1899

Acanthagrion latapistylum Calvert, 1899: 26, figs 1-3 (description of male and female; illustrations of male cerci); — Leonard (1977: 129; transcription of original description).

Calvert (1899) described this species based on a pair from Paraguay, deposited at the Museo Bernandino Rivadavia in Buenos Aires, Argentina, and apparently lost. His description of color pattern agrees with that of a typical *Acanthagrion*, and although drawings of male cerci are schematic and their description is incomplete – no mention of presence of basal tubercles is made – they seem similar to those of *A. abunae* and *A. jessei*. Like Leonard (1977), we chose to retain this species in *Acanthagrion*, pending examination of the genital ligula and other structural characters of the types. We excluded it from the cladistic analysis due to the high number of unknown character states.

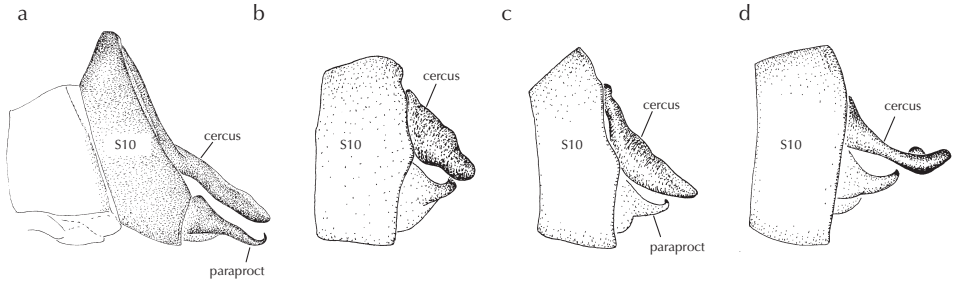


Figure 3: Male S10 in lateral view — (a) *Acanthagrion aepiolum* (AR, Salta, Arroyo del Medio); (b) *A. lancea* (AR, Salta, Dique Itiyuro); (c) *Oxyagrion ablutum* (AR, Salta, Río La Caldera); (d) *O. rubidum* (AR, Salta, Pulares).

'Acanthagrion' taxaense Santos, 1965

Acanthagrion taxaensis Santos, 1965: 60, figs 1-13 (description of male and female; illustrations of head, thorax, male S10 and genital ligula, female ovipositor); — Machado & Brescovit (2005: 95; presumed extinct).
Acanthagrion taxaense Santos — De Marmels (1984: 25; mention).

Santos' (1965) brief original description and schematic drawings are not sufficient to assign this species to a current genus. Although color pattern would be encompassed in that known for *Acanthagrion*, it is shared also by other Neotropical genera (*Cyanallagma*, *Enallagma*, *Homeoura*), and the character states of female mesepisterna, male cerci and genital ligula characteristic of *Acanthagrion* and *Oxyagrion* are not illustrated or mentioned. We consider the position of this species in *Acanthagrion* as doubtful, and its generic placement unsolved pending examination of types.

Oxyagrion Selys, 1876: 290 [46 reprint]

Type species: *Agrion rubidum* Rambur, 1842 [Kirby 1890 by subsequent designation].

Diagnosis

Color pattern including red and/or light blue pale areas on head, thorax and abdomen, and restricted dark areas (Figs 4a-e, 8c, 9c). Head with rounded frons, usually red, although in mature males of *O. ablutum* it is blue, in *O. rubidum* and *O. sulinum* dorsum can be entirely darkened by pruinescence, in some species stippled with brown, and in others (*O. ablutum, O. basale, O. imeriense, O. impunctatum, O. machadoi* and *O. santosi*) with pale postocular spots, which are light blue or

