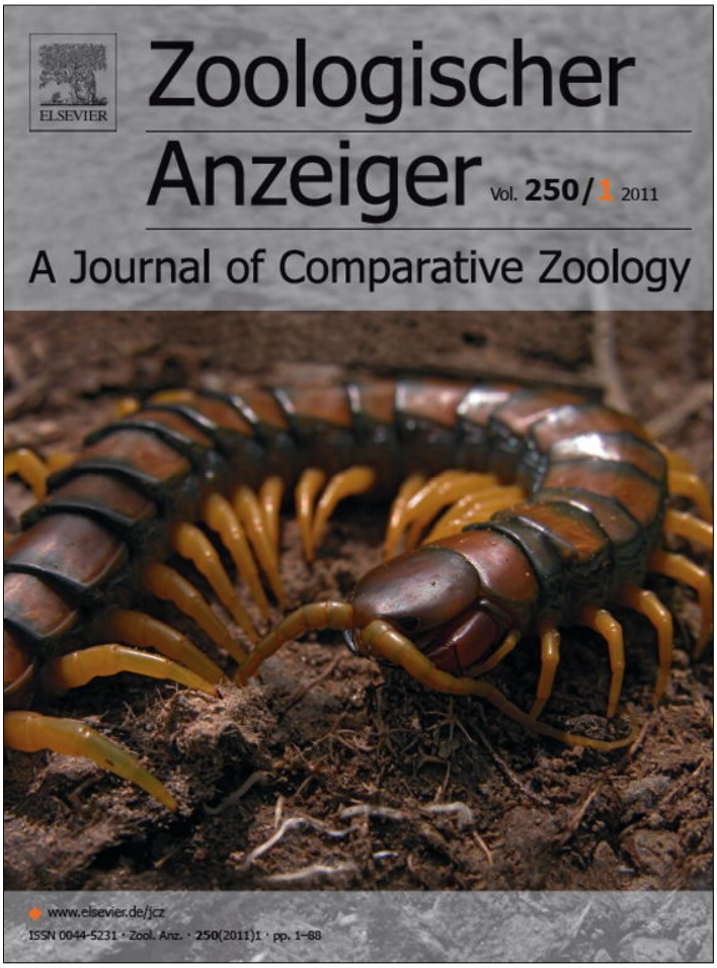
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Weberiella De Carlo, 1966 (Insecta: Heteroptera: Belostomatidae) revisited: Redescription with a key to the genera of Belostomatidae and considerations on back-brooding behaviour

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Abstract

Males of some subgroups of Belostomatidae brood the eggs attached to their backs, whereas the eggs are attached to the vegetation by females in others. Male brood care is obligatory in the belostomatine species of *Abedus* Stål, 1862, *Belostoma* Latreille, 1807, *Diplonychus* Laporte, 1833, *Hydrocyrius* Spinola, 1850, and *Limnogeton* Mayr, 1853. Recent investigations into relationships among Neotropical Belostomatinae have led authors to recognize a clade Belostomatinae, which is mainly characterized by back-brooding behaviour. It is likely that *Weberiella* belongs to this clade. Males of the only described species *W. rhomboides* (Menke, 1965) are reported as carrying eggs on their back for the first time here. Since this species was described based on a single female specimen from French Guiana, *W. rhomboides* is redescribed based on specimens from Amazonas, Mato Grosso, Rondônia, and Roraima States, Brazil. Its distribution in Brazil is mapped. The scale-like abdomen is a presumably autapomorphic condition not found in the other belostomatid species. A key to the genera of Belostomatidae including Lethocerinae and Horvathiniinae is provided. Even though a formal parsimony analysis is not presented here, a placement of *W. rhomboides* in Belostomatinae is tentatively suggested based on the back-brooding behaviour of males as a shared apomorphy. Convergent evolution cannot be excluded as suitable vegetation for depositing eggs is not available in the specific habitat (kinon) of *W. rhomboides*.

Keywords: Giant water bugs; Kinon; Paternal care; Systematics

1. Introduction

Giant water bugs or Belostomatidae contain over 140 species in eleven genera. Polhemus (1995) and Perez-Goodwyn (2006) have recently re-erected three of these genera: *Appasus* Amyot and Serville, 1843, *Benacus* Stål, 1861 and *Kirkaldyia* Montandon, 1909. According to Lauck and Menke (1961), the family is divided into three subfamilies. The subfamily Belostomatinae was originally erected by Lauck and Menke in 1961 to include *Abedus* Stål, 1862, *Belostoma* Latreille, 1807, *Diplonychus* Laporte, 1833, *Hydrocyrius* Spinola, 1850, and *Limnogeton* Mayr, 1853. Mahner (1993) carried out the first phylogenetic analysis of Belostomatidae based on morphological characters using the "classical" Hennigian approach. The results supported the monophyly of Belostomatinae, which is a diverse assemblage of six monophyletic groups recognized, and each was given generic status in accordance with traditional

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concepts (Lauck and Menke, 1961). In addition, characters of the head, thorax, abdomen, male genitalia and reproductive behaviour led Mahner (1993) also to recognize more two main monophyletic lineages, Lethocerinae and Horvathiniinae. Lethocerinae containing only the genus *Lethocerus* Mayr, 1853 is placed as the sister group of a clade comprising Horvathiniinae and Belostomatinae. In Mahner's (1993) work, Belostomatinae comprises three from the Old World (*Diplonychus*, *Hydrocyrius* and *Limnogeton*) and two from the New World (*Abedus* and *Belostoma*). Belostomatinae was characterized by Lauck and Menke (1961) and Mahner (1993) by several autapomorphic features, including the back-brooding behaviour. Among the Belostomatinae, only the New World genus *Weberiella* De Carlo, 1965, which is an enigmatic South American genus with a strangely limited distribution (Fig. 3), has been erroneously considered a taxon without apparent morphological features by Mahner (1993, see for more details). Assuming this genus monophyly for the moment, a recent analysis indicates that *Weberiella* is probably basal relative to *Appasus* + *Diplonychus* + Belostomatini otherwise (Ribeiro, in preparation).

