Revalidation of *Argentagrion* and redefinition of *Homeoura*, with the description of *H. obrieni* n. sp. (Odonata: Coenagrionidae)

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Revalidación de *Argentagrion* y redefinición de *Homeoura*, con la descripción de *H. obrieni* n. sp. (Odonata: Coenagrionidae)

RESUMEN. Se revalida *Argentagrion* Fraser, considerado actualmente como un sinónimo de *Homeoura* Kennedy; ambos géneros son rediagnosticados y se proporcionan ilustraciones, claves y mapas para sus especies. Se considera que *Ischnura sobrina* Schmidt pertenece a *Homeoura* y una nueva especie, *H. obrieni*, es descripta, resultando un total de cinco especies incluidas en *Homeoura* (*H. chelifera* (Selys), *H. lindneri* (Ris), *H. nepos* (Selys), *H. obrieni* sp. nov. y *H. sobrina* (Schmidt) comb. nov.) y dos en *Argentagrion* (*A. ambiguum* (Ris) y *A. silviae* Bulla).

PALABRAS CLAVE. Odonata. Coenagrionidae. *Argentagrion. Homeoura*. América del Sur.

■ ABSTRACT. Argentagrion Fraser, currently considered a synonym of Homeoura Kennedy, is revalidated; both genera are rediagnosed and their species illustrated, keyed and mapped. Ischnura sobrina Schmidt is transferred to Homeoura, and a new species, H. obrieni is described, resulting in five species being included in Homeoura (H. chelifera (Selys), H. lindneri (Ris), H. nepos (Selys), H. obrieni sp. nov. and H. sobrina (Schmidt) comb. nov.) and two in Argentagrion (A. ambiguum (Ris) and A. silviae Bulla).

KEY WORDS. Odonata. Coenagrionidae, *Argentagrion. Homeoura*. South America.

INTRODUCTION

Generic concepts within Neotropical Coenagrionidae are still not fully resolved, with poorly defined and/or artificial genera (May, 2002; De Marmels & Garrison, 2005; De Marmels 2007; von Ellenrieder & Lozano, 2008). In this paper I revise the genus *Homeoura* Kennedy, 1920. According to recent usage (Bridges, 1994; Muzón & von Ellenrieder, 1998; Costa *et al.* 2000; Lencioni, 2006), the genus currently includes five species: *H. ambigua* (Ris), *H. chelifera* (Selys), *H. lindneri* (Ris), *H. nepos* (Selys) and *H. silviae* (Bulla). The history of how this genus came to be is complex and tortuous with various species being transferred from one genus to another. Its species were originally described in the genera *Acanthagrion* Selys, *Agrion* Fabricius, *Argentagrion* Fraser and *Ischnura* Charpentier, and their generic position shifted over the years, involving the passage of some of them also through *Enallagma* Charpentier.

Selys (1876) described Acanthagrion? cheliferum under his 'Acanthagrion interruptum' group, with vein A₁ originating anteriorly to CuA in FW and male S10 slightly elevated forming two points. He (Selys, 1876) also described Agrion? nepos based on a single male, but stated that if the then unknown female was found to have a vulvar spine, it should then be considered as an aberrant species of Ischnura. Calvert (1909) described the female, and transferred this species to Ischnura due to the presence of a vulvar spine.

Ris (1904) expressed doubts in describing *Acanthagrion ambiguum* as to its correct generic placement. Fraser (1948) created the genus *Argentagrion* for reception of this species and diagnosed it from *Acanthagrion* by its small size, delicate build and greatly reduced wing venation.

Kennedy (1920) created the genus Cyanallagma to include species of Selys' 'interruptum' group and "perhaps cheliferum", and Homeoura to include Agrion? nepos. Kennedy's diagnoses were extremely brief and inconclusive; Cyanallagma was characterized as «an Acanthagrion but with male cerci not decumbent and usually forked», and Homeoura as «an Ischnura but more Enallagmine, with proximal and distal sides of pterostigmata rounded, costal slightly indented at nodus and second segment of male genital ligula with large lateral patches of spines.»

Probably unaware of Kennedy's (1920) generic descriptions, Ris (1928) described *Acanthagrion lindneri* stating that it was similar to *A. cheliferum* and *A. ambiguum*, and Schmidt (1942) described *Ischnura sobrina*, noting its similarity to *I. nepos*.

Santos (1956) shifted *Acanthagrion cheliferum* to *Enallagma*, based on the petiolation of the wings ending proximal to anal crossing as in the latter, and the male

cerci with a ventral process at base as in some species of the primarily Nearctic genus Enallagma. However, he offered no comments on the placement of the other species described under Acanthagrion which shared these characters. Rácenis (1958) disagreed with Santos (1956), noting that wing petiolation also ends proximal to anal crossing in all other species of Selys' second section of Acanthagrion, and even in some species of Acanthagrion sensu stricto. He (Rácenis, 1958) concluded that the species of Selys' second section should be placed in two different genera: Cyanallagma, with venation complete, 11-14 postnodals, male paraprocts at least as long as half of the cerci and larger size (abdomen 21.5-28; HW 16-19.5), and Argentagrion, with venation reduced, 6-10 postnodals, male paraprocts shorter than half of cerci, and smaller size (abdomen 18-23; HW 12.5-15). Besides A. ambiguum he included A. cheliferum and A. lindneri in Argentagrion but did not mention H. nepos. The similarity of A. cheliferum with Homeoura, especially regarding genital ligula morphology, was first noted by Donnelly & Alayo (1966).

Bulla (1971b) described Argentagrion silviae, and since the generic redefinition by Rácenis (1958) for Argentagrion did not allow the inclusion of his new species, he transferred A. cheliferum and A. lindneri back to Acanthagrion «...until their placement could be reanalyzed», and restricted Argentagrion to include only A. ambiguum and A. silviae as follows: more slender species, HW of 10-12.5 mm, postocular spots triangular, very elongated transversally and partially or completely fused to pale occipital bar, posterior margin of prothorax not projected, pterostigma as long as half a cell, apical margin of male \$10 with a pointed or blunt medial apophysis, ventral process of male cerci apical, represented by the ventrally bent tips of unforked cerci, and male paraprocts as long as or longer than half of cerci. Bulla (1971a) also noted the different shape of larval caudal lamellae of A. cheliferum and A. ambiguum. He (Bulla, 1973) later described the similarities in male caudal appendages, female thorax

and larval lamellae between *Cyanallagma bonariense* - *C. interruptum* and *Acanthagrion cheliferum* - *A. lindneri*, and suggested the possibility of placing the latter pair of species in *Cyanallagma*.

De Marmels (1989) redefined *Cyanallagma*, and diagnosed it from *Argentagrion ambiguum*, *Acanthagrion cheliferum*, *Homeoura nepos* and *H. lindneri*, and later (De Marmels, 1997) also placed *Acanthagrion cheliferum* in *Homeoura*.

Davies & Tobin (1984) listed A. ambiguum, A. silviae, A. cheliferum, A. nepos, A. lindneri and A. silviae under Argentagrion, and incorrectly treated Homeoura as its junior synonym without providing any explanation. This was followed by Steinmann (1997) who, however, incorrectly attributed the synonymy of Homeoura with Argentagrion to Fraser (1948). Following the principle of priority, Garrison (1991) had previously inverted the synonymy.

Lencioni (2006) characterized the genus Homeoura, with Argentagrion as its junior synonym, by the different size of quadrangles in FW and HW, and also small size, overall black coloration with light blue and yellow pale areas, presence of pale postocular spots, and females with a vulvar spine on S8. However, FW and HW quadrangles differ in size (costal side of FW quadrangle is shorter than half of HW quadrangle costal side) not only in Argentagrion and Homeoura, but also in Oxyallagma Kennedy, Tigriagrion Calvert and several Enallagma and Ischnura species, and the particular combination of small size and color pattern is also present in other neotropical Coenagrionidae (i.e. some species of Ischnura).

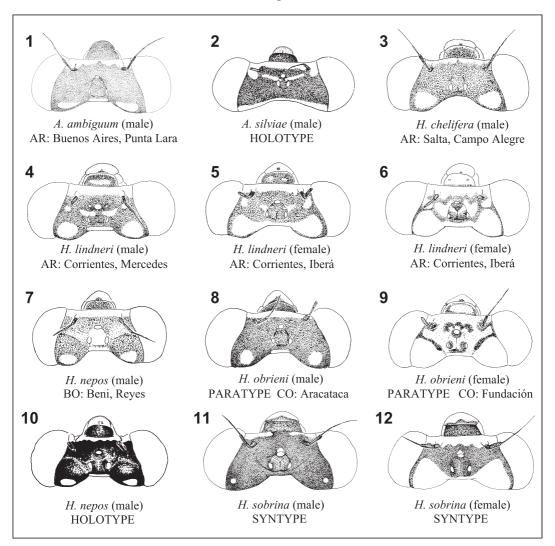
Based on morphological evidence, I contend that the species included in *Homeoura* belong to two separate genera (*A. ambiguum* and *A. silviae* in *Argentagrion* and *H. cheliferum, H. nepos* and *H. lindneri* in *Homeoura*); I also place *Ischnura sobrina* in *Homeoura*, describe a new species of *Homeoura* and provide keys, diagnoses, illustrations and distribution maps for all involved species.

MATERIAL AND METHODS

Adults of all described species of *Argentagrion* and *Homeoura*, with the sole exception of *H. sobrina*, the types of which are apparently lost (see remarks under this species account), and all original descriptions and revisions were analyzed. Additionally, several species of other coenagrionid genera were examined to establish generic boundaries. Acronyms used for collections are as follows:

- DRP D.R. Paulson personal collection, Tacoma, Washington, USA;
- FML Fundación Miguel Lillo, Tucumán, Argentina;
- FNS Forschungsinstitut und Naturmuseum Senckenberg, Frankfurtam-Main, Germany;
- IRSNB Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium;
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;
- MLP Departamento Científico de Entomología, Museo de La Plata, Argentina;
- MNRJ Departamento de Entomología, Museu Nacional, Río de Janeiro, Brazil;
- RWG R.W. Garrison personal collection, Sacramento, California, USA;
- SWD S.W. Dunkle personal collection, Tucson, Arizona, USA;
- UMMZ University of Michigan, Museum of Zoology, Ann Arbor, Michigan, USA.

