

**Intraspecific morphological polymorphism in Naucoridae
(Hemiptera: Heteroptera)
with notes on nomenclature and synonymy**

John T. POLHEMUS¹⁾ & Dan A. POLHEMUS²⁾

¹⁾ Colorado Entomological Institute, 3115 S. York St., Englewood, CO 80113, USA;
e-mail: jtpolhemus@msn.com

²⁾ Dept. of Natural Sciences, Bishop Museum, 1525 Bernice St., Honolulu, HI 96817, USA;
e-mail: bugman@bishopmuseum.org

Abstract. Trends in intraspecific variation among certain aspects of pronotal and tarsal morphology within the family Naucoridae are reviewed, and linked to previously flawed taxonomic decisions regarding species separation or generic assignments within this group, particularly in the subfamily Laccocorinae. In particular, we review evidence that the shape of the posterolateral pronotal angles is linked to differing degrees of fore- and hindwing development across the family as a whole, and that members of the subfamily Laccocorinae exhibit intersexual variation in both fore tarsal segmentation and the number of claws on the foreleg. Misinterpretation of such character state variation has been utilized as an invalid basis for separation of putatively distinct species by many authors over the past 50 years. Based on this analysis, we propose the following taxonomic changes (valid names listed first): *Laccocoris staudingeri* Montandon, 1897 = *Laccocoris maai* La Rivers, 1970, syn. nov. = *Laccocoris lipogonia* La Rivers, 1970, syn. nov.; *Interocoris* La Rivers, 1974, stat. nov. (currently subgenus of *Heleocoris* Stål, 1876) is raised to full generic status to contain *Interocoris mexicanus* (Usinger, 1935), comb. nov. (formerly held under *Heleocoris (Interocoris) mexicanus* Usinger, 1935); the following Neotropical species are transferred from *Heleocoris* to *Ctenipocoris* Montandon, 1897: *Ctenipocoris brasiliensis* (De Carlo, 1968), comb. nov., *Ctenipocoris peruvianus* (La Rivers, 1974), comb. nov., *Ctenipocoris schadei* (De Carlo, 1940), comb. nov., *Ctenipocoris spinipes* (Montandon, 1897), comb. nov.; and *Heleocoris faradjensis* La Rivers, 1960 is transferred to *Ctenipocoris* and synonymized such that *Ctenipocoris africanus* Poisson, 1948 = *Heleocoris faradjensis* La Rivers, 1960, syn. nov.

Key words. Heteroptera, Naucoridae, Laccocorinae, morphology, variability, sexual dimorphism, taxonomy, new synonymy, new combination

Introduction

During a series of expeditions supported by the National Geographic Society over the past 25 years, we have collected numerous specimens of Naucoridae, or creeping water bugs, from most tropical regions of the planet. At this point we have studied most of world's naucorid taxa, and have documented many overlooked intraspecific morphological polymorphisms. In this paper we discuss specific instances of such polymorphisms, which were either unknown, or have escaped notice in recent times in spite of their mention in previous publications. Analysis of these intraspecific variations has in turn led to the realization that nomenclatural synonymies exist within certain taxa, and new nomenclatural proposals are advanced to rectify these problems.

Materials and methods

When quoting the data on type labels, a double slash (//) is used to divide separate labels; authors comments are given in square brackets [].

The following abbreviations of collections are used:

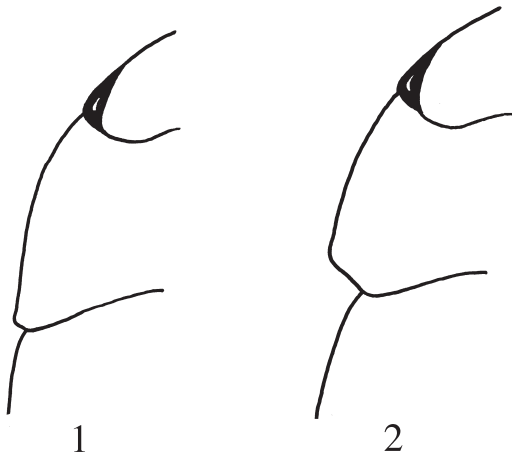
BMNH	The Natural History Museum, London, United Kingdom;
CAS	California Academy of Sciences, San Francisco, USA;
JTPC	John T. Polhemus Collection, Englewood, Colorado, USA;
NHMW	Naturhistorisches Museum, Wien, Austria.

Results

Comparative morphology

The fact that variation in certain aspects of pronotal morphology, particularly in regard to the shape of the posterolateral angles (Figs. 1-2), is linked to differing degrees of fore- and hindwing development has long been recognized in the Naucoridae, particularly among members of the subfamily Laccocorinae. Most genera in this same subfamily also exhibit intersexual variation in fore tarsal segmentation (Table 1). Despite this, differences in such character states have continued to be utilized for as a basis for separation of putatively distinct species by many authors over the past 50 years.