In contrast to the emergent-brooding Lethocerinae belostomatine bugs are back-brooders, i.e., females lay eggs on the backs of the males, where they remain until the hatching of larvae. A position of *Horvathinia* Montandon, 1911 and *Weberiella* between Lethocerinae and Belostomatinae was suggested by Mahner (1993), in his phylogenetic analysis, and Smith (1997). No member of *Horvathinia* has ever been collected in its aquatic habitat, and there is almost nothing published on their ecology or reproductive behaviour. *Horvathinia* species could be emergent-brooders (Smith, 1997) as females were observed in the laboratory depositing eggs in moist sand outside of the water. However, this may not have been the regular behaviour as none of these eggs hatched. Females of back-brooding belostomatine bugs are known to use alternative depositing sites if suitable males are unavailable. For instance, *Belostoma elegans* (Mayr, 1871) females have been obeserved depositing eggs on small rocks in the laboratory (Schnack and Estévez, 2005).

Among insects, the back-brooding behaviour of males (an exclusive postcopulatory paternal care) is restricted to few families of Hemiptera, and all but a few of them are water bugs of the subfamily Belostomatinae. Male belostomatine bugs invest time and energy in brooding eggs attached to their backs by females (Smith, 1980), even though this phenomenon of egg nursery can vary in some details within the subfamily (Schnack and Estévez, 1990).

Up to now nothing was known about oviposition and life history of *Weberiella*, one that is a lineage of apparently basal Belostomatinae and a monotypic genus restricted to small areas in Guyana and Brazil (Menke, 1965; De Carlo, 1966; Nieser, 1975). The only known living species was described by Menke (1965) as *B. rhomboides* Menke, 1965 (based on a single female). He pointed out the presence of air straps and a narrow hemelytral membrane like in *Belostoma* species, and one-segmented foretarsi like in *Horvathinia pelocoroides* Montandon, 1911 and *Diplonychus urinator urinator* (Dufour, 1863). The type-specimen designated by Menke is from French Guiana and is deposited in the Los Angeles County Museum, USA.

Additionally, De Carlo (1966) examined male and female specimens of *B. rhomboides* from Branquinho river and Marauá river, Amazonas State, Brazil, which he erroneously considered as "paratypes" (a male allotype and four paratypes deposited in the Max-Planck-Institut für Limnologie, Plön, Germany; a male paratype and two female paratypes deposited in the Museo Argentino de Ciencias Naturales, Argentina [De Carlo, 1966: 100]). This allowed him to describe and figure both sexes of this species and to establish the new monotypic genus *Weberiella* for Menke's species, *B. rhomboides*, characterised by a phallobase without arms, serrate abdominal margins, and allegedly "one-segmented foretarsi". He was the first to use male genitalia in his taxonomic treatment. Later, Nieser (1975) redescribed the type material from French Guiana as well as the supposed male allotype from Amazonas (Menke, 1965). He remarked that *Weberiella* differs from the other genera of Belostomatidae by the generic characteristics given by De Carlo (1966). Based on similarities of the antennae of *Weberiella* and *Belostoma* and the reduced hemelytral membrane, he included *Weberiella* in the subfamily Belostomatinae.

Study of specimens from the surface film of freshwaters (an entire coenosis of the surface film of freshwaters called "kinon", as defined by Fittkau, 1977) in Brazil and Guyana resulted in the discovery of males with eggs on the dorsum. After studying them, other conspecific male and female specimens were found at the collections of the Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil), Museo Argentino de Ciencias Naturales "B. Rivadavia" (Buenos Aires, Argentina) and Museo de Ciencias Naturales de La Plata (La Plata, Argentina). A more comprehensive redescription of *W. rhomboides* is presented herein, and the number of segments of the foretarsi (De Carlo, 1966; Menke, 1965; Nieser, 1975) is corrected. The redescription includes modifications and clarifications of non-genitalic and male genitalic features, which were inaccurately described by De Carlo (1966) and Nieser (1975). As emergent-brooders require emergent vegetation, which is absent from many aquatic habits (Smith, 1997) such as for instance the kinal, i.e., the biotope of the surface drift, we briefly discuss here the possibility of the placement of kinobiontic forms of *Weberiella* in the subfamily Belostomatinae.

Finally, new locality records for the species are provided and its distribution in Brazil is mapped. We also present the first taxonomic key to all genera of Belostomatidae including those recently re-erected.