Diagnostic 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 terminology follows Kennedy (1916). 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



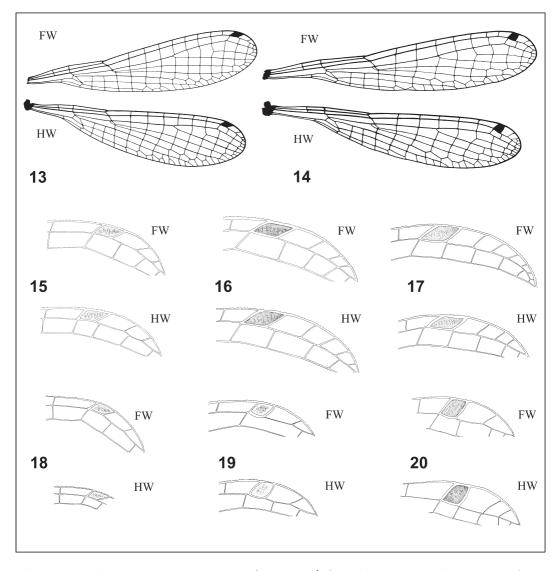
Figs. 1-12. Head, dorsal view. 1, *Argentagrion ambiguum*, male (Argentina, Buenos Aires, Punta Lara); 2, *A. silviae*, male (Holotype: Paraguay, Caaguazú); 3, *Homeoura chelifera*, male (Argentina, Salta, Campo Alegre); 4, *H. lindneri*, male (Argentina, Corrientes, Mercedes); 5-6, *H. lindneri*, female (Argentina, Corrientes, Iberá); 7, *H. nepos*, male (Bolivia, Beni, Reyes); 8, *H. obrieni*, male (Paratype: Colombia, Magdalena, Aracataca); 9, *H. obrieni*, female (Paratype: Colombia, Magdalena, Fundación); 10, *H. nepos*, male (Holotype: Amazon); 11-12, *H. sobrina*, male and female respectively (Syntypes: Peru, Pasco, Oxapampa). Fig. 10 by RWG; Figs. 11-12 redrawn from Schmidt (1942).

longitude/latitude coordinates were culled from the Global Gazetteer website (<http:// w w w.fallingrain.com/world/>). Abbreviations for structures used throughout the text are as follows: FW: forewing; HW: hindwing; pt: pterostigma; Px: postnodal crossveins; S1-10: abdominal segments 1 to 10; SD: standard deviation.

RESULTS

Argentagrion Fraser, 1948

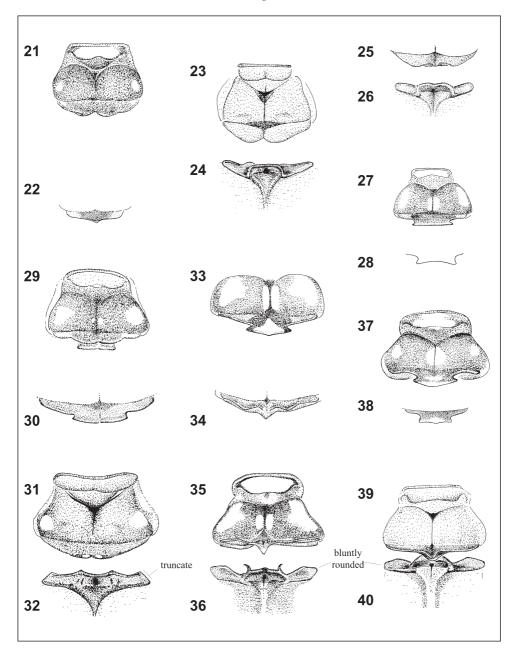
Argentagrion Fraser, 1948: 48-50 (diagnosis); Rácenis, 1958: 190-192 (generic redefinition); St. Quentin, 1960: 52, 58 (generic key, diagnosis); Donnelly &



Figs. 13-20. Wings. 13, 15, *Argentagrion ambiguum*, male (Argentina, Buenos Aires, Punta Lara); 14, 20, *Homeoura obrieni*, male (Paratype: Colombia, Magdalena, Aracataca); 16, *H. chelifera*, male (Argentina, Salta, Campo Alegre); 17, *H. lindneri*, male (Argentina, Corrientes, Mercedes); 18, *A. silviae*, male (Holotype: Paraguay, Caaguazú); 19, *H. nepos*, male (Bolivia, Beni, Reyes).

Alayo, 1966: 108-109 (comparison to *Enacantha*); Bulla, 1971b: 49-54 (generic redefinition); Bulla, 1973: 95 (discussion of generic placement); Davies & Tobin, 1984: 65; Bridges, 1994: III.6 (as junior synonym of *Homeoura*); Steinmann, 1997: 245; Tsuda, 2000: 34 (as junior synonym of *Homeoura*). Type species: *Acanthagrion ambiguum* Ris, 1904 by original designation.

Characterization. Small (HW 10.4-15mm, abdomen 17.5-21.5mm) and largely black (brown in heterochromatic females) damselflies with pale blue to pale yellow areas. Head with rounded frons, longest at level of eyes; pale postocular spots present, transversely elongated and about twice as wide as long or wider, usually concave anteriorly (Figs. 1-2), except in some heteromorphic females whose entire



Figs. 21-38. Thorax, dorsal view. 21, *Argentagrion ambiguum*, male pronotum (Argentina, Buenos Aires, Punta Lara); 22, *A. silviae*, male pronotum (Holotype: Paraguay, Caaguazú); 23-24, *A. ambiguum*, female pronotum and mesostigmal plates respectively (Argentina, Buenos Aires, Punta Lara); 25-28, *Homeoura nepos*, 25-26, female pronotum and mesostigmal plates respectively (Bolivia, Santa Cruz, Urubicha), 27. male pronotum (Bolivia, Beni, Reyes); 28, posterior lobe of male pronotum (Holotype: Amazon); 29-32, *H. chelifera* (Argentina, Salta, Campo Alegre), 29, male pronotum, 30-32, 30, female. posterior lobe of pronotum, 31, pronotum, 32, mesotigmal plates; 33-36, *H. lindneri*, 33, male pronotum (Argentina, Corrientes, Mercedes), 34-36, female (Argentina, Corrientes, Iberá), 34, posterior lobe of pronotum, 36, mesotigmal plates; 37-40, *H. obrieni*, 37, male pronotum (Paratype: Colombia, Magdalena, Aracataca), 38, posterior lobe of male pronotum (Paratype: Colombia, Magdalena, Fundación). Fig. 28 by RWG.

posterior area of head dorsum is pale; pale occipital bar is present and usually confluent to postocular spots (except in some males of A. ambiguum in which they are adjacent but not fused). Posterior lobe of prothorax either bilobate (Figs. 21, 23, in both male and female of A. ambiguum) or with a short triangular apophysis (Fig. 22, in male of A. silviae), lacking a differentiated medial lobe; pterothorax with complete antehumeral pale stripe, and no black stripe over metapleural suture (Fig. 60); tibial spurs as long as or intervening shorter than spaces; supplementary teeth of pretarsal claws well developed. CuP reaching CuPAA (Fig. 13); petiolation ending at or proximal to CuP (variable intraspecifically); pt rhomboidal (Figs. 13, 15, 18). Male genital ligula with one latero-distal lobe on each side, lacking inner fold, with an inner process (Figs. 41, 43, ip) in the center of a transverse fold distal to flexure, and with no projections proximal to flexure; setae on sides of ligula second segment usually present. Posterior margin of male S10 entire (Figs. 65-70), usually with a medial apophysis. Distal half of male cercus bent ventrally into a triangular laminar process (Figs. 65, 67-68, 70); paraprocts short with dorsal branch rounded (in A. ambiguum, Fig. 67) or ending in a sclerotized tooth (in A. silviae, Fig. 70, to). Female vulvar spine of S8 well developed; outer valves of ovipositor with one row of spines, and extending to posterior margin of \$10.

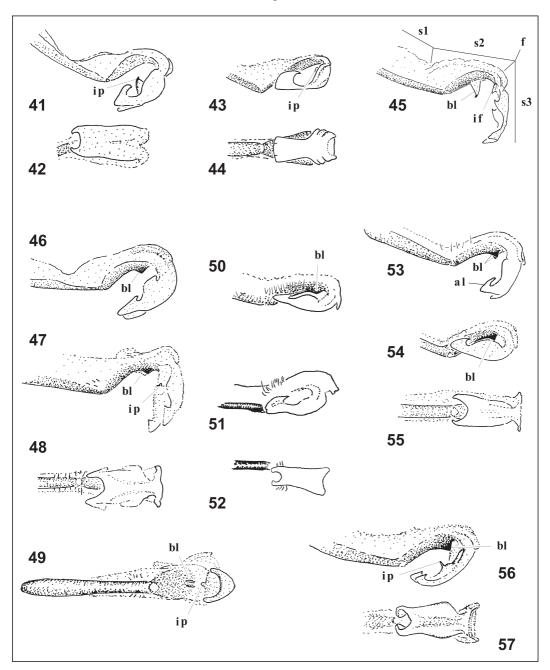
Diagnosis. Argentagrion can be diagnosed from all other coenagrionid genera based on its unique combination of characters: pale postocular spots transversely elongated in males and andromorphic females, about as wide as twice their length or wider (Figs. 1-2); posterior prothoracic lobe either bilobate or with a small medial triangular apophysis (Figs. 21-23); posterodorsal margin of male \$10 entire with a small medio-dorsal triangular apophysis (Figs. 65-70); distal half of male cercus bent ventrally into a triangular process (Figs. 65, 67-68, 70; as in Andinagrion, Leucobasis Rácenis, 1959 and Zoniagrion Kennedy, 1917); male genital ligula lacking inner fold and sclerotized inner bladed projections proximal to flexure, and with an inner bladed process distal to flexure (Figs. 41, 43, ip).

Species included. *A. ambiguum* (Ris, 1904) and *A. silviae* Bulla, 1971.