In diverse naucoroid lineages (= Naucoroidea sensu MAHNER (1993)) such as the Old World genera *Laccocoris* Stål, 1856 and *Heleocoris* Stål, 1876 (Laccocorinae), *Coptocatus* Montandon, 1909 (Cheirochelinae), and *Aphelocheirus* Westwood, 1833 (Aphelocheiridae), and the New World genera *Limnocoris* Stål, 1860 (Limnocorinae) and *Cryphocricos* Signoret, 1850 (Cryphocricinae), pronotal polymorphism is a common occurrence and is apparently genetically linked to wing length, especially that of the hind (flight) wings. For instance, in single populations of *Heleocoris floresensis* Nieser & Chen, 1992 from Flores (Indonesia), *Laccocoris spurcus congoensis* Poisson, 1949 from Africa, *L. hoogstaali* La Rivers, 1970 from the Philippines, *L. staudingeri* Montandon, 1897, *Coptocatus kinabalu* D. Polhemus, 1986 and *C. oblongulus* Montandon, 1909 all three from Borneo, species of *Temnocoris* Montandon, 1897 from Madagascar, and *Limnocoris virescens* Montandon, 1897 from Costa



Figs. 1-2. *Laccocoris staudingeri* Montandon, 1897, intraspecific variation in the posterolateral angles of the pronotum. 1 – ‘Sharp’ morph, with reduced hind wing; 2 – ‘Rounded’ morph, fully macropterous.

Rica, the posterolateral angles of the pronotum are posterolaterally produced and more or less angulate in individuals with reduced hind wings, but truncate and rounded in those with fully developed hind wings. D. POLHEMUS (1986) illustrated and discussed this polymorphism for the genus *Coptocatus*.

Conversely, the genus *Ambrysus* Stål, 1862, subgenus *Syncollus* La Rivers, 1965, exhibits wing polymorphism, but apparently not linked pronotal characters. In a population of *Ambrysus circumcinctus circumcinctus* Montandon, 1910 from Texas, there are two wing morphs. The flightless morph has reduced hind wings, reaching tergite IV, and the claval suture is essentially obliterated. In the alate morph the hind wings reach tergite VI, and the claval suture is well developed. In contrast to the genera discussed above, there is no discernable pronotal polymorphism in this species.

DE CARLO (1951) showed that in *Limnocoris*, acute posterolateral pronotal angles are not consistently linked to a reduced hemelytral membrane. Although this is true, the posterolaterally produced angle is indeed linked to reduced hind wings, whether or not the angle is acute or somewhat rounded apically. In addition, membrane development is not necessarily correlated with hind wing development. In *Limnocoris borellii* Montandon, 1897 and *L. uhleri* Montandon, 1910 all specimens have a well developed membrane, yet some have reduced hind wings coupled with produced, acute posterolateral pronotal angles. In *Limnocoris rotundatus* De Carlo, 1951, which has reduced hind wings and a reduced membrane, the posterolateral angles are produced posterolaterally but the apices are somewhat rounded. In all species of *Limnocoris* with well developed hind wings, the posterolateral pronotal angles are not produced, but are instead obtuse, and notched or angled anteriorly.

In all of the taxa discussed above, except *Cryphocricos*, the hemelytra (fore wings) are fully developed and cover most or all of the abdominal dorsum; in order to inspect the state of the hind wings, the hemelytra must be lifted or removed. In terrestrial bugs the length of the hemelytra and hind wings are usually rather closely coordinated, thus brachyptery implies that both sets of wings are considerably shortened (see classification of seven fore wing types by SLATER (1975) pertaining especially to Lygaeidae). In several genera of intertidal Saldidae,

terrestrial air breathers that are regularly submerged for extended periods, the hemelytra cover almost the entire abdominal dorsum but the membrane and hind wings are much reduced; J. POLHEMUS (1985: 31) described this as brachyptery. In bugs that live under water, hind wing reduction is not accompanied by fore wing reduction because the long hemelytra are needed to break the surface film and capture an air bubble to replenish the air store, unless the taxon has developed a plastron (see discussion in J. POLHEMUS (1991) and references therein). In plastron-bearing naucorids and aphelocheirids a reduction in hind wings is accompanied by a similar reduction in fore wings.

The plastron bearing genera *Cryphocricos*, *Procryphocricos* J. Polhemus, 1991, *Idiocarus* Montandon, 1897, and *Aphelocheirus* exhibit extreme brachyptery not seen in other genera of Naucoroidea, along with macroptery. In the New World genus *Cryphocricos* the modification of the posterolateral pronotal angles is the reverse of the genera discussed above, slightly more pronounced in the long winged forms, but this genus is not directly comparable to those discussed previously because the posterolateral angles slope anteriorly in both morphs and are not sharply produced posterolaterally. SITES (1990) illustrated three morphs in a population of *Cryphocricos hungerfordi* Usinger, 1947: brachypterous, submacropterous and macropterous, with each state progressively having the posterolateral pronotal angles slightly more angulate.