2. Material and methods

Acronyms of collections in which the specimens are deposited are the following: INPA (Instituto Nacional de

Pesquisas da Amazônia, Manaus, Brazil); MACN (Museo de Ciencias Naturales "B. Rivadavia", Buenos Aires, Argentina); and MLPA (Museo de Ciencias Naturales de La Plata, Universidad Nacional de La Plata, La Plata, Argentina). In quotations of label data, a comma separates different information and a period separates information on different specimens. Collectors and insect collection institutions are cited in parentheses. The full citation of individual specimens collected at the same locality on different dates is not cited. A semicolon separates different specimens with same information. The letter "m" refers to male specimens and the letter "f" to female ones. All localities are listed geographically from North to South. The known geographic distribution of each genus is given in the key. All measurements are in mm and based on all examined specimens. Measurements were made with an ocular micrometer on a stereoscopic microscope, except those of total body length and largest width of body, which were made with manual calipers accurate to 0.1 mm. The dissected genital structures are stored in microvials with glycerin.

The terminology of the head, thorax, and abdomen follows Menke (1965) and De Carlo (1966). The studied material was described using the structural characteristics which are of taxonomic importance in describing other members of Belostomatinae (Lauck and Menke, 1961; Kopelke, 1978; Estévez and Polhemus, 2001; Ribeiro and Estévez, 2009).

To avoid redundant situations created by the use of monotypic supraspecific categories (see Papavero and Llorente-Bousquets, 1993), i.e., names including a single taxon, Belostomatidae species were used instead of monotypic genera.

3. Results

3.1. Taxonomic key to Belostomatidae genera (based on Lauck and Menke, 1961, Polhemus, 1995 and Perez-Goodwyn, 2006)

Since numerous figures have been published for each of the remaining genera treated here, and in the absence of male specimens of some genera, only drawings and photographs of *W. rhomboides*, in particular those concerning male genitalia, were included in this key.

1a. Segment 1 of rostrum short, thicker than long and obviously shorter than segment 2; abdominal sternites 5 and 6 subdivided laterally by suture-like fold; spiracles located on or adjacent to mesal margins of ventral laterotergites ("connexiva" of authors)... 2

1b. Segment 1 of rostrum much longer than greatest thickness (Fig. 1C and D), subequal in length to segment 2; abdominal sternites not subdivided by a suture (Fig. 1F); spiracles located near center of ventral laterotergites (subfamily Belostomatinae)... 5

2a (*1a*). Antennal segments 2 and 3 with long, sometimes angular, finger-like projections; segment 4 with two projections; foretarsus 3-segmented (often appearing 2-segmented externally) and bearing one long claw; mesal margins of ventral laterotergites meeting genital plate near its apex; tibia and tarsus of hind leg thinly compressed, much more dilated than middle tibia and tarsus; aedeagus and ventral diverticulum separate; genital operculum of females with spines and acutely rounded at apex (subfamily Lethocerinae)... 3

2b. Antennal segment 2 large, expanded and flattened ventrally, bearing finger-like projection dorsally; segment 3 with large expanded and flattened dorsal lobe; segment 4 short, dorsoventrally elongate; foretarsus 2-segmented (often appearing 1-segmented), bearing two very short, vestigial claws; mesal margins of ventral laterotergites ending at basal angle of genital plate; tibia and tarsus of middle and hind legs similar, narrow, flattened but not broadly dilated; aedeagus and ventral diverticulum fused; genital operculum of females fringed with hairs, rounded at apex... (subfamily Horvathiniinae) *Horvathinia* Montandon [Argentina, Bolivia, Brazil, Paraguay]

3a (*2a*). Inner pad of setae of forefemur with two furrows; pads of hind femur with just one; external borders of ventral laterotergites 2 and 3 narrowed, almost straight... 4

3b. Inner pad of setae of forefemur without any trace of furrow; pads of hind femur with just a deep cleft, but not divided; external borders of ventral laterotergites 2 and 3 not narrowed, arcuate, following borderline of abdomen... *Benacus griseus* (Say) [Canada, Colombia, Cuba, Honduras, Jamaica, Mexico, United States of America]

4a (*3a*). Inner pad of setae of forefemur with two symmetrical furrows; setae of tarsomeres following the line of those of tibia or slightly curved outwards... *Lethocerus* Mayr [cosmopolitan]

4b. Inner pad of setae of forefemur with two asymmetrical furrows; setae of tarsomeres curved outwards... *Kirkaldyia deyrolli* (Vuillefroy) [China, Japan, Korea, southeastern Asia, Taiwan]

5a (*1b*). Foretarsus obviously 2-segmented (Fig. 1E), possessing one long anterior claw and one vestigial to absent posterior claw... 6

5b. Foretarsus 3-segmented (often appearing 2-segmented externally), possessing two very short, inconspicuous claws, or two large equal or subequal claws... 8

6a (*5a*). Membrane of hemelytron well developed, with its greatest width more than that of clavus; most of its cells equal in length, in the form of long, narrow rectangles... *Belostoma* Latreille [North and South America]

6b. Membrane of hemelytron distinctly reduced, with its greatest width equal to or less than that of clavus (Figs. 1A and 2A); most of its cells usually small or feebly defined, or short and rectangular, of various lengths... 7

7a (*6b*). Lateral margins of abdomen not smooth, interrupted at borders between segments (laterotergites