Argentagrion ambiguum (Ris, 1904) (Figs. 1, 13, 15, 21, 23-24, 41-42, 58, 65-67, 86, 88)

- Acanthagrion ambiguum Ris, 1904: 13-14, fig. 8 (description of male and female, illustration of male S10); Calvert, 1909: 176 (comments on color and venation); Ris, 1913: 14 [reprint 68] (mention from Argentina); Ris, 1918: 120 (mention from Catamarca, Argentina); Ris, 1928: 42 (comparison with *A. lindneri*); Fraser, 1947: 430 (mention from Argentina); Calvert, 1948: 24-25 (variability of female color and venation); St. Quentin, 1960: 58 (mention from Paraguay, Argentina and Brazil).
- Argentagrion ambiguum; Fraser, 1948: 48-50, figs. 1-5 (designation as type species of Argentagrion, illustration of wings, pterothorax, female S8-10, male genital ligula and S10); Rácenis, 1958: 190-193 (discussion of generic placement); Donnelly & Alayo, 1966: 107-108, fig. 3 (discussion of history and comparison to Enacantha, illustration of genital ligula); Gloger, 1967: 45-46, 50-51, 57 (distribution in Argentina, discussion of history and generic placement); Bulla, 1970: 95-97, pl. 2 figs. 1-5, pl. 3 fig. 2 (description of last larval instar); Bulla, 1971a: 135-142, figs. 139-155 (redescription of adult and larva); Bulla, 1971b: 50-54, figs. 7-10 (discussion of relationship with Acanthagrion cheliferum and A. lindneri); Bulla, 1973: 95 (discussion of generic placement); Davies & Tobin, 1984: 65 (listed); De Marmels, 248 (comparison 1989: with Cyanallagma); Rodrigues Capítulo et al., 1991: 61 (listed); Steinmann, 1997: 245-246 (synonymic list); May, 2002: 407 (character matrix).

Homeoura ambigua; Garrison, 1991: 12



Figs. 41-57. Male genital ligula. 41-42, *Argentagrion ambiguum*, lateral and ectal views respectively (Argentina, Buenos Aires, Punta Lara); 43-44, *A. silviae*, lateral and ectal views respectively (Holotype: Paraguay, Caaguazú); 45, *Enallagma signatum*, lateral view (USA, Virginia, Shenandoah); 46-49, *Homeoura lindneri* (Argentina, Corrientes, Mercedes), 46-47, lateral view, 48, ectal view, 49, inner view of first and second segments, frontal view of third segment; 50-52, *H. nepos*, 50, lateral view (Bolivia, Santa Cruz, Urubicha), 51-52, lateral and ectal views respectively (Holotype: Amazon); 53-55, *H. obrieni* (Paratypes: Colombia, Magdalena, Aracataca), 53-54, lateral view, 55, ectal view; 56-57, *H. chelifera*, lateral and ectal views respectively (Argentina, Salta, Campo Alegre). al: apical lobe; bl: bladed projections; f: flexure; if: inner fold; ip: inner process; s1-s3: genital ligula segments 1-3. Figs. 51-52 by RWG.

(synonymic list); Rodrigues Capítulo, 1992: 54 (mention and distribution in Argentina); Bridges, 1994: VII.10 (list); Muzón & von Ellenrieder, 1998: 23 (mention and distribution in Argentina); Tsuda, 2000: 34 (synonymic list); Costa et al., 2000: 12 (mention from São Paulo); von Ellenrieder, 2000: 20-21, 23-25 (population dynamics); O'Grady & May, 2003: 2833 (character matrix); Lencioni, 2006: 36, 127, figs. B10B, 70A-I (distribution, illustration of wings, male genital ligula, abdomen and S10, female pronotum and \$8-10); von Ellenrieder & Garrison, 2007: 52-53, figs. 112, 114 (characterization, illustrations of male \$10 and female mesostigmal plates).

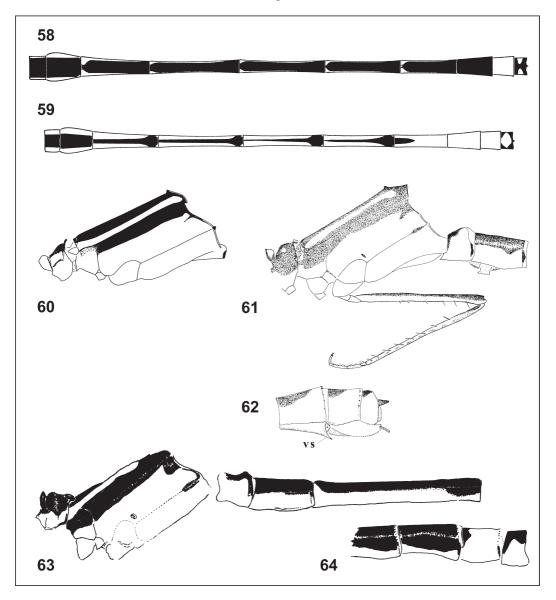
Diagnosis. Black male labrum; dorsum of head between antennae and black pale postocular spots (Fig. 1); pale in heteromorphic female labrum and entire posterior area of head. Posterior lobe of prothorax widely bilobate (Figs. 21, 23). Lateral margins of female mesostigmal plates (Fig. 24) bluntly pointed. Pt (Figs. 13, 15) rhomboidal. Dorsum of male \$3-8 mostly black (Fig. 58). Male cercus about twice as long as wide in dorsal view (Fig. 66); dorsal branch of male paraproct rounded (Figs. 67). Larval prementum with three mental and five palpal setae; base of caudal lamella dark with non-discernible tracheae, primary and secondary tracheae on distal portion equally pigmented (Fig. 86).

Biology. Adults perch on twigs and leaves of emergent vegetation close to water surface and on bushes and grass blades near shores of ponds, pools, dams and slow streams rich in aquatic vegetation within grasslands and marginal forests, and fly in a slow steady beat when sunny. Bulla (1970) described the larva, which lives among filamentous algae and roots of aquatic plants; von Ellenrieder (2000) studied seasonal variations in populations of Buenos Aires.

Distribution (Fig. 88). Bolivia (Santa Cruz department), Brazil (São Paulo, Santa Catarina and Rio Grande do Sul states), Paraguay (Amambay, Concepción, San Pedro, Central and Guaira departments), Argentina (Salta, Tucumán, Catamarca, Chaco, Formosa, Corrientes, Misiones, Santa Fe, Entre Ríos and Buenos Aires provinces) and Uruguay (Florida department), from 2 to 1040 m a.s.l.

Type material. 3 σ 3 Q syntypes in FNS [not examined].

Material examined (390360). BOLIVIA. Santa Cruz: Robore, Chiquitos, xi 1960, 1 o (UMMZ). BRAZIL. Santa Catarina: Nova Teutonia, 10 v 1939, Fritz Plaumann col., 1 o (RWG). PARAGUAY. Concepción: Concepción, 24 viii 1956, C. J. D. Brown col., $5 \sigma 8 \circ (UMMZ)$, same but $2 \sigma 1 \circ (RWG)$, Asunción, 1 viii 1956, C. J. D. Brown col., 1 o (RWG). Guaira: Villarica, 7 iv/ 21 v 1911, 9 ♂ 9 ♀ (UMMZ), Mbuvevo, 9 iv/ 21 v 1911, 5 of 2 o (UMMZ). ARGENTINA. Misiones: Puerto Rico, 04-08 iv 1971, C. M. & O. S. Flint, Jr. col., 1 o (RWG). Corrientes: Pariopá marsh and stream, on prov. road 94, aprox. 12 km N of Santo Tomé, 21 ix 2005, N. v. Ellenrieder col., 1 o 1 o (RWG), Mburucuyá National Park, central station, 12-14 xii 1999, C. Molineri col., 1 ç (FML). Formosa: ditch 10 km N of Formosa on route 11, 5 xi 2007, R.W. Garrison & N. v. Ellenrieder col., 5 of 4 o (RWG), same but ditch 12 km E from route 11 on route 2 to Mojón de Fierro, 1 o 1 o (RWG), same but roadside pond and grassy ditches by route 81, 40 km W of Formosa, 6 xi 2007, $1 \circ 1_Q$ (RWG), same but ponds 12 km S of Gran Guardia on road 16, 1_Q (RWG), slough 2 km S of Bañado La Estrella, 43 km N of Las Lomitas on road 28, 2 of (RWG). Salta: Campamento Jakulica, 40 km W to Aguas Blancas, 20 xi 1971, Porter col., 1 o (FML), km 327 on National road 81, between Hickmann and Dragones, sloughs with pleuston, 30 xi 2007, N. v. Ellenrieder col., $1 \circ 1 \circ (RWG)$. Santa Fe: Esperanza, $10 \times 10^{\circ}$ 1896, 1 of (UMMZ). Entre Ríos: P.N. El Palmar, 20 xi 1987, J. Muzón col., 1 o (MLP). Buenos Aires: Arroyo Zapata, Rt. 11, 25 km E La Plata, 24 xi 1969, C. M. & O. S. Flint, Jr. col., 1 o (RWG), Punta Lara, road to Villa Elisa, 06 iv 1990, J. Muzón col., 2 o 1 o (RWG),



Figs. 58-64. Color pattern. 58, *Argentagrion ambiguum*, 59, *A. silviae*, 58-59, male abdomen, dorsal view; 60, *A. silviae* thorax, lateral view (Holotype: Paraguay, Caaguazú); 61-62, *Homeoura obrieni*, 61, male thorax and S1-2, lateral view (Paratype: Colombia, Magdalena, Aracataca), 62, female S8-10, lateral view (Paratype: Colombia, Magdalena, Fundación); 63-64, *Homeoura nepos* male, lateral view (Holotype: Amazon), 63, thorax and S1-2, 64, part of S7-10. vs: vulvar spine. Figs. 63-64 by RWG; Figs. 58-60 from Bulla (1971b).

same but 24 viii 1997, N. v. Ellenrieder col., 1 \circ (RWG), Punta Blonce, 07 xi 1989, J. Muzón & Aguirre col., 1 σ (RWG), Punta Indio, Arroyo Villoldo (North), 24 xi 1998, J. Muzón & N. v. Ellenrieder col., 1 σ (RWG).

Argentagrion silviae Bulla, 1971 (Figs. 2, 18, 22, 43-44, 59-60, 68-70, 88)

- Argentagrion silviae Bulla, 1971b: 51-54, figs. 1-6 (description of male, illustration of head, thorax, abdomen, genital ligula and S10); Davies & Tobin, 1984: 66 (listed); Steinmann, 1997: 246 (synonymic list).
- Homeoura silviae; Garrison, 1991: 12 (synonymic list); Bridges, 1994: VII.217 (list); Tsuda, 2000: 34 (synonymic list);

Costa *et al.*, 2000: 12 (mention from São Paulo); Lencioni, 2006: 36, 131 (distribution and illustration of head, thorax, male genital ligula, abdomen and S10); Muzón *et al.*, 2007: 303 (type catalog MLP).