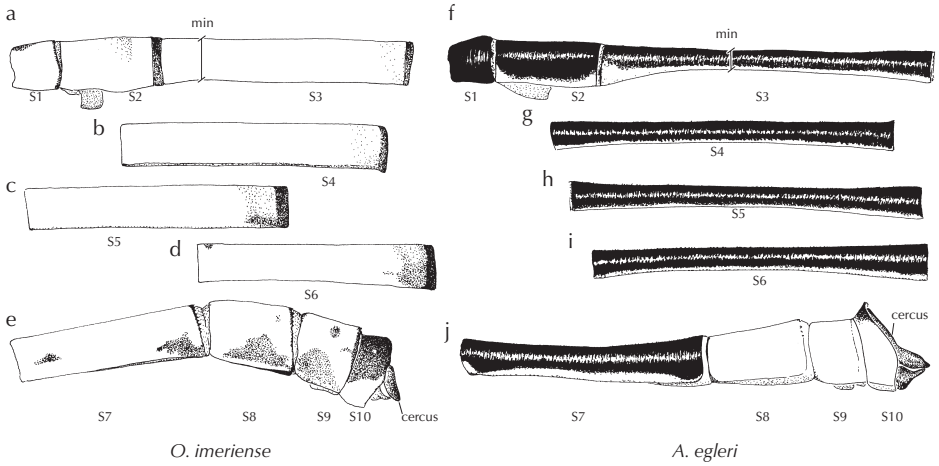


Figure 4: Male abdomen in lateral view — (a-e) *Oxyagrion imeriense* (VE, Amazonas, Cerro Yutajé); (f-j) *Acanthagrion egleri* (FG, Rorota).

light brown with irregular margins and stippled with brown (Fig. 8c). Posterior prothoracic lobe straight or moderately bi- or trilobate; pterothorax usually red (blue in *O. ablutum*), with a dark mid-dorsal ill-defined stripe in males of *O. ablutum*, *O. basale*, *O. chapadense*, *O. imeriense* and *O. sulinum*, and dorsum entirely dark in *O. hempeli*, *O. hermosae* and *O. machadoi*; only *O. imeriense* with narrow dark humeral stripe. CuP reaching hind margin of wing (as in Fig. 1b). Abdomen dorsum dark on S1-2; S3-6 are mostly red (Figs 4a-e), with the exceptions of *O. ablutum* and females of *O. bruchi* and *O. imeriense* which have dorsum of S1-7 and 10 also mostly black, and *O. sulinum*, in which mature male abdomen is entirely dark dorsally. Most species have light blue spots on dorsum of apical segments (S8 to/ or S9 to/ or S10), but *O. basale*, *O. chapadense*, *O. imeriense*, *O. impunctatum*, *O. miniopsis*, *O. pavidum* and *O. zielma* lack them. Female vulvar spine of sternum S8 present (Fig. 7b) except in *O. evanescens*. Male abdomen robust with minimum width (at S3) of 0.40-0.65 mm in lateral view (Fig. 4a). Male cerci decumbent from their bases (Figs 2c, 3c, d), except in *O. microstigma* (Fig. 2d), with a dorso-basal tubercle (Fig. 2c) correlated with presence of mesepisternal fossae in female (Figs 6b, d, e); basal tubercles on male cerci and female mesepisterna are lacking only in *O. microstigma* and *O. hempeli* (Fig. 6b). Female with well defined mesepisternal carinae between mesostigmal plates and medial carina (Figs 6b-d), except in *O. chapadense* and *O. rubidum* (Fig. 6e). Length of male genital ligula distal to flexure about as long as flexure surface, so that the distal portion of the ligula is 'C'-shaped in lateral view (Figs 5b-f), and lateral lobes of distal segment always at flexure (usually near base of flexure, Figs 5b, c, e, f; only in *O. imeriense* near distal portion of flexure, Fig. 5d).