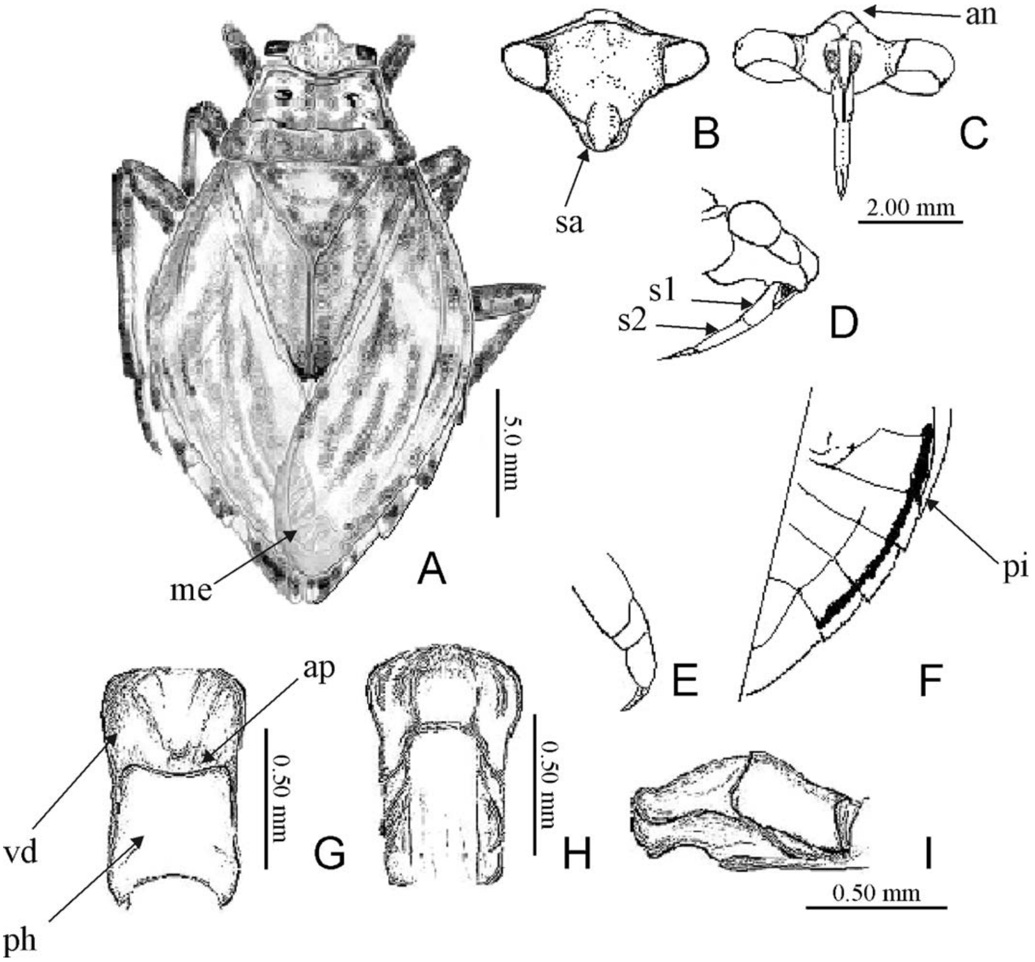

Fig. 1. *Weberiella rhomboides* (Menke). Body, dorsal view (A); head: dorsal view (B); frontal view (C); lateral view (D); foretarsus (E); abdomen showing abdominal pilosity, ventral view (F); male genitalia: dorsal view (G); ventral view (H); lateral view (I). an, anteclypeus; ap, apical portion of phallotheca; me, membrane of hemelytron; ph, phallotheca; pi, abdominal pilosity; sa, anteclypeal-loral plate suture; s1, segment 1 of rostrum; s2, segment 2 of rostrum; vd, ventral diverticulum.

scale-like) (Fig. 2A); phallotheca with its apical portion dorsally slightly concave; arms poorly developed, vestigial (Figs. 1G and 2D)... *Weberiella rhomboides* (Menke) (Figs. 1 and 2) [Brazil, French Guiana]

7b. Lateral margins of abdomen smooth, not scale-like; phallosoma with its apical portion dorsally bifurcate and arms developed... *Abedus* Stål [Central and the southern part of North America; and including the Isthmus of Panama]

8a (*5b*). Pubescence of ventral laterotergites 4 not attaining external margin; arms of phallosoma enclosing ventral diverticulum; genital operculum of females with two tufts of setae on apex... 9

8b. Pubescence of ventral laterotergites 4 attaining external margin along its entire length (Fig. 1F); arms of phallosoma scarcely developed, or short; genital operculum of females never bearing two tufts of setae on apex... 10

9a (*8a*). Lateral eye margins flushed with lateral margin of head; eyes not protruding laterally from such a margin; antennal segment 1 equal to or longer than lateral prolongations of segments 2 and 3, and segment 4; pygophore tapering more or less evenly between basal portion and apical semitubular portion; arms of phallosoma each with low angular medial projection; phallus laterally flat; endosoma laterally flat, hatchet-shaped... *Diplonychus* Laporte [Africa, Australia, East Indies, southern Asia]

9b. Lateral eye margins not flush with lateral margin of head; eyes prominent, protruding laterally from lateral margin of head; antennal segment 1 shorter than lateral prolongations of segments 2 and 3, and segment 4; pygophore with abrupt sculptured shoulder between basal portion and apical semitubular portion; arms of phallosoma without projections, smooth; phallus tubular; endosoma tubular, not hatchet-shaped... *Appasus* Amyot and Serville [Africa, Australia, East Indies, southern Asia]