Diagnosis. Labrum pale; dorsum of head between antennae and pale postocular spots with two transversely elongated spots between medial and posterior ocelli (Fig. 2). Posterior lobe of prothorax with a short medial triangular apophysis (Fig. 22). Pt (Fig. 18) rhomboidal. Dorsum of male S3-6 with black restricted to narrow mediolongitudinal stripe, limited to basal half on S7, and dorsum of S8 entirely pale (Fig. 59). Male cercus about as long as wide in dorsal view (Fig. 69); dorsal branch of male paraproct ending in a sclerotized tooth (Fig. 70). Female unknown.

Biology. Larva and habits unknown.

Distribution (Fig. 88). Paraguay (Caaguazú department) at 300 m a.s.l.

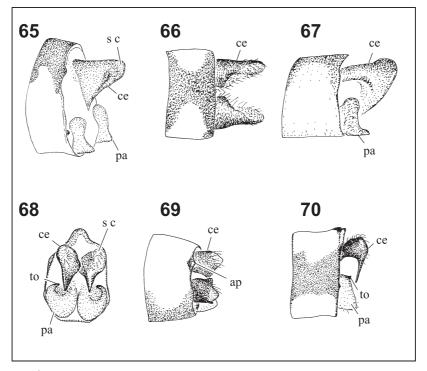
Type material. Holotype σ in MLP, with following labels: [Museo de La Plata/ Holotipo/ Argentagrion/ silviae Bulla] [Caaguazu/ Paraguay/ 10/3/70/ Bulla col.] [3484] [examined].

Remarks. The record from São Paulo state, Brazil, has not been verified because the specimen(s) upon which Costa *et al.* (2000) and Lencioni (2006) have based their records is/ are lost (Costa *pers. comm.*). The only known *bona fide* specimen in existence is therefore the holotype, deposited at the MLP. However, the locality belongs to the same biogeographic province (Amazon province of the Neotropical region) and the species could possibly be present there.

Homeoura Kennedy, 1920

Homeoura Kennedy, 1920: 88 (diagnosis); Davies & Tobin, 1984: 65 (listed as junior synonym of *Argentagrion*); Bridges, 1994: III.22 (synonymic list); Steinmann, 1997: 246 (listed as senior synonym of *Argentagrion*); Tsuda, 2000: 34 (synonymic list); Lencioni, 2006: 26, 36, fig. B10 (generic key and diagnosis). Type species: *Ischnura neops* [*sic* for *Agrion? nepos*] by original designation.

Characterization. Small (HW 10.2-17.5mm, abdomen 16.5-26mm) and largely black (brown in heterochromatic females) damselflies with pale blue to pale yellow areas. Head with rounded frons, longest at level of eyes; pale postocular spots present, approximately oval to rounded or triangular, narrower than twice their length, with anterior margin usually convex (Figs. 3-12), concave in some *H. nepos*; pale occipital bar usually present (Figs. 4-10, 12), absent in males of H. chelifera and H. sobrina (Figs. 3, 11), and usually separated from postocular spots (except in some males of H. lindneri and heteromorphic females where the entire posterior area of head dorsum is pale, *i.e.* Figs. 6, 9, 12). Posterior lobe of prothorax with medial portion differentiated into a trapezoidal or rectangular lobe in male (Figs. 27-29, 33, 37-38), usually into a triangular or rectangular lobe in female (Figs. 25, 30, 34-35, 39; in some females of H. chelifera and *H. nepos* barely bilobate, Fig. 31); pterothorax (Fig. 61) with black medio-dorsal and humeral stripes and usually a complete antehumeral pale stripe (interrupted distally in some *H. nepos*), usually lacking a complete black stripe over metapleural suture (present only in *H. sobrina*); in some heteromorphic females thorax entirely pale; tibial spurs as long as or shorter than intervening spaces; supplementary teeth of pretarsal claws well developed. CuP reaching CuPAA (Fig. 14), petiolation of wing ending at or proximal to CuP (variable intraspecifically), pt quadrangular (H. nepos and H. obrieni, Figs. 14, 19-20) or rhomboidal (H. chelifera and H. lindneri, Figs. 16-17). Male genital ligula with one latero-distal lobe on each side, lacking inner fold, with a small digitiform inner process in the center of a transverse fold distal to flexure, and with a pair of unique sclerotized projections shaped as triangular blades proximal to flexure (Figs. 46, 47, 50,



Figs. 65-70. male S10. 65-67, *Argentagrion ambiguum* (Argentina, Buenos Aires, Punta Lara), 65, medio-dorsal view (left cercus and hairs omitted), 66, dorsal view, 67, lateral view (hairs omitted); 68-70, *A. silviae* (Holotype: Paraguay, Caaguazú), 68, posterior view, 69, dorsal view, 70, lateral view. ap: apophysis; ce: cercus; pa: paraprocts; sc: scalariformlike cuticle; to: tooth.

53-56, bl), setae on sides of second segment usually present. Posterior margin of male S10 with a 'u' shaped medial cleft with two apical tubercles (Figs. 71-72, 74-85, ct). Male cerci approximately horizontal with inner margin projected ventro-basally into a laminar process (Figs. 71-76, 78, 80, 82, 85); paraprocts short with dorsal branch ending in a sclerotized tip (Figs. 74-76, 78, 80, to). Female vulvar spine of S8 well developed; outer valves of ovipositor with one row of spines, and extending slightly beyond posterior margin of S10 (Fig. 62).

Diagnosis. *Homeoura* differs from *Argentagrion* by the medial lobe of posterior lobe of prothorax projected into a rectangular or trapezoidal process in males (projected medial lobe shared with *Andinagrion* Bulla, *Cyanallagma*, *Hesperagrion* Calvert, *Mesamphiagrion* Kennedy, *Oxyallagma* Kennedy and *Protallagma* Kennedy), the presence of a 'u' shaped cleft with two apical tubercles on postero-dorsal margin of male S10 (shared with previous genera and with *Enallagma, Enacantha* Donnelly & Alayo and some *Ischnura* species) and male cercus approximately horizontal with a ventro-basal branch, which is a projection of its ventromesal margin (as in *Enallagma* and *Mesamphiagrion*). The paired sclerotized projections shaped as triangular blades proximal to flexure on second segment of male genital ligula of *Homeoura* distinguish it from all other genera of New World Coenagrionidae.

Remarks. The «bladed projection» (De Marmels, 1989) observed in *Enallagma signatum* (Hagen, 1861) is single (Fig. 45), and therefore not equal to the projection of all *Homeoura* species, which is composed of two parallel blades (Figs. 46-47, 49-50, 53-54, 56, bl).

Species included. H. chelifera (Selys,

1876), *H. lindneri* (Ris, 1928), *H. nepos* (Selys, 1876), *H. obrieni* n. sp. and *H. sobrina* (Schmidt, 1942) n. comb.

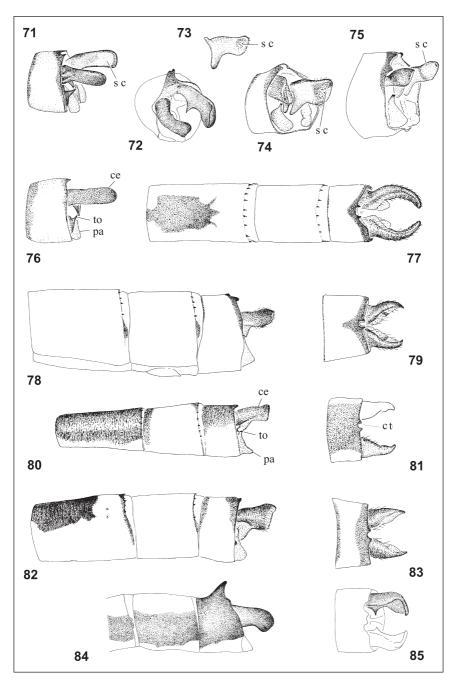
Homeoura chelifera (Selys, 1876) (Figs. 3, 16, 29-32, 56-57, 71, 76-77, 87, 89)

- Acanthagrion? cheliferum Selys, 1876: 319-321 [reprint 75-77] (description of male).
- Acanthagrion cheliferum? rusticum Calvert, 1909: 175-176 (description as possible subspecies).
- Acanthagrion cheliferum; Ris, 1904: 12-13, fig. 7 (description of female, illustration of male \$10); Needham, 1904: 717 (incomplete larval description); Calvert, 1909: 175-176 (comments on color and venation); Ris, 1913: 14 [reprint 68] (mention from Argentina); Ris, 1928: 41, 44 (comparison with A. lindneri); Fraser, 1947: 430 (mention from Argentina); Bulla, 1971a: 159-166, figs. 175-182, 246 (redescription of adult and larva); Bulla, 1971b: 49-51 (discussion of relationship with Argentagrion); Bulla, 1973: 95 (comparison with Cyanallagma bonariense and C. interruptum).
- *Enallagma cheliferum*; Santos, 1956: 571-576, figs. 1-12 (new combination proposed, discussion of similarity with *Enallagma* species, redescription of male and female, illustrations of head, thorax, abdomen, wings); De Marmels, 1990: 335 (mention for Venezuela).
- Argentagrion cheliferum; Rácenis, 1958: 190-192 (mention from Venezuela, discussion of generic placement); Donnelly & Alayo, 1966: 108-109, fig. 3 (discussion of history and comparison with *Enacantha*, illustration of genital ligula); Gloger, 1967: 45-46, 50, 55, 57 (distribution in Argentina, discussion of history and generic placement); Davies & Tobin, 1984: 65 (listed); Rodrigues Capítulo *et al.*, 1991: 61, 66 (chromosomal data); Steinmann, 1997: 246 (synonymic list); May, 2002: 407 (character matrix).
- *Cianallagma chelifera*; Cruz, 1986: 745-747, fig. 8 (comparison with *C. demarmelsi*, illustration female posterior prothoracic

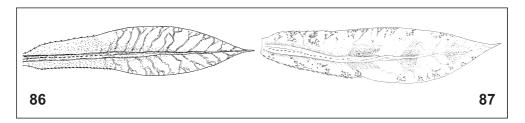
lobe and mesostigmal plates).