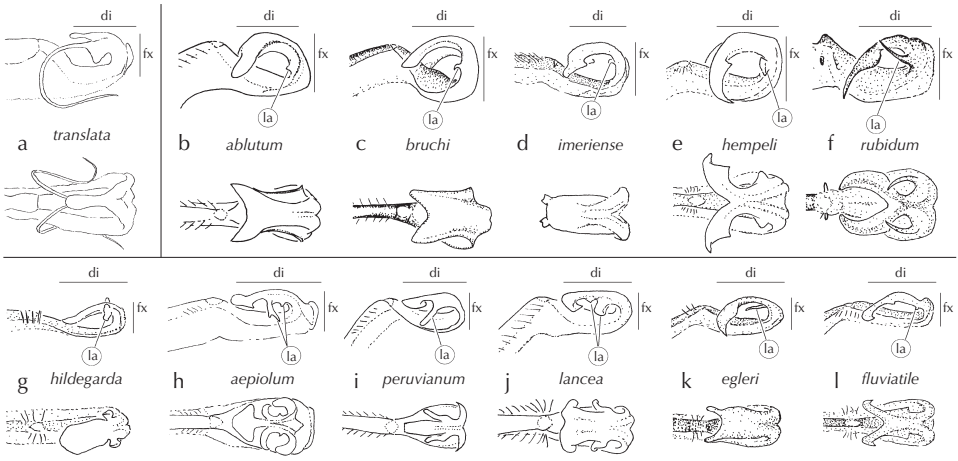


Figure 5: Distal portion of male genital ligula in lateral (above) and ventral (below) views — (a) *Argia translata* (AR, Jujuy, Arroyo Zanjón Seco); (b) *Oxyagrion ablutum* (AR, Salta, Río La Caldera); (c) *O. bruchi* (AR, Salta, Lesser); (d) *O. imeriense* (VE, Amazonas, Cerro Yutajé); (e) *O. hempeli* (AR, Misiones, Uruzú); (f) *O. rubidum* (AR, Salta, Pulares); (g) *Acanthagrion hildegarda* (AR, Buenos Aires, Arroyo N Matilde); (h) *A. aepiolum* (AR, Salta, Arroyo del Medio); (i) *A. peruvianum* (AR, Salta, Arroyo Yacuy); (j) *A. lancea* (AR, Salta, Dique Itiyuro); (k) *A. egleri* (FG, Rorota); (l) *A. fluviatile* (VE, Yaracuy, Nirgua). di: distal to flexure; fx: flexure; la: lateral lobes.

Larvae: Caudal lamellae are shorter than abdomen (95% of its length or less; Fig. 10a) in all known larvae (61.5% of the species), and are usually foliate with width/length ratio 0.20 or more (Fig. 10a; in *O. hempeli*, *O. microstigma* and *O. pavidum* lanceolate as in Fig. 10b).
Distribution: Colombia and N Brazil to central Chile and southern Argentina.
Habitat: Slow backwaters of streams and rivers, weedy ponds, and temporary pools.

Species included

O. ablutum (Calvert, 1909) — [L: Pessacq et al. 2005]*
O. basale Selys, 1876 — [L: Bulla 1973; Costa et al. 2000]*
O. brevistigma Selys, 1876*
O. bruchi Navás, 1924 — [L: von Ellenrieder & Garrison 2006]*
O. chapadense Costa, 1978 — [L: Costa et al. 2000]*
O. evanescens Calvert, 1909 — [L: Costa 1979b]*