10a (*8b*). Forefemur with a single, flat groove for reception of the tibia; foretarsus with segments 2 and 3 equal in length and twice as long as wide; foretibiae and foretarsi subcylindrical; genital operculum of females fringed with hairs, rounded at apex... *Limnogeton* Mayr [northern part of Africa

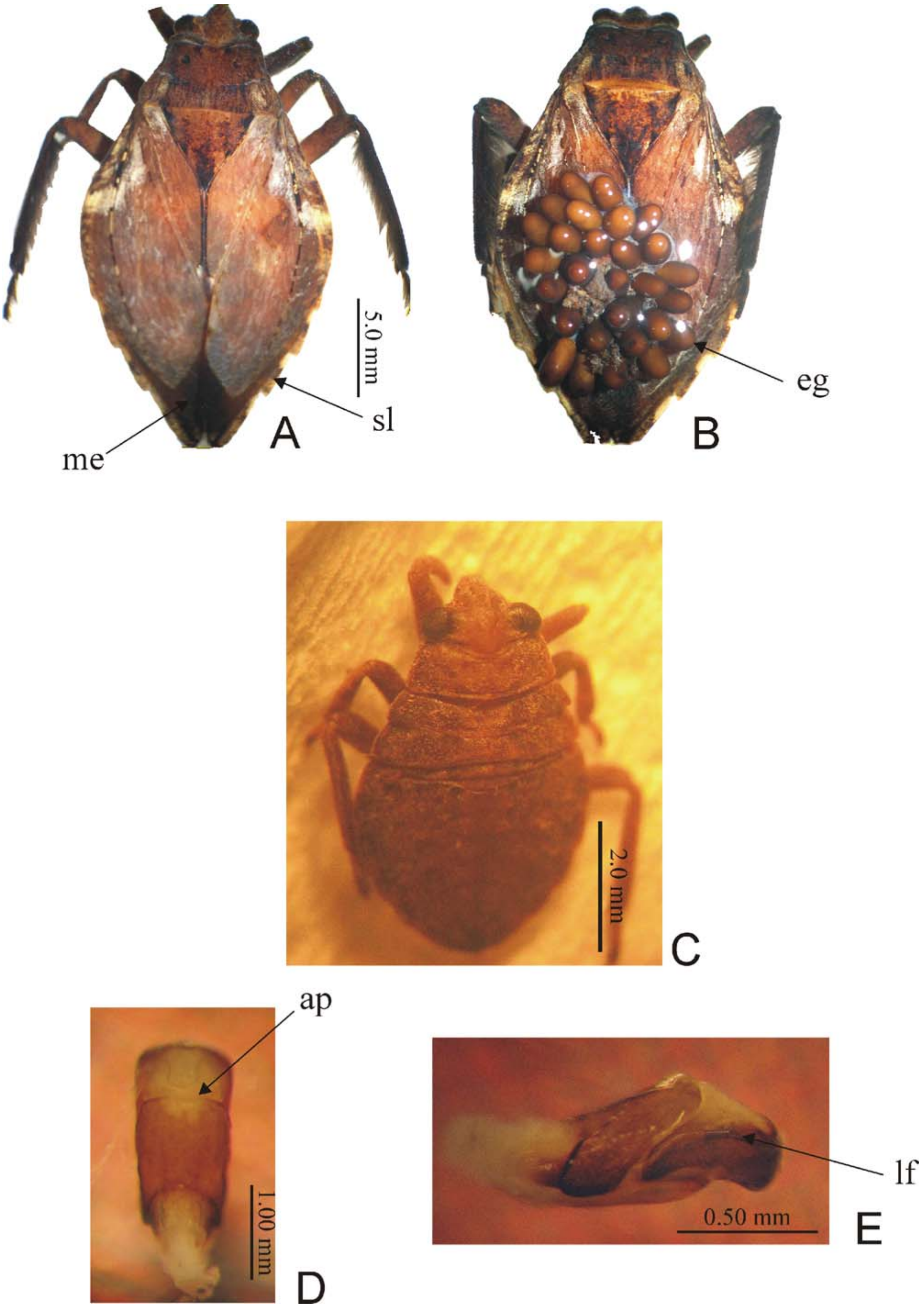

Fig. 2. *Weberiella rhomboides* (Menke), dorsal habitus. Female (A); encumbered male (B); nymph (C). Male genitalia: dorsal view (D); lateral view (E). ap, apical portion of phallotheca; eg, eggs; lf, lateral flanges; me, membrane of hemelytron; sl, scale-like laterotergites.

(extending westward to the Cameroon and southward to Tanganyika and the Republic of Congo)]

10b. Forefemur with two grooves for reception of the tibia; foretarsus with segment 2 shorter than 3, both segments short, rhomboidal; foretibiae and foretarsi laterally flattened; genital operculum of females with one apical tuft of setae on apex, somewhat notched apically. . . *Hydrocyrius* Spinola [restricted to Africa and Madagascar]

3.2. Redescription of *W. rhomboides* (Menke) based on males and females

Belostoma rhomboides Menke, 1965: 1 (description of female holotype).