Homeoura chelifera; Garrison, 1991: 12 (synonymic list); Rodrigues Capítulo, 1992: 54 (mention and distribution in Argentina); Bridges, 1994: VII.49 (list); De Marmels, 1997: 136 (comparison with Cyanallagma); Muzón & von Ellenrieder, 1998: 23 (mention and distribution in Argentina); Tsuda, 2000: 34 (synonymic list); Costa et al., 2000: 12 (mention from São Paulo); von Ellenrieder, 2000: 20-21, 23-25 (population dynamics); Lencioni, 2006: 36, 128, figs. B10A, 71A-I (distribution, illustration of wings, head, thorax, male genital ligula, abdomen and S10, female pronotum, mesostigmal plates and S8-10); von Ellenrieder & Garrison, 2007: 52-53, figs. 110-111, 113 (characterization, picture, illustrations of male S10 and female mesostigmal plates).

Diagnosis. Pale postocular spots on dorsum of male head (Fig. 3) large (larger than 1/3 of postocular lobe's width) and approximately oval (shared with H. lindneri and H. nepos), and pale postocular bar absent (shared with H. sobrina); in heteromorphic female entire posterior area of head pale (shared with all Homeoura species). Medial projection of posterior lobe of prothorax rectangular (Figs. 29-30) (shared with H. nepos) or narrowly bilobate (Fig. 31) in some females (unique). Lateral margins of female mesostigmal plates (Fig. 32) truncated (unique). Pt (Fig. 16) rhomboidal (shared with H. lindneri). Second segment of genital ligula with a few thin hairs on each side or lacking hairs (Figs. 56-57), and bladed projections proximal to flexure in the shape of equilateral triangles, with acutely pointed apex and about as high as wide (Fig. 56; both shared with H. lindneri and H. obrieni). Dorsum of male S8 partially or entirely black, S9 entirely pale and S10 mostly pale, with black posterior margin (Figs. 76, 77; shared with H. obrieni). Dorsal and ventral margins of male cercus (Fig. 76) approximately parallel and of equal length in lateral view, so that apical width is approximately the same as basal width and apex is roundly truncated (shared with H.



Figs. 71-85. Male abdomen. 71, *Homeoura chelifera* (Argentina, Salta, Campo Alegre), 72, *H. sobrina* (Syntype: Peru, Pasco, Oxapampa), modified from Schmidt (1942), 73, *H. nepos*, right cercus, inner view (Bolivia, Beni, Reyes), 74, *H. obrieni* (Paratype: Colombia, Magdalena, Aracataca), 75, *H. lindneri* (Argentina, Corrientes, Mercedes), 71, 72, 74-75, S10, medio-dorsal view; 76-77, *H. chelifera* (Argentina, Salta, Campo Alegre), 76, S10, lateral view, 77, S8-10, dorsal view; 78-79, *H. lindneri* (Argentina, Corrientes, Mercedes), 78, S8-10, lateral view, 79, S10, dorsal view; 80-81. *H. nepos* (Bolivia, Beni, Reyes), 80, S8-10, lateral view, 81, S10, dorsal view; 82-83, *H. obrieni* (Paratype: Colombia, Magdalena, Aracataca), 82, 84, 85, *H. sobrina* (Syntype: Peru, Pasco, Oxapampa), redrawn from Schmidt (1942), 84, part of S8-10, lateral view, 85, S10, dorsal view. ce: cercus; ct: S10 postero-dorsal cleft with tubercles; pa: paraprocts; sc: scalariformlike cuticle; to: tooth.



Figs. 86-87. Larval lateral caudal lamella. 86, *Argentagrion ambiguum*; 87, *Homeoura chelifera*. Fig. 86 from Bulla (1970); Fig. 87 from Bulla (1971a).

sobrina). Larval prementum with three mental and five palpal setae; caudal lamella with three diffuse dark spots along midline and secondary tracheae much darker than primary (Fig. 87).

Biology. Adults perch on twigs and leaves of emergent vegetation close to water surface and on bushes and grass blades near the shores of ponds, pools, dams and slow streams rich in aquatic vegetation, and fly in a slow steady beat when sunny (von Ellenrieder & Garrison, 2007). Needham (1904) provided a short description of the larva based on an incomplete putative specimen of *H. chelifera* from São Paulo, which was later complemented by Bulla (1971a); von Ellenrieder (2000) studied seasonal variations in populations from Buenos Aires.

Distribution (Fig. 89). Colombia (Antioquia department), Venezuela (Aragua, Guárico, Barinas and Apure states), Guyana (Upper Takutu-Upper Essequibo region), Brazil (Bahia, Minas Gerais, Espirito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul states), (Guaira and Paraguarí Paraguay departments), Uruguay (de Rocha department) and Argentina (Jujuy, Salta, Tucumán, Corrientes, Santa Fe, Entre Ríos and Buenos Aires provinces), from 4 to 1530 m a.s.l.

Type material. Types of *Acanthagrion*? *cheliferum:* 1 σ lectotype by present designation; 7 σ paralectotypes in IRSNB [examined]. In order to clarify application of the name, I designate the syntype male from

Brazil, Minas Gerais, Entre Ríos, ix, Walthère de Selys col. as LECTOTYPE; labels: *Entrerios; cheliferum; W. de Selys.* Paralectotypes: Minas Gerais, 3σ (IRSNB), Santa Teresa, 1σ (IRSNB), Rio de Janeiro, 2σ (IRSNB), Rio Grande, 1σ (IRSNB). Types of *Acanthagrion? cheliferum rusticum*: 2σ , 1φ syntypes in MCZ [not examined].

Material examined $(44 \circ 13 \circ)$. VENEZUELA. Barinas: NE to Mantecal, marshy pond at entrance to Hato El Frío, 27 xii 2000, D.R. Paulson & N. Smith col., 1 o 1 o (DRP). COLOMBIA. Antioquia: Represa La Fe, W of La Fe, 26 ii 1984, C.M. & O.S. Flint, Jr. col., 1 of 1 o (RWG). BRAZIL. Minas Gerais: Entre Ríos, ix, Walthère de Selys col., 1 σ lectotype (IRSNB), Minas Gerais, 3 σ paralectotypes (IRSNB), Belo Horizonte, Lagoa Santa, 15 x 1978, D.A.L. Davies col., 1 σ (RWG). Espirito Santo: Santa Teresa, 1 σ paralectotype (IRSNB). Rio de Janeiro: Rio de Janeiro, 2 o paralectotypes (IRSNB), same but 27 ix 1922, J.H. Williamson col., 3 o (RWG). Santa Catarina: Nova Teutonia, 3 iv /25 iii 1945, F. Plaumann col., 6 o 1 o (RWG). São Paulo: Fazenda Santana do Rio Abaixo, Jacareí, 08 xii 1998, F. A. A. Lencioni col., 2 σ1 φ (RWG), same but 15 ix 1996, 1 σ (RWG), Salesopolis, 14 iii 1999, F. A. A. Lencioni col., 1 o (RWG), Campos do Jordão, 02 xi 1999, F. A. A. Lencioni col., 1 o (RWG), Rio Claro, 10 ix 1996, F. A. A. Lencioni col., 1 o (RWG), São Paulo (RWG), 3 çCipó, 8 iv 1967/ 2 iii 1968, V. N. Alin, 2 o 1 o (DRP). **Rio Grande do Sul:** Rio Grande do Sul, 1 o paralectotype (IRSNB). PARAGUAY. Guaira: Mbuevo, 9 iv 1911, 1 of (RWG). ARGENTINA. Jujuy: La Angostura, pond at house, 1 o (RWG). Salta: pond between La Angostura and

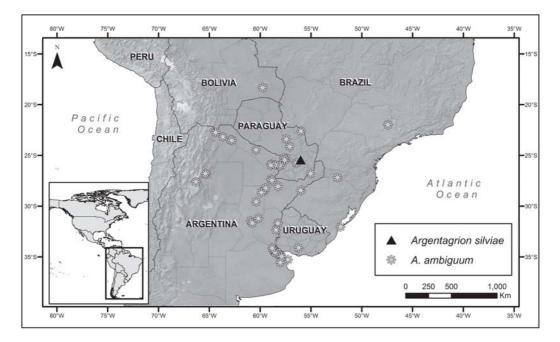


Fig. 88. Distribution of Argentagrion in South America.

Campo Alegre, 21 iv 2001, N. v. Ellenrieder col., $6 \circ 1_{\varphi}$ (RWG), Campo Alegre Dam, 12 i 1997, T.W. Donnelly col., 1 o (RWG), same but J. Muzón & N. v. Ellenrieder col., 1 o 1 o (RWG). Tucumán: pond at Museo, 23 xi 1968, L.A. Bulla col., 2 o (MLP). Corrientes: Pariopá marsh and stream, on prov. road 94, aprox. 12 km N of Santo Tomé, 21 ix 2005, N. v. Ellenrieder col., 2 o (RWG), Mburucuyá National Park, central station, 12-14 xii 1999, C. Molineri col., 1 o (FML). Santa Fe: Santo Tomé, Río Salado, 30-31 iii 1971, C.M. & O.S. Flint, Jr., 1 o (RWG). Buenos Aires: Punta Lara, grassland, 07 xi 1997, N. v. Ellenrieder col., 1 o (RWG), Punta Indio, stream on km 223 of road 11, 1,5 km N Arroyo La Matilde, 25 xi 1998, J. Muzón & N. v. Ellenrieder col., 1 σ (MLP), Lima, Club de Pesca near Central Nuclear Atucha I, 31 x 1995, N. v. Ellenrieder col., 2 o (MLP).

Remarks. Needham (1904) mentioned one mental seta and seven palpal setae for the single «mutilated» larva at his disposal, which he identified by association with adults from the same locality. This does not agree with *bona fide* reared material of *H. chelifera* from Argentina, which shows three and five setae respectively (Bulla, 1971a). Needham's description (1904) probably does not apply to this species.