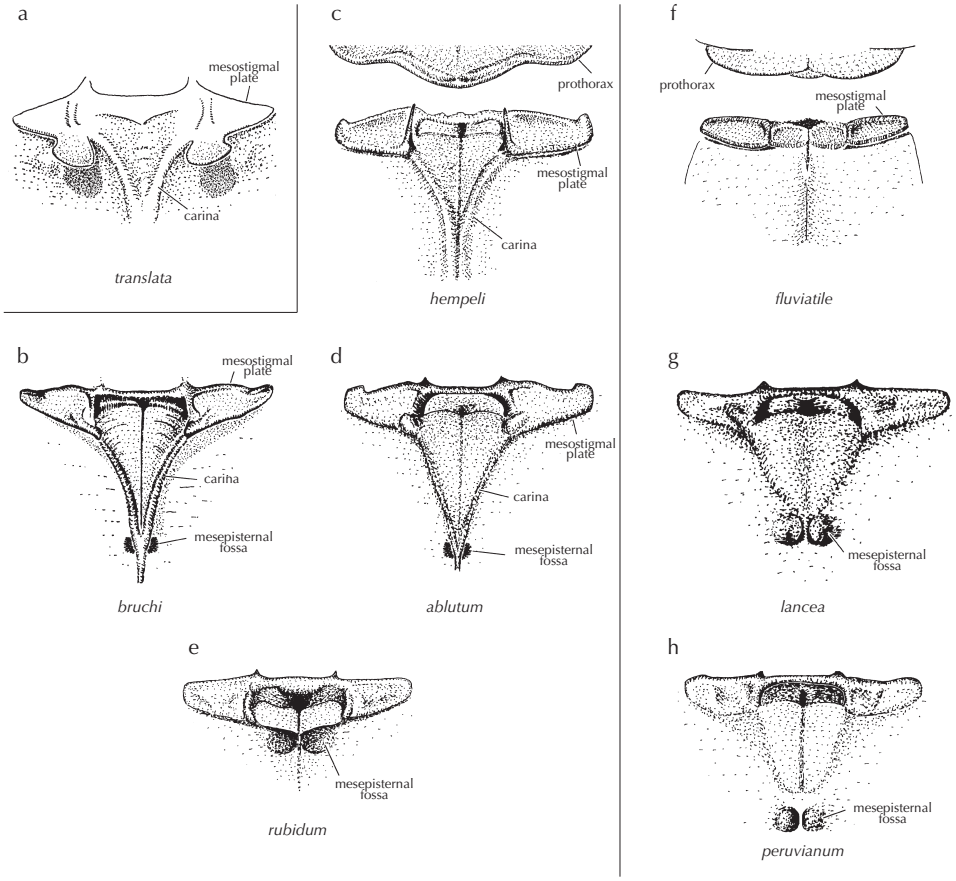


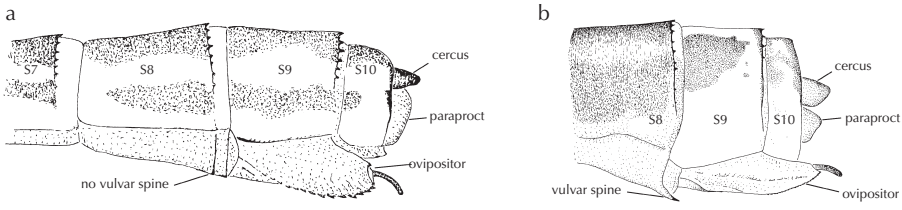
Figure 6: Female mesepisterna in dorsal view, and for (c, f) also posterior lobe of prothorax (above) — (a) *Argia translata* (USA, Arizona, Maricopa; by RWG); (b) *Oxyagrion bruchi* (AR, Salta, Lesser); (c) *O. hempeli* (AR, Misiones, Uruzú); (d) *O. ablutum* (AR, Salta, Río La Caldera); (e) *O. rubidum* (AR, Salta, Pulares); (f) *Acanthagrion fluviatile* (VE, Yaracuy, Nirgua); (g) *A. lancea* (AR, Salta, Dique Itiyuro); (h) *A. peruvianum* (AR, Salta, Arroyo Yacuy).

O. fernandoi Costa, 1988
O. haematinum Selys, 1876 — [L: Costa et al. 2000]*
O. hermosae (Leonard, 1977)
O. hempeli Calvert, 1909 — [L: Bulla 1973]*
O. imeriense (De Marmels, 1989) — [L: De Marmels 2007]*
O. impunctatum Calvert, 1909 — [L: Costa 1981]*
O. machadoi Costa, 1978*
O. microstigma Selys, 1876 — [L: Costa 1979a]*
  syn. *divaricatum* Calvert, 1909
O. miniopsis Selys, 1876
O. pavidum Hagen in Selys, 1876 — [L: Costa et al. 2000]*
? *O. pseudocardinale* Costa, Souza & Santos 2000
O. rubidum (Rambur, 1842) — [L: Needham & Bullock 1943]*
  syn. *rufulum* (Hagen, 1861)
O. santosi Martins, 1967 — [L: Costa et al. 2000]
O. simile Costa, 1978 — [L: Santos 1966 as *O. brevistigma*]
O. sulinum Costa, 1978 — [L: Costa et al. 2000]*
O. sulmatogrossense Costa, Souza & Santos 2000
O. tennesseni Mauffray, 1999*
O. terminale Selys, 1876 — [L: Bulla 1973]*
O. zielmae Costa, Souza & Muzón, 2006

Oxyagrion ablutum (Calvert, 1909) comb. nov.