Weberiella rhomboides: De Carlo, 1966: 97 (new genus, description of male allotype, two male paratypes, and five female paratypes).

Weberiella rhomboides: Nieser, 1975: 119 (record, redescription, comments).

Weberiella rhomboides: Lanzer-de-Souza, 1980: 77 (list).

Weberiella rhomboides: Mahner, 1993: 65 (phylogeny).

Weberiella rhomboides: Smith, 1997: 120 (taxonomy).

Weberiella rhomboides: Ribeiro, 2005: 247 (citation).

Weberiella rhomboides: Pereira et al., 2007: 216 (list).

Type – *Weberiella rhomboides* was described based on a female (from French Guiana) deposited in LACM. According to Recommendation 72A of the Code (Iczn, 1999), the term "allotype", usually adopted by De Carlo (1966), has no name-bearing function, but it may be used to indicate a type-specimen of opposite sex to the holotype. The use of the term "paratype" should be only applied to specimens without a name-bearing function when an author designates a holotype. After the holotype has been labelled, any remaining specimens of the type series should be viewed as "paratypes" to identify the components of the original type series. There is no reason to believe that the specimens mentioned by De Carlo (1966) as allotype and paratypes are in fact type-specimens of *W. rhomboides*. Therefore, those specimens erroneously used by De Carlo (1966) for describing *W. rhomboides* must be viewed neither as paratypes nor allotypes.

Material examined – Brazil, Roraima State, Basin of Urubu river, kinon, 18.IX.2006 (L.F. da Silva): 2 f; Urubu river, quinta ordem [fifth order tributary], 19.IX.2006: 1 f; 20.IX.2006: 1 m, 1 f, and 1 nymph (INPA), new State record. Amazonas State, Branquinho river, 23.VII.1962 (Fittkau), J.A. De Carlo det.: 1 m and 1 f (MACN). Rondônia State, *lgarapé* [intermittent stream] Tambaqui (near Amazonas), tributário na margem direita do Abunã [stream tributary along right margin of Abunã], *Igarapé* do Garimpo, em macrófitas aquáticas [on marsh-plants], 03.VI.2004 (N. Hamada, R.L.M. Ferreira, and J. Silva): 1 m (MLPA), new State record. Mato Grosso State, Sinop, X.1976 (M. Alvarenga), J.R.I. Ribeiro det.: 1 f (AMNH), new State record.

Measurements (m/f) – Body length (from apex of head to apex of abdomen at rest): 21.0–22.4/22.0–23.3; greatest width of body: 12.5–13.0/12.6–13.0.

Coloration – General coloration: brown, with yellowish, pale and dark brown spots.

External morphology – Body rhomboidal, flattened, widened at level of third and fourth abdominal segments, densely covered with short setae; external margin of laterotergites scale-like (Figs. 1A and 2A, sl). Head triangular; eyes widely separated, densely covered with stout hairs; anteclypeal-maxillary plate suture (=anterior portion of frontogenal suture) as long as anteclypeal-lorum suture (=posterior portion of frontogenal suture); anteclypeal-loral plate sutures slightly convergent and open distad (Fig. 1B, sa); anteclypeus elevated (Fig. 1C, an), with median longitudinal pubescence; vertex with three elevations; eyes globose, as wide as long, protruding from lateral margin of head; margins of eyes with scarce setae (Fig. 1B); antennae 4-segmented; segments 2 and 3 with finger-like projections, not flattened on segment 2, flattened, broad and short on segment 3; segment 4 with more bulbous compared to those on the preceeding antennonmeres 2 and 3; segment 1 shorter than lateral projections of segments 2, 3, and segment 4; anteoculus shorter than interoculus; bucculae with short and stout hairs; segment 1 of rostrum longer than wide, shorter than 2, densely covered with hairs (Fig. 1C and D, s1, s2). Prosternal keel rounded, flat; pronotum covered with short hairs, with distinctly concave anterior margin; transverse furrow delimiting anterior wide lobe of pronotum bordered by deep, glabrous groove; with two black, glabrous pits and posterior area with longitudinal elevations (Figs. 1A and 2A); narrow membrane of forewings with greatest width (combined with translucent margin) equal to greatest width of clavus; most cells of hemielytral membrane small or feebly defined, each cell rectangular, and of various lengths (Figs. 1A and 2A, me); scutellum with transverse furrow on anterior area; with two kidney-shaped elevations close to the lateral margins and numerous short hairs; elevated area close to posterior vertices without hairs (Fig. 1A); forelegs slightly dilated; forefemur with one wide flat groove for reception of the tibia; groove delimited by three rows of short setae; outer rows broader than middle row; foretarsus with two segments (externally appearing 1-segmented), bearing a well developed internal claw and a reduced external one (Fig. 1E); middle and hind legs slender, with long swimming hairs along inner margins of tibiae and tarsi; metathoracic scent glands not developed. Abdomen without suture-like fold; lateral sulcus terminating near proximal angles of mesal plate 7; ventral pubescence profuse; abdominal pilosity narrow, covering less than half of ventral laterotergites and attaining entire external margin of ventral laterotergites 4 (Fig. 1F, pi); spiracles located near external margin of ventral laterotergites; proximal portions of lateral lobes on segment 7 formed entirely or largely by lateral plates, with sublateral plates absent or not visible externally (when visible, developed as minute triangular sclerites) (Fig. 1F); genital operculum of females possessing two tufts of setae; air straps spatulate, bearing transverse bands of pubescence dorsally.