Homeoura lindneri (Ris, 1928) (Figs. 4-6, 17, 33-36, 46-49, 75, 78-79, 89)

- Acanthagrion lindneri Ris, 1928: 41-44, figs. 1-2 (description of male and female, illustration of male \$10, comparison with A. ambiguum and A. cheliferum); Calvert, 1948: 23-24, figs. 18-22 (illustrations of male \$10, posterior lobe of prothorax and genital ligula based on specimen from Pirassununga, São Paulo state, Brazil); Fraser, 1947: 431 (mention from Argentina); Bulla, 1971a: 167-171, figs. 183-191 (redescription of adult); Bulla, 1971b: 49-51 (discussion of relationship with Argentagrion); Bulla, 1973: 95 (discussion of generic affinities, comparison with Cyanallagma bonariense and C. interruptum).
- Argentagrion lindneri; Donnelly & Alayo, 1966: 108-109 (discussion of history); Davies & Tobin, 1984: 66 (listed); Kiauta, 1988: 438 (incorrect statement of Argentagrion lindneri being a junior

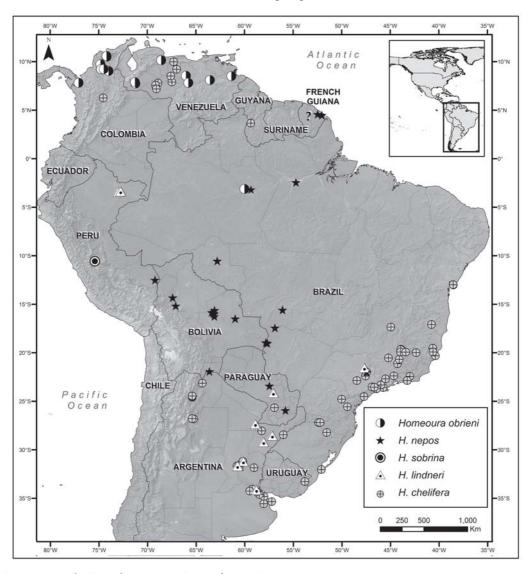


Fig. 89. Distribution of Homeoura in South America.

synonym of *A. nepos*); Rodrigues Capítulo *et al.*, 1991: 61 (listed); Steinmann, 1997: 246 (synonymic list).

- *Cianallagma lindneri*; Cruz, 1986: 745-747, fig. 8 (comparison with *C. demarmelsi*, illustration of female posterior prothoracic lobe and mesostigmal plates).
- Homeoura lindneri; De Marmels, 1989: 248 (comparison with Cyanallagma); Garrison (1991: 12; synonymic list); Rodrigues Capítulo, 1992: 54 (mention and distribution in Argentina); Bridges (1994: VII.135; list); Muzón & von Ellenrieder, 1998: 23 (mention and distribution in

Argentina); Tsuda, 2000: 34 (synonymic list); Costa *et al.*, 2000: 12 (mention from São Paulo); Lencioni, 2006: 36, 129, figs. 72A-C (distribution, illustration of male S10 and pt).

Ischnura sobrina; O'Grady & May, 2003: 2826, 2833 (character matrix based on male from Peru, Explorama Lodge) misidentified material.

Diagnosis. Pale postocular spots on dorsum of male and andromorphic female head (Figs. 4-5) large (larger than 1/3 of postocular lobe's width) and approximately oval (shared with *H. chelifera* and *H. nepos*), and pale postocular bar present (shared with H. nepos and H. obrieni), sometimes both are fused (Fig. 5); in heteromorphic female (Fig. 6) entire posterior area of dorsum pale (shared with all Homeoura species). Medial projection of posterior lobe of prothorax trapezoidal to rectangular in male (Fig. 33) and triangular to rectangular (Figs. 34-35) in female (shared with H. obrieni). Lateral margins of female mesostigmal plates (Fig. 36) are bluntly pointed (shared with H. obrieni). Pt (Fig. 17) rhomboidal (shared with H. chelifera). Second segment of genital ligula with a few thin hairs on each side or lacking hairs (Figs. 46-49), and bladed projections proximal to flexure in the shape of equilateral triangles, with acutely pointed apex and about as high as wide (Figs. 46-47; both shared with H. chelifera and H. obrieni). Male S8-9 entirely pale and S10 mostly pale, with black posterior margin (Figs. 78-79; unique). Dorsal and ventral margins of male cercus (Fig. 78) in lateral view diverging apically, and dorsal margin longer than ventral, so that apical width is larger than basal width, and apex is obliquely truncated dorso-ventrally (shared with *H. nepos* and *H. obrieni*).

Biology. Adults collected at ponds and marshes (locality data from collections). Larva unknown.

Distribution (Fig. 89). Peru (Loreto department), Brazil (São Paulo state), Paraguay (San Pedro department) and Argentina (Corrientes, Formosa, Chaco, Santa Fe and Buenos Aires provinces), from 14 to 630 m a.s.l.

Type material. $1 \circ 1 \circ 1$ syntypes in FNS [not examined].

Material examined ($12 \sigma 3 \phi$). PERU. Loreto: Explorama Lodge, 25 mi NE lquitos on Amazon River, 17/21 vii 1989, G. B. Edwards col., 1σ (SWD), Explorama Lodge, 50 mi NE lquitos on Amazon River at junction with Yanamono River, Manatí river and pasture pond at Lodge, 16/31 viii 1989, S.W. Dunkle col., $2 \sigma 1 \circ (SWD)$, same but 4 vii 1991, S.W. Dunkle col., $1 \sigma (SWD)$. **PARAGUAY. San Pedro:** Antequera, xii 1979, L. Strickman col., $1 \sigma (DRP)$. **ARGENTINA. Corrientes:** Laguna Iberá, 3 xi 2003, J. Muzón & P. Pessacq, $3 \sigma 2 \circ (MLP)$, Mercedes, 03 x 2004, F. Lozano & A. Garré col., $1 \sigma (MLP)$, same but $2 \sigma (RWG)$. **Santa Fe:** Laguna Don Felipe, E of Santa Fe, 01 iv 1971, C.M. & O.S. Flint, Jr. col., $1 \sigma (RWG)$.

Remarks. Kiauta (1988) in an abstract review declared «*Argentagrion*» *lindneri* a synonym of «*A*.» *nepos* with no further discussion («....further, *lindneri* is in *Argentagrion*, and is a junior synonym of *nepos*.»). My examination shows them to be distinct.

Homeoura nepos (Selys, 1876) (Figs. 7, 10, 19, 25-27, 50-52, 63-64, 73, 80-81, 89)

- Agrion? nepos Selys, 1876: 1246-1247, 1249-1250 [reprint 136-137, 139-140] (description of male).
- *Coenagrion? nepos*; Kirby, 1890: 148 (mention).
- *Ischnura? nepos*; Calvert, 1909: 206-209, figs. 121-122 (description of female, illustration of male S10); Calvert, 1948: 9-10 (incomplete description of larva by supposition).
- Homeoura nepos; Kennedy, 1920: 88 (designation as type species of Homeoura); De Marmels, 1989: 248 (comparison to Cyanallagma); De Marmels, 1990: 335 (mention from Venezuela); Garrison, 1991: 12 (synonymic list); Bridges (1994: VII.163; list); Tsuda, 2000: 34 (synonymic list); Costa et al., 2000: 12 (mention from São Paulo); May, 2002: 407 (character matrix); Lencioni, 2006: 36, 130, figs. 73A-H (distribution, illustration of male head, thorax, pronotum, pt, abdomen, genital ligula and S10).
- Argentagrion nepos; Davies & Tobin, 1984: 66 (listed); Kiauta, 1988: 438 (incorrect statement of Argentagrion lindneri being a junior synonym of A. nepos); Machet,

1989: 11 (mention from French Guiana); Steinmann, 1997: 246 (synonymic list).

Diagnosis. Pale postocular spots on dorsum of male head (Figs. 7, 10) large (larger than 1/3 of postocular lobe's width) and approximately oval (shared with H. chelifera and H. lindneri), sometimes with concave anterior margin and pale postocular bar present (shared with H. lindneri and H. obrieni), in heteromorphic female entire posterior area of dorsum pale (shared with all Homeoura species). Medial projection of posterior lobe of prothorax approximately rectangular (shared with H. chelifera) with posterior margin slightly concave to linear (Figs. 27-28), reduced to absent in some females (Fig. 25). Lateral margins of female mesostigmal plates (Fig. 26) bluntly rounded, anterior and posterior margins approximately parallel-sided (Fig. 26; unique). Pt (Fig. 19) quadrangular (shared with H. obrieni). Second segment of genital ligula with a dense row of strong hairs on each side (Figs. 50-52; unique), and bladed projections are proximal to flexure with bluntly pointed apex and considerably wider than high (Fig. 50; unique). Dorsum of male S8 entirely black, of S9 mostly pale with black anterior margin, of \$10 entirely or mostly black (Figs. 64, 80-81; unique). Dorsal and ventral margins of male cercus (Fig. 80) in lateral view diverging apically, and dorsal margin longer than ventral, so that apical width is larger than basal width and apex is obliquely truncated dorsoventrally (shared with H. lindneri and H. obrieni).

Larval prementum with two long and two short mental setae and four palpal setae (Calvert, 1948).

Biology. Adults found at lentic environments (locality data from collections). Larva described by supposition by Calvert (1948) based on an incomplete specimen from a dam in Pirassununga, Brazil.

Distribution (Fig. 89). Brazil (Amazonas, Pará, Rondônia, São Paulo, Mato Grosso and Mato Grosso do Sul states), Paraguay (Concepción and Amambay departments) and Bolivia (Beni, Santa Cruz and Tarija departments), from 10 to 635 m a.s.l.

Type material. Holotype σ from IRSNB currently on loan to MNRJ [not examined].

Material examined (23 of 14 o). PERU. Madre de Dios: Explorer's Inn on Rio Tambopata, 30 km SW Puerto Maldonado, oxbow lake, 15 /16 vi 1977, D.R. Paulson col., 1 o 1 o (DRP). BRAZIL. Pará: Santarem, 1-31 v 1919, S. M. Klages col., 1 o 1 o (RWG), same but iv/ vii 1919, 4 o 2 o (FSCA). Rondônia: 60 km S of Ariquemes, Fazenda Rancho Grande, farm of Harold Schmitz and environs within about 15 km radius, 16/24 iii 1989, S. W. Dunkle, $1 \sigma 3 \circ$ (SWD), same but 15/ 22 iii 1991, F. W. Skillman Jr. col., 1 o (SWD). BOLIVIA. Beni: Reyes, 27-30 xi 1957, L. Peña col., 1 o (RWG). Santa Cruz: Provincia del Sara: J. Steinbach col., 1 o (FSCA), Puerto Suárez, xi 1960, 5 o 4 o (RWG), Los Lajas hacienda and lagunas, 5 km S Guarayos, 27 viii 2003, B. Mauffray col., 1 o (FSCA), 1.5 km N Urubicha, Río Blanco and adjacent laguna Guarayos, 19 viii 2003, B. Mauffray col., 1 o 1 o (FSCA), 1.7 km W Ascención de Guarayos, laguna La Tejerina, 14 viii 2003, B. Mauffray col., 2 o (FSCA), 15 km W Yotau, Cachuelos de Yotau, 15 viii 2003, B. Mauffray col., 1 o (FSCA), hacienda Progreso and lagunas, 13 km S on Hwy 9, 17 viii 2003, B. Mauffray col., 1 o 1 o (FSCA), 23.5 km N on Hwy 9 of Ascención de Guarayos, borrow pit pond and adjacent forest, 26 viii 2003, B. Mauffray col., 1 o (FSCA). PARAGUAY. Amambay: Cerro Cora, 16/17 viii 1980, L. Strickman col., 1 o 1 o (DRP).