(Figs 2c, 3c, 5b, 6d, 8c, 10a)

Acanthagrion gracile ablutum Calvert, 1909: 164, 165, fig. 80 (description of male and female; illustration male S10); — Ris (1913: 66, 94; mention).
Acanthagrion ablutum Calvert — Kennedy (1916: 327, figs 10, 11; illustrations of male genital ligula); — Ris (1918: 123, 124; mention); — Leonard (1977: 20, 23, 48-50, figs 15, 16, 72, 79, 80, 150, 173; keys, redescription, illustrations of male genital ligula and S10, female mesepisternum, map); — De Marmels (1984: 25; mention); — Pessacq et al. (2005: 73-76, figs 1-12; description of larva, illustrations of head, antenna, prementum, mandibles, female gonapophyses, cerci, caudal lamellae); — De Marmels (2007: 43; comparison with '*A.*' *imeriense*); — von Ellenrieder & Garrison (2007a: 48, 50, figs 98; 101, 105; diagnosis, distribution and habitat; 2008: 10, 33, 70, cover picture, ad. figs 118, 120, 121, 132, larv. fig. 39, pl. 9; keys).



translata *bruchi*

Figure 7: Female abdominal end in lateral view — (a) *Argia translata* (AR, Jujuy, Arroyo Zanjón Seco); (b) *Oxyagrion bruchi* (AR, Salta, Lesser).

Calvert (1909) described this species as a subspecies of *A. gracile*, and named it *ablutum* referring to the absence of dark humeral stripes. Due to its overall blue coloration with no hints of red and presence of pale postocular spots, its generic placement was never questioned. Leonard (1977) mentioned that it differs from all other *Acanthagrion* species by postero-lateral boundaries of interlaminal sinus of female mesepisternum represented by sharply defined carinae, and because of that reason and due to its male C-shaped genital ligula, with lateral lobes at the base of the flexure (Fig. 5a), robust male abdomen (minimum width in lateral view (at S3) of 0.60 mm), and larval caudal lamellae shorter than abdomen (Fig. 10a; as long as 0.78-0.91 of abdomen length) as in all other *Oxyagrion* species, we place this species in *Oxyagrion*. Excepting mature males of *O. sulinum* which turn entirely blue due to pruinescence, *O. ablutum* is the only *Oxyagrion* lacking any red. Its female abdominal color pattern of dark and pale areas is however almost identical to that of *O. bruchi*.

Oxyagrion hermosae (Leonard, 1977) comb. nov.

Acanthagrion hermosae Leonard, 1977: 20, 51, 52, figs 17, 18, 81, 85, 86, 173 (key, description of male, illustrations of male genital ligula and S10, map); — De Marmels (1984: 25; mention); — De Marmels (1989: 30; comparison with '*A.*' *imeriense*).

Leonard (1977) noted the similarity of this species to *O. ablutum* as regards genital ligula and male cerci morphology, and tendency toward obliteration of pale postocular spots, describing it in his revision of *Acanthagrion* as part of the '*ablutum*' group including only *A. ablutum* and *A. hermosae*. It shares with *O. rubidum* and *O. sulinum* an entirely dark head dorsum, and with *O. hempeli* and *O. machadoi* entirely dark thoracic dorsum. Leonard (1977) mentioned presence of red areas on metepimeron and S1-7 of male. Leonard's (1977) description and drawings of male genital ligula – C-shaped and with lateral lobes at flexure surface – indicates it belongs to *Oxyagrion* rather than *Acanthagrion*. This species is known only from its original description, and female and larvae are still unknown. Types deposited at the Collection of the University of Michigan (Garrison et al. 2003).