Male genitalia (Figs. 1G–I and 2D, E) – Parameres markedly widened at proximal two thirds; phallotheca (sclerotized proximal part of phallosoma, "phallobase" by Lauck and Menke, 1961) rather short (about one third the length of ventral diverticulum), sinuose, concave; apical portion in dorsal view with vestigial dorsal arms (Figs. 1G and 2D); phallosoma fused with ventral diverticulum; ventral diverticulum conspicuous, strongly expanded at apex, angularly widened, somewhat curved ventrad, with apicoventral protuberance poorly developed; lateral margins thickened and sinuous, with lateral flanges.

3.3. Taxonomic notes

Weberiella rhomboides shares with members of *Limnogeton* and *Hydrocyrius* the plesiomorphic api-

Table 1. Summary of morphological similarities and differences found in the genera *Hydrocyrius* Mayr, *Limnogeton* Spinola, and *Weberiella* De Carlo (related according to Mahner, 1993) based on personal observations and data from Lauck and Menke (1961), Kopelke (1978), and Mahner (1993).

	Hydrocyrius	*Limnogeton*	*Weberiella*
Head	– Segment 4 of antennae more bulbous than prolongations of segments 2 and 3 – Anteoculus shorter than interoculus – Frontogenal sutures distally closed	–Segment 4 of antennae more bulbous than prolongations of segments 2 and 3 – Anteoculus longer than interoculus – Frontogenal sutures slightly convergent and opened distad	– Segment 4 of antennae more bulbous than prolongations of segments 2 and 3 – Anteoculus shorter than interoculus – Frontogenal sutures slightly convergent and opened distad
Thorax	– Membrane of hemelytron approximately equal to greatest width of clavus, with its cells usually small or feebly defined and of various lengths – Forefemur with two grooves for reception of tibia – Foretarsi 3-segemented (often appearing 2-segmented externally), with two large equal or subequal claws – Middle and hind tibia and tarsus flattened, not broadly dilated, with swimming setae	– Membrane of hemelytron approximately equal to greatest width of clavus, with its cells usually small or feebly defined and of various lengths – Forefemur with one wide flat groove for reception of tibia – Foretarsi 3-segmented (often appearing 2-segmented externally), with two very short, inconspicuous claws – Middle and hind tibia and tarsus simple, slender, and cursorial	– Membrane of hemelytron approximately equal to greatest width of clavus, with its cells usually small or feebly defined and of various lengths – Forefemur with one wide flat groove for reception of tibia – Foretarsi obviously 2-segmented, with one long anterior claw and one vestigial posterior claw – Middle and hind tibia and tarsus flattened, not broadly dilated, with swimming setae
Abdomen	– Lateral margins of abdomen smooth – Genital operculum of female with one apical tuft of setae – Phallosoma with apical portion dorsally bifurcate and arms developed – Ventral diverticulum with its external margin broadly expanded with lateral flanges	– Lateral margins of abdomen smooth – Genital operculum of female fringed with hairs – Phallosoma with apical portion dorsally slightly concave and vestigial arms – Ventral diverticulum with its external margin slightly expanded, with apex acute	– Lateral margins of abdomen scale-like – Genital operculum of female with two apical tufts of setae – Phallosoma with apical portion dorsally slightly concave and vestigial arms – Ventral diverticulum with its external margin broadly expanded with lateral flanges

cal portion of the phallotheca with vestigial dorsal arms (Fig. 2D, ap; see Mahner, 1993: 66), and the greatest width of the membrane of the hemelytron subequal or equal to the greatest width of the clavus (Figs. 1A and 2A).

Despite nymphs with smooth lateral margins of abdomen (Fig. 2C), *W. rhomboides* itself is easily distinguished from other Belostomatinae by the particular scale-like abdominal margins (Figs. 1A and 2A, sl). Shared and distinguishing morphological characters of *Weberiella* and the other two genera with back-brooding males (*Limnogeton* and *Hydrocyrius*) are summarized in Table 1.

The foretarsi are 2-segmented in *W. rhomboides* (Fig. 1E), although they have been described as one-segmented (see Menke, 1965 that found segment 1 short, strikingly reduced, making this segment difficult to distinguish from segments 2 and 3, which are fused; De Carlo, 1966; Nieser, 1975 in his key to Belostomatidae occurring in Guyana).

3.4. Notes on biology

Members of *W. rhomboides* have been exclusively collected from the surface film of freshwaters ("kinon", as defined by Fittkau, 1977). It seems to be a rare species and apparently confined to northern South America. Recently, Pereira et al. (2007) expanded its range to some turbulent narrow streams (*Igarapé*) and white-water floodplain (*várzea*) lakes from Presidente Figueiredo and Manaus, as well as from Rio Negro black-water flooded forest (*igapó*) adding, in this way, new records for this species. Males brood the eggs, exposing them to atmospheric air, deposited on their backs by the females (Fig. 2B, eg) (back-brooders *sensu* Smith, 1997). Various authors have described this distinctive behaviour displayed by encumbered belostomatine males as "surfacing" (Venkatesan, 1983 and Volker, 1968) or as "surface brooding" (Volker, 1968; Smith, 1976a,b, 1980, 1997; Kopelke, 1982; Venkatesan, 1983; Jawale and Ranade, 1988; Schnack et al., 1990).