Remarks. As stated above, the holotype is currently deposited in the MNRJ, where RWG examined it and illustrated the head (Fig. 10), thorax (Figs. 28, 63), genital ligula (Figs. 51, 52), and S1-3, 7-10 (Fig. 64). Although the appendages are missing, comparisons of RWG illustrations of pronotum and color pattern with material I have identified as this species show that I have correctly applied the name to material

discussed here. Synonymy of «*Argentagrion» lindneri* with «*A.» nepos* by Kiauta (1988) is discussed under *H. lindneri* above. The records of *H. nepos* from la Guyane department, French Guiana (Machet, 1989) need to be confirmed by examination of specimens, since they could as well correspond to *H. obrieni* (Fig. 89).

Homeoura obrieni sp. nov. (Figs. 8-9, 14, 20, 37-40, 53-55, 61-62, 74, 82-83, 89)

- Argentagrion lindneri; Rácenis, 1958: 191-193 (placement in Argentagrion, comparison with original description and redescription of *A. lindneri* by Calvert, 1948, based on male from Suripá, Estado Barinas, 14.iii.1954, Szumkowsky leg.) misidentified material.
- Argentagrion nepos; Donnelly & Alayo (1966: 108-109, fig. 3; at least in part, specimen from Aracataca, Colombia; illustration of genital ligula) misidentified material.
- *Homeoura nepos*; De Marmels (1990: 335; mention from Venezuela) misidentified material.

Diagnosis. Pale postocular spots on dorsum of male head (Fig. 8) about as large as 1/3 of postocular lobe width and approximately rounded, and pale postocular bar present (shared with H. lindneri and H. nepos). Medial projection of posterior lobe of prothorax is rhomboidal in male (Figs. 37-38) and triangular (Fig. 39) in female (shared with H. lindneri). Lateral margins of females' mesostigmal plates (Fig. 40) are bluntly pointed (shared with H. lindneri). Pt (Figs. 14, 20) quadrangular (shared with *H. nepos*). Dorsum of male S8 partially black, always distally pale, S9 entirely pale and S10 mostly pale, with black posterior margin (Figs. 82-83; shared with H. chelifera) or black anterior and posterior margins, occasionally joined by black narrow mid-dorsal stripe. Dorsal and ventral margins of male cercus (Fig. 82) in lateral view diverging apically, and dorsal margin longer than ventral, so that apical width is larger than basal width and apex is obliquely truncated dorso-ventrally (shared with *H. lindneri* and *H. nepos*).

Description. Male holotype. Head: labium pale yellow; labrum, base of mandibles, anterior surface of genae and anteclypeus light blue, with a basal black stripe on labrum and two short black stripes on anteclypeus; postclypeus, dorsal surface of genae, frons, antennae and top of head black, with a small pale blue spot anterior to lateral ocellus, large pale blue postocular spot and occipital bar; back of head pale blue, with a black rounded spot to each side of occipital foramen. Frons in profile rounded. Thorax: prothorax black with pale blue spots; medial lobe of posterior prothoracic lobe trapezoidal (as in Figs. 37-38). Dorsum of pterothorax black with complete pale blue antehumeral stripe about as wide as a fourth of mesepisternum, slightly widened at anterior and posterior ends; sides pale blue with a small black spot on posterior end of metapleural suture (as in Fig. 61). Venter of thorax pale yellow, with a low postero-medial rounded tubercle. Legs yellow with black spurs, extensor surface of femora, a narrow stripe along outer side of tibiae and distal tip of tarsi and pretarsi (as in Fig. 61). Spurs on femora and tibiae shorter than intervening spaces; pretarsal claw with well developed supplementary tooth (as in Fig. 61). Wings (as in Fig. 14) hyaline; pt reddish brown, quadrangular, shorter than underlying cell, with anterior (costal) margin the shortest (as in Fig. 20); CuP reaching CuPAA distal to confluence of CuPAA with A, for a distance equal to CuP in FW, and shorter than CuP in HW, petiolation ending at about a third of the distance between Ax 1 and Ax 2; Px 7 in FW, 6 in right HW, 8 in left HW; RP2 branching between Px 3 and 4 but closer to 4 in FW and right HW, midway between Px 3 and 4 in left HW. Abdomen: S1pale blue with dorsal black spot on basal two thirds; dorsum of S2 black, sides pale blue; dorsum of \$3-7 black except basal pale blue ring, sides pale blue; S8 pale blue with black spot on an antero-dorsal three fifths; S9 pale blue; S10 pale blue with narrow transverse anterodorsal and postero-dorsal black stripes. Cercus (as Figs. 74, 82-83) shorter than S10,

with a ventro-basal triangular process directed anteriorly on inner margin; a distal area of differentiated scalariform like cuticle (May, 2002) on mesal surface (as in Fig. 74); dorsal margin slightly longer than and diverging gradually from ventral margin, so that posterior margin is oblique (as in Fig. 82); color black except pale brown mesal surface and distal portion of outer surface. Paraproct yellow, with a small medially directed black tooth on dorsal end (as in Fig. 74). Second segment of genital ligula with a few thin hairs on each side (as in Figs. 53-55), and bladed projections proximal to flexure in the shape of equilateral triangles, with acutely pointed apex and about as high as wide (as in Figs. 53-54).

Dimensions: total length 25.7 mm; abdomen length 20.6 mm; FW 13mm; HW 12.2 mm.

Female allotype. Head: as in holotype but postclypeus pale blue with anterior margin black; pale spot anterior to lateral ocellus larger; additional small pale spot posterior to base of antenna; pale blue postocular spot confluent with pale occipital bar. Thorax: color pattern as in holotype but pale blue areas on prothorax more extensive; and a narrow yellow stripe along humeral suture; legs as in holotype but black areas brown. Medial lobe of posterior prothoracic lobe bluntly triangular (as in Fig. 39); mesostigmal plate with basal constriction, so that anterior and posterior margins diverge basally; lateral sides bluntly rounded (as in Fig. 40). Wings as in holotype but pt yellow, Px 10 in right FW, 8 in left FW, 7 in right HW, 7 in left Hw; RP2 branching between Px 3 and 4 but closer to 4 in all wings. Abdomen: color pattern as in male holotype, except for dorsum of \$1-7 black with only very narrow pale anterior ring, black on dorsum of S8 reaching posterior margin but very narrowly along posterior fourth of S8; dorsum of S9 with a black triangular spot on each side of anterior margin (as in Fig. 62). Cercus shorter than S10, conical and dark reddish brown; paraprocts yellow. Vulvar spine on S8 well developed, with black tip. Sub-basal plate of ovipositor small and

triangular; outer valve of ovipositor with a single row of teeth; tip of ovipositor (excluding stylus) extending slightly beyond posterodorsal margin of S10 (as in Fig. 62).

Dimensions: total length 27.8 mm; abdomen length 22.3 mm; FW 15.3 mm; HW 14.5 mm.

Variation in paratypes. Heteromorphic females with entire posterior area of head dorsum pale (Fig. 9), and thorax entirely pale. Dorsum of S8 and S9 as holotype in some females. Male paratypes Px in FW 8-6, in HW 5-7; RP2 branching between Px 3 and 4 in FW, usually closer to 4, at Px 3 or 4 in HW, usually closer to 4. Female paratypes Px in FW 7-9, in HW 6-7; RP2 branching between Px 3 and 4 in FW, usually closer to 4, at Px 3 or 4 in HW, usually closer to 4. Dimensions: abdomen length in males 18.5-22.2 mm [mean 20.73 mm; SD 0.79; n 40]; abdomen length in females 20-22.3 mm [mean 21.29 mm; SD 0.61; n 23]; HW males 11.1-13.5 [mean 12.54 mm; SD 0.52; n 40]; HW females 13.2-14.75 mm [mean 13.9 mm; SD 0.5; n 23].

Biology. Adults found at lentic environments (locality data from collections). Larva and habits are unknown.

Distribution (Fig. 89). Venezuela (Barinas, Delta Amacuro, Guárico and Yaracuy states), Colombia (Bolívar, Magdalena and Chocó departments) and Brazil (Amazonas state), from 0 to 870 m a.s.l.

Etymology. Named after my colleague Mark O' Brien, in gratitude for his manifold assistance to students interested in the rich dragonfly collection in UMMZ.

Type material. Holotype σ : COLOMBIA. Bolívar: Palermo, 19 i 1917, E.B. & J.H. Williamson col. (UMMZ). Allotype φ : COLOMBIA. Magdalena: Aracataca, 9 i 1917, E.B. & J.H. Williamson col. (UMMZ). Paratypes (40 σ 23 φ): VENEZUELA. Yaracuy: Nirgua, 28 ii 1920, J.H. & E.B. Williamson col., 1 σ (RWG). COLOMBIA. Magdalena: same as allotype but 6 σ 6 φ (UMMZ), 2 σ 2 φ (FSCA), 2 σ (RWG), 2 σ 1 φ (MLP), 15 xii 1916, 2 σ (UMMZ), Fundación, S of Aracataca, 12-14 i 1917, E.B. & J.H. Williamson col., 1 φ (RWG), same but 1 σ (UMMZ), El Banco, 24 I 1917, E.B. & J.H. Williamson col., 1 σ 1 φ (UMMZ). **Bolívar**: same as holotype but 5 σ 2 φ (UMMZ), 6 σ 1 φ (RWG), Zambrano, 20 i 1917, E.B. & J.H. Williamson col., 3 σ 1 φ (RWG), same but 1 σ 1 φ (UMMZ), near Magangue, 21 i 1917, E.B. & J.H. Williamson col., 1 σ 5 φ (RWG), same but 2 σ 2 φ (UMMZ). **Chocó:** Sautatá, 6 ii 1918, M.A. Carriker col., 3 σ (UMMZ).