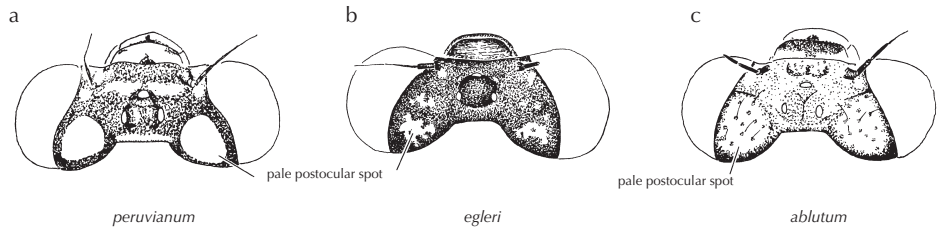


Figure 8: Head in dorsal view — (a) *Acanthagrion peruvianum* (AR, Jujuy, Río Pantanoso); (b) *A. egleri* (FG, Rorota); (c) *Oxyagrion ablutum* (AR, Salta, Río La Caldera).

Oxyagrion imeriense (De Marmels, 1989) comb. nov.
(Figs 4a-e, 5d)

Acanthagrion imeriense De Marmels (1989: 29, 30, figs 102-109; description of male and female, illustrations of head, prothorax, mesepisternum, pterostigma, male S10 and genital ligula); — De Marmels (2007: 41-43, figs 62-73; description of larva, illustrations of habit, antenna, prementum, mandibles, S9-10, caudal lamellae).

In his description De Marmels (1989) remarked on the similarity of this species with '*A.*' *hermosae*, particularly regarding shape of male genital ligula with two ental lobes near the base of the distal segment (Fig. 5d). Male abdomen is robust (minimum width in lateral view of 0.60 mm; Fig. 4a) and caudal lamellae of the recently described larva (De Marmels 2007) are shorter than abdomen as in all known *Oxyagrion*. It also differs from all *Acanthagrion* species by male dorsum of S3-6 lacking extensive dark markings (entirely red; Figs 4a-d), and by the presence of well defined female mesepisternal carinae (De Marmels 1989: fig. 108).

'Oxyagrion' pseudocardinale (Costa, Souza & Santos 2000)

Oxyagrion pseudocardinale Costa et al., 2000: 1-3, figs 1-6 (description of male, illustrations of prothorax, mesepisternum, male S10 and genital ligula, comparison with '*O.*' *cardinale*).

Costa et al. (2000) included this species, known so far only from the holotype male, in *Oxyagrion* due to the presence of red color and absence of pale postocular spots and of dark areas on head and mesepisternum. They noted its similarity to '*O.*' *cardinale* by the upright quadrangular prothoracic posterior lobe (Costa et al. 2000: figs 1, 2); however, '*O.*' *cardinale* is a *Leptobasis* (von Ellenrieder & Garrison 2007b), and all *Acanthagrion* and *Oxyagrion* species have a straight or moderately bi- or trilobate posterior prothoracic lobe (Figs 6c, f). According to the original drawings and description (Costa et al. 2000: figs 3, 4), cerci in '*O.*' *pseudocardinale* are not decumbent and lack the dorso-basal tubercle typical of *Oxyagrion* and *Acanthagrion* males, and the genital ligula, unlike that of these other two genera, has no lateral lobes (Costa et al. 2000: figs 5, 6). For all these reasons, we consider that correct generic placement of '*O.*' *pseudocardinale* is uncertain pending examination of the holotype.

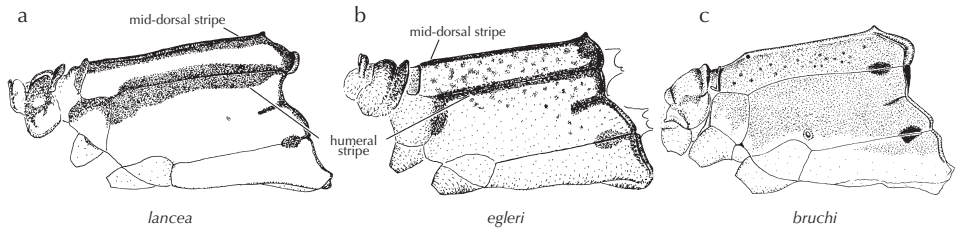


Figure 9: Thorax in lateral view — (a) male *Acanthagrion lancea* (AR, Salta, Dique Itiyuro); (b) male *A. egleri* (FG, Rorota); (c) female *Oxyagrion bruchi* (AR, Salta, Lesser).