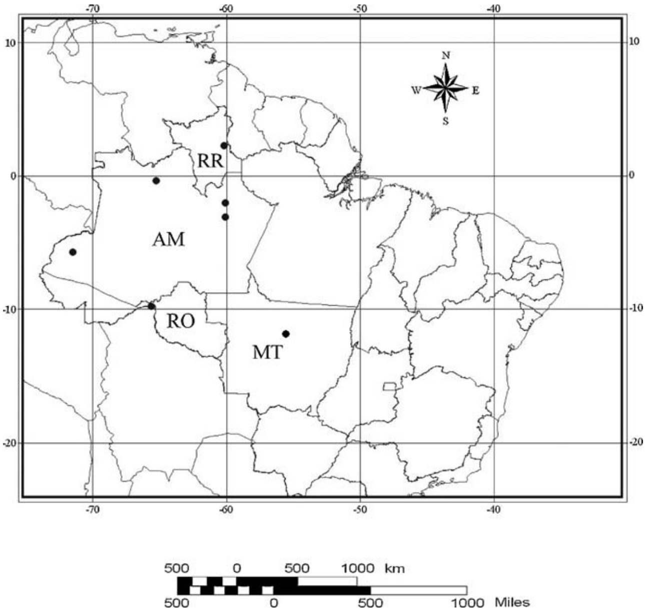

Fig. 3. Geographic distribution map of *Weberiella rhomboides* (Menke) in northern Brazil. AM, Amazonas State; MT, Mato Grosso State; RO, Rondônia State; RR, Roraima State.

3.5. New records of Brazilian *Weberiella*

Weberiella rhomboides was described based on material collected by Menke at an unknown locality in French Guiana. Only a female was known until De Carlo (1966) discovered more specimens collected by Fittkau from Amazonas State in Brazil. After having studied these specimens, De Carlo (1966) reported *W. rhomboides* from Marauá river, Amazonas, which is a very suspicious record, probably corresponding to Marauiá river, near the Rio Negro. According to Fittkau's handwritten manuscript entitled "Protokoll über das hydrobiologische Sammlungsmaterial aus dem brasilianischen Amazonasgebiet, gesammelt von E.J. Fittkau in den Jahren 1960–1963", his expedition from December 1962 to February 1963 was almost entirely restricted to that river instead of the Marauá river.

Here this species is newly recorded from the Brazilian States of Roraima, Rondônia, and Mato Grosso. This expands the range of *W. rhomboides* to the south (Fig. 3).

4. Discussion

Weberiella rhomboides has been found in the surface drift of Amazonian lotic waters, which are entirely dynamic and very often unstable biotopes with limited resources and without emergent vegetation. According to Fittkau (1977), *W. rhomboides* seems to exhibit a close connection to that habitat like the epineustic species of the genera *Rhagovelia* Mayr, 1865 and *Microvelia* Westwood, 1834.

It is conceivable that male investment is higher in the emergent-brooders than in the back-brooders. According to Smith (1997), emergent-brooders have to service clutches of eggs outside of the water where no prey is available. They are deposited on stems of emergent vegetation or tree branches that project into aquatic habitats. Despite the scarcity of prey items, they cannot change their location or only to a limited degree during brooding for much of the time while brooding and they could not change locations if prey availability were poor in the vicinity of the brooded eggs. Back-brooders are somewhat restricted in their movabilty. However, high mobility is not required because they are almost always in the aquatic environment where prey is available. Thus emergent-brooders would not be true kinobionts because of clearly unvailable good places to establish for laying and caring eggs. Finally, based on his extensive ecological and behavioural research and observations on belostomatids, Smith (1997, references therein) presented an adaptative scenario explaining the evolution of paternal care in giant water bug life history. The fact that extant emergent-brooding species require emergent vegetation, which is absent from kinal, corroborates the hypothetical evolutionary scenario of Smith. In such a hypothetical temporal succession scenario, considering the most parsimonious reconstruction, basal belostomatids are held to be emergent-brooders and more derived clades would show the back-brooding behaviour as a derived condition. Emergent-brooders are limited in their ecological distribution, whereas back-brooders are not. With this in mind and considering this fragmentary information, we assume that *W. rhomboides* belongs to Belostomatinae. This species shares with related genera the abdominal sternites 3–7 undivided laterally by weak folds. Mahner (1993) came to the conclusion that there are insufficient characters for including *W. rhomboides* under *Belostoma* (as suggested by Menke). In turn, if our hypothesis is correct, features of the apical portion of the phallotheca of *Weberiella*, i.e. slightly concave dorsally, with vestigial arms (Fig. 2D, ap), could be considered as ancestral for Belostomatinae, as a similar condition occurs in *Limnogeton* (see phylogeny of belostomatid genera in Mahner, 1993). Moreover *W. rhomboides* can be easily separated from *Belostoma* species by its laterotergite morphology, being the only Belostomatidae species with laterotergites scale-like (Figs. 1A and 2A, sl). Nevertheless, the taxonomic position of *Weberiella* within Belostomatinae is still doubtful. The life history of the genus *Weberiella* is largely unknown and therefore capturing material for rearing as well as new data might clarify the relationships among the genera and will allow establishing the definite position of this enigmatic genus.

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