Other material examined. BRAZIL. Amazonas: Manaus, 16 vi 1922, J.H. Williamson & J.W. Strohm col., 1 incomplete σ, lacking S8-10 (FSCA).

Remarks. This species most closely approaches *H. nepos* and was so confused with it in the past, but it differs (alternative characters for *H. nepos* in square brackets) by medial portion of posterior lobe of prothorax rhomboidal or triangular, roundly (Fig. 37) to angularly (Fig. 38) convex in male [rectangular with posterior margin linear to concave, Figs. 27-28], forming a triangular lobe in female (Fig. 39) [slightly sinuate, Fig. 25]; female mesostigmal plates with anterior and posterior margins not parallel sided, and lateral margins bluntly pointed (Fig. 40) [anterior and posterior margins approximately parallel-sided, and lateral margins bluntly rounded, Fig. 26]; second segment of genital ligula with a few thin hairs on each side (Figs. 53-55) or lacking hairs [second segment of genital ligula with a dense row of strong hairs on each side (Figs. 50-52)], and bladed projections proximal to flexure in the shape of equilateral triangles, with acutely pointed apex and about as high as wide (Figs. 53-54)[bladed projections with bluntly pointed apex and much wider than high (Fig. 50)]; dorsum of male S8 distally pale (Figs. 82-83) [dorsum of male S8 distally black, Figs. 80-81]; larger species: male abdomen length 18.5-22.2 mm, mean 20.73 mm, SD 0.79; female abdomen length 20-22.3 mm,

mean 21.29 mm, SD 0.61 [smaller species: male abdomen length 16.5-18.5 mm, mean, 17.74 mm, SD 0.64; female abdomen length 16.9-19.8 mm, mean 18.61 mm, SD 1.05].

The distributions of *H. nepos* and *H.* obrieni are apparently allopatric (Fig. 89) along most of their ranges, meeting only in Amazonas state, Brazil. The only male I examined from Manaus, Amazonas state (UMMZ) agrees with H. obrieni in the shape of its pronotal posterior lobe, larger size (HW of 13.5 mm; range in males of H. nepos (n 17): 10.2-12 mm; in males of H. obrieni (n 42): 11.1-13.5 mm), and genital ligula characters (second segment devoid of evident hairs on each side, and bladed projections proximal to flexure with acutely pointed apex and about as high as wide).Since S8-10 are missing, I did not include it in the type series. J. De Marmels (pers. comm.) kindly shared his records (MIZA) and confirmed the presence of H. nepos in Manaus, Amazonas state. The records of H. nepos from French Guiana (Machet, 1989) could correspond to this species (see remarks under H. nepos).

Homeoura sobrina (Schmidt, 1942) comb. nov.

(Figs. 11-12, 72, 84-85, 89)

Ischnura sobrina Schmidt, 1942: 237-239, figs. 7a-f (description of male and female, illustrations of male and female head, male S8-10); Rácenis, 1959: 477 (mention from Peru); Garrison, 1991: 12 (synonymic list); Bridges, 1994: VII.220 (list); Steinmann, 1997: 277 (synonymic list); Tsuda, 2000: 37 (synonymic list).

Diagnosis [based on original description]. Pale postocular spots on dorsum of male head (Fig. 11) rounded and minute (smaller than 1/6 of postocular lobe's width; unique), and no pale postocular bar present (shared with *H. chelifera*); in heteromorphic female (Fig. 12) entire posterior area of head dorsum pale (shared with all *Homeoura* species). Male pterothorax with black stripe along metapleural suture (unique); in heteromorphic female there is a black narrow stripe along metapleural suture (unique) beside the medio-longitudinal black stripe on dorsum. Dorsum of male S8-9 pale and sides black (unique), both dorsum and sides of S10 black (Fig. 84). Dorsal and ventral margins of male cercus (Fig. 84) approximately parallel and of equal length in lateral view, so that apical width is approximately the same as basal width, and apex is roundly truncated (shared with *H. chelifera*); apex slightly bent ventrally. Dorso-posterior margin of male S10 (Figs. 72, 84-85) with u-shaped cleft and two marginal tubercles situated on apex of a projection (unique).

Biology. Larva and habits are unknown.

Distribution (Fig. 89). Peru (Pasco department) at 3000 m a.s.l.

Remarks. Based on its description, this species belongs in Homeoura, displaying diagnostic characters of this genus as regards male cerci morphology. Schmidt (1942) already noted its similarity to 'Ischnura' nepos. He did not describe its genital ligula, and the only specimens so far known comprise the type series originally deposited in Schmidt's collection. Unfortunately, their current location is unknown. Dr. E. Schmidt's collection was inherited by Dr. S. Asahina (Dr. W. Schneider pers. comm.), and Dr. Asahina's collection was in turn donated to the National Museum of Nature and Science in Tokyo, Japan (Dr. H. Ubukata pers. comm.). However, no type specimens from Schmidt are found in this collection (http:// www.type.kahaku.go.jp/TypeDB).

Key to species of Argentagrion and Homeoura

1- Posterior lobe of prothorax in both sexes broadly bilobate (Figs. 21, 23) or with a medial triangular apophysis (Fig. 22); postero-dorsal margin of male S10 entire (Figs. 65, 68-70), usually with a small medio-dorsal apophysis (Figs. 69, 70); inner surface of genital ligula proximal to flexure smooth (Figs. 41, 43); distal

- 1'- Posterior lobe of prothorax trilobate with a differentiated medial process, which is trapezoidal (Figs. 33, 37-38) or rectangular (Figs. 27-30) in male, triangular (Figs. 34-35, 39), rectangular (as in Fig. 30) or barely bilobate(Fig. 31) in female; postero-dorsal margin of male S10 with a u-shaped medial cleft with a tubercle on each side (Figs. 71-85); inner surface of male genital ligula proximal to flexure provided with a pair of sclerotized projections shaped as triangular blades (Figs. 46-47, 49-50, 53-54, 56, bl); male cercus approximately horizontal with a ventrally directed laminar branch at base (Figs. 71-85 Homeoura ... 3

- 3- Pale postocular spots of male (Fig. 11) minute (less than 1/6 of postocular lobe's width); complete black stripe on male metapleural suture, and narrow black stripe on metapleural suture of

- 4- Pt approximately quadrangular, with costal side the shortest (Figs. 14, 19-20)
- 4'- Pt approximately rhomboidal, with costal side the longest (Figs. 16-17) ... 6
- 5- Medial portion of posterior lobe of prothorax approximately rectangular, with posterior margin slightly concave (Fig. 28) to linear (Fig. 27) in male, and slightly sinuate in female (Fig. 25); female mesostigmal plates with anterior and posterior margins approximately parallel sided, and lateral margins bluntly rounded (Fig. 26); second segment of genital ligula with a dense row of strong hairs on each side (Figs. 50-52), and bladed projections proximal to flexure with bluntly pointed apex and much wider than high (Fig. 50); dorsum of male S8 entirely black (Figs. 80, 81); smaller species (males' abdomen length 16.5-19.1 mm, mean, 17.82 mm, SD 0.7; females' abdomen length 16.9-19.8 mm, mean 18.61 mm, SD 1.05) Homeoura nepos (Selys)
- 5'- Medial portion of posterior lobe of prothorax rhomboidal or triangular, with posterior margin roundly (Fig. 37) to angularly (Fig. 38) convex in male, forming a triangular lobe in female (Fig. 39); female mesostigmal plates with anterior and posterior margins not parallel sided, and lateral margins bluntly pointed (Fig. 40); second segment of genital ligula with a few thin hairs on each side (Figs. 53-55) or

lacking hairs, and bladed projections proximal to flexure in the shape of equilateral triangles, with acutely pointed apex and about as high as wide (Figs. 53-54); dorsum of male S8 distally pale (Figs. 82-83); larger species (males' abdomen length 18.5-22.2 mm, mean 20.73 mm, SD 0.79; females' abdomen length 20-22.3 mm, mean 21.29 mm, SD 0.61) *Homeoura obrieni* sp. nov.

DISCUSSION

As pointed out by Bulla (1971b), Rácenis' (1958) rediagnosis of *Argentagrion* (venation reduced, 6-10 postnodals, male paraprocts shorter than half of cerci, and smaller size: abdomen 18-23 mm; HW 12.5-15 mm) will not allow for the inclusion of *A. silviae* (with

paraprocts almost as long as cerci), and both A. ambiguum and A. silviae differ in several characters from H. cheliferum and H. lindneri, precluding their placement in the same genus. Although he did not study all species involved, when redefining Cyanallagma De Marmels (1989, 1997) advocated the same placement I am proposing here for these species: Argentagrion ambiguum, Homeoura chelifera, H. nepos and H. lindneri. Unfortunately these observations went unnoticed, and the treatment of all species as congeneric by Rácenis (1958) and Davies & Tobin (1984) was instead followed (Garrison, 1991; Steinmann, 1997; Muzón & von Ellenrieder, 1998; Costa et al. 2000; Tsuda, 2000; Lencioni, 2006).

In their cladistic analysis designed to test sub-familiar divisions within Coenagrionidae, O'Grady & May (2003) included one species, each of Argentagrion (A. ambiguum as Homeoura ambigua) and Homeoura (H. lindneri as Ischnura sobrina). These two species clustered together only in the analysis based solely on sub-familiar characters used by Fraser (1957) and Davies & Tobin (1984), but not in their analyses when based on all characters and on non-continuous and unambiguously defined characters (O'Grady & May, 2003: 2820-2821), supporting my hypothesis that Homeoura sensu lato (including all species treated here under Argentagrion and Homeoura) constitutes a polyphyletic assemblage.

The last larval instar of only one species is known satisfactorily for each Argentagrion and Homeoura, differing by the shape of caudal lamellae: in A. ambiguum, the base of the caudal lamella is dark with nondiscernible tracheae, and primary and secondary tracheae on the distal portion are equally pigmented (Fig. 86), whereas in H. chelifera, the base of the caudal lamella is not differentiated from the distal portion: there are three diffuse dark spots along its midline, and secondary tracheae are much darker than primary (Fig. 87). Whether these differences are of generic value will be established only when larvae of more species are known.

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