Conclusions

Acanthagrion and *Oxyagrion* are diagnosed from other neotropical coenagrionids by the morphology of male cerci and correlated female mesepisternal fossae; mesepisternal fossae are found also only in females of *Acanthallagma luteum* Williamson & Williamson, 1924, *Amphiagrion* Selys, 1876, *Argia apicalis* (Say, 1840), *A. lilacina* Selys, 1865, *Enallagma clausum* Morse, 1895, some *Telebasis* Selys, 1865 spp. and *Tepuibasis rubicunda* De Marmels, 2007. With the sole exception of *O. microstigma* which has straight horizontal cerci (Fig. 2d), male cerci are decumbent from their bases (Figs 2b, c, 3), and except in *O. hempeli* and *O. microstigma* (Fig. 2d), there is a tubercle on their dorsal bases (Figs 2b, c) which is usually correlated with the presence of paired depressions on the female mesepisterna (the mesepisternal fossae; Figs 6b, d, e, g, h). In the few known cases where tubercles in male cerci (*O. hempeli* and *O. microstigma*) or female fossae (*A. chararum*, *A. fluviatile*, *A. hildegarda*, *O. hempeli* and *O. microstigma*) are absent, structure of geni-tal ligula lacking an inner lobe and with 1 or 2 pairs of lateral lobes, color pattern and remaining morphological and venational characters correspond to the two ge-nera in question, thus we consider that their absence is due to a reversion to a plesio-morphic state for the clade including both genera (Fig. 11).

Males of *Acanthagrion* and *Oxyagrion* can be separated from each other by the minimum width of abdomen (0.25-0.35 mm at S3 as in Fig. 4f, versus 0.40-0.65 mm, as in Fig. 4a; respectively), shape of distal portion of genital ligula (flexure considerably shorter than distal portion as in Figs 5e-l, versus about as long as distal portion as in Figs 5b-f; respectively), and position of ligula lateral lobes relative to flexure (distal to flexure as in Figs 5e-l, versus at flexure as in Figs 5b-f; respectively). Females of *Oxyagrion*, with the possible exception of *O. imeriense* (not examined here), can be recognized from those of *Acanthagrion* by the absence of well defined mid-dorsal and humeral dark stripes; in females of *O. imeriense* and in most *Oxyagrion* species (known exceptions are *O. chapadense* and *O. rubidum*) there are well defined mesepisternal carinae (Figs 6b-d), which are absent in all *Acanthagrion* species (Figs 6f-h). All ultimate instar larvae so far known differ by length of caudal lamellae relative to abdomen length – lamellae are longer than abdomen in *Acanthagrion* (Fig. 10a) and shorter in *Oxyagrion* (Fig. 10b).

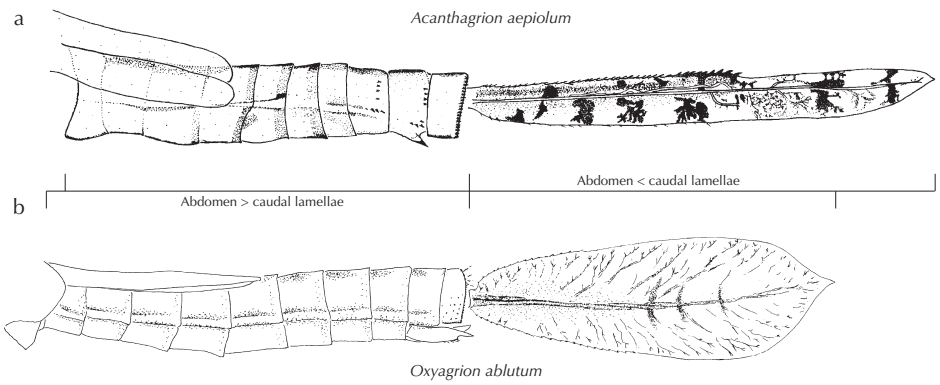


Figure 10: Larval abdomen in lateral view — (a) male *Acanthagrion aepiolum* (AR, Corrientes, Arroyo Pay Ubre); (b) female *Oxyagrion ablutum* (AR, Tucumán, Lillo).

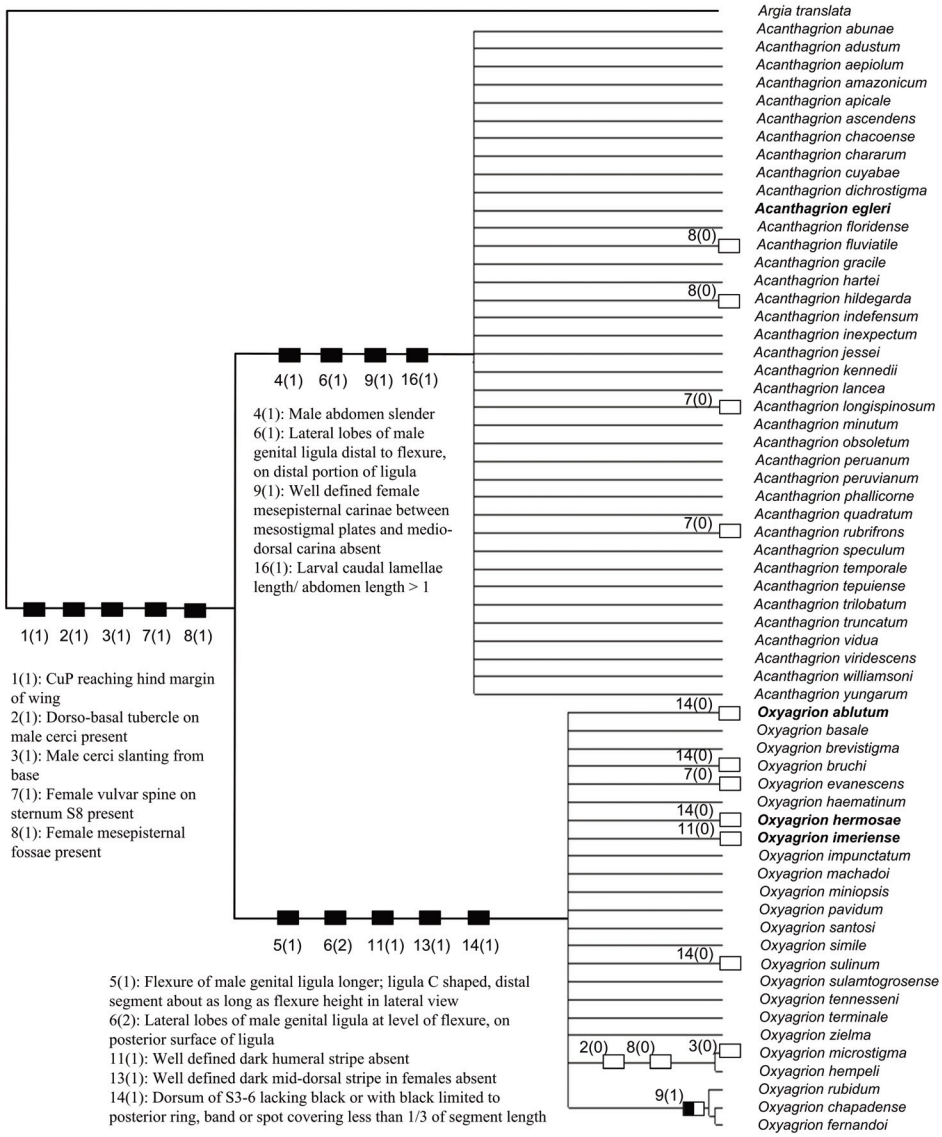


Figure 11: Strict consensus tree (length 54, ci 31, ri 81) showing derived characters (■: homology) and homoplasies (□: reversion; ◧: convergence) for *Acanthagrion* and *Oxyagrion* taxa. New generic combinations in bold text.

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