In the genus *Aphelocheirus* the modification of the posterolateral angles is not consistent with wing morph, but varies from species to species, although apparently still genetically linked to wing length and consistent within each species. This was illustrated for a number of species by D. POLHEMUS & J. POLHEMUS (1989). In *Aphelocheirus zamboanga* D. Polhemus & J. Polhemus, 1989 the posterolateral pronotal angles are shaped quite similarly in the two morphs, but as in all macropterous specimens of *Aphelocheirus* the pronotum is longer and the scutellum larger than in the brachypterous morph. In *A. sculpuratus* D. Polhemus & J. Polhemus, 1989 and *A. kinabalu* D. Polhemus & J. Polhemus, 1989 the posterolateral angles are more pronounced in the brachypterous form, whereas in *A. breviostrus* D. Polhemus & J. Polhemus, 1989 the reverse is true.

Almost fifty years ago POISSON (1949) recognized the linkage of pronotal morphology to wing development in the genus *Laccocoris*, elaborated on it, showed that it also affects the length of the claval commissure, and illustrated abnormal specimens with the right and left sides dimorphic. In spite of his long association with Naucoridae, the late Ira La Rivers either ignored or never recognized this phenomenon, an oversight that led him to describe the two morphs from a single population as two new species as discussed further below.

In addition to the hindwing and associated pronotal polymorphism, all genera currently placed in Laccocorinae, except the genus *Ctenipocoris* Montandon, 1897 and the recently described genus *Namtokocoris* Sites, 2007 (SITES & VITHEEPADIT 2007), exhibit sexual dimorphism of the anterior tarsi, with a single segment in the females but two in the males. LA RIVERS (1970) described two new species of *Laccocoris* from Borneo, and although he had both sexes of each, he characterized the anterior tarsi of both species as single segmented.

La Rivers was preceded in his ignorance of these nuances of naucorid morphology by such august workers as Stål and Montandon, probably because these early workers usually had only a paucity of material. STÅL (1876: 42) at least recognized a possible problem with tarsal

Table 1. Foreleg characters for genera of Laccocorinae (Naucoridae).

Genus	Male tarsal segments	Female tarsal segments	Claws
<i>Ctenipocoris</i>	2	2	2 large
<i>Namtokocoris</i>	1	1	1
<i>Aneurocoris</i>	2	1	2
<i>Decarlea</i>	2	1	2 large
<i>Diaphorocoris</i>	2	1	2
<i>Heleocoris</i>	2	1	2
<i>Interocoris</i>	2	1	2
<i>Laccocoris</i>	2	1	2
<i>Temnocoris</i>	2	1	2

Note. SITES & VITHEEPRAKIT (2007: 4), stated that all Laccocorinae except the genus *Namtokocoris* Sites, 2007 have 2 tarsal segments in the male and 1 in the female. As shown in the table above this is not correct, because *Ctenipocoris* Montandon, 1897 possess 2 tarsal segments on the foreleg in both sexes.

segmentation, for in his characterization of the division 'Laccocoraria' he has the notation 'in *Laccocori limigeno* uniarticulatis?' (= in *Laccocoris limigenus* with one segment). MONTANDON (1897b), in his pioneer work on the subfamily Laccocorinae, characterized his new genus *Aneurocoris* Montandon, 1897 as having 'tarses antérieurs paraissant uniarticulés et bionguiculés ...' (= one segment with two claws), but he had only a single specimen before him. In this work he attributes two anterior tarsal segments to all of the species of *Laccocoris* and *Heleocoris* for which he mentions this character. Oddly, such careful workers as USINGER (1941) and NIESER (1975) also characterized the anterior tarsi of the Laccocorinae as having two segments and the Naucoridae as having one, even though LUNDBLAD (1933) had noted the sexual dimorphism of several *Laccocoris* species in regard to this character state.

We have studied males and females of at least one species of every genus-group taxon of the subfamily Laccocorinae, as presently construed, and all except *Ctenipocoris* (with two anterior tarsal segments in both sexes) and *Namtokocoris* (with single segmented tarsi in both sexes), have sexually dimorphic anterior tarsi. Both sexes of the two Old World species originally described in the genus *Ctenipocoris* have also been studied, i. e. *C. africanus* Poisson, 1948 and *C. asiaticus* Montandon, 1897. D. POLHEMUS (1987) recently transferred the South American *Heleocoris brasiliensis* DeCarlo, 1968 to *Ctenipocoris*; the males have two segmented anterior tarsi, as does a female of this species in the J. T. Polhemus collection, thus further supporting this generic assignment. DE CARLO (1940) described *Heleocoris schadei* De Carlo, 1940 from two females from Paraguay, and noted that they had two claws, but did not mention the anterior tarsal segmentation. Later DE CARLO (1965) illustrated the two segmented anterior tarsi with two large claws of *H. schadei*, but did not mention the sex, however in his description of *H. brasiliensis* (DE CARLO 1968a) he noted that the male has two

segmented anterior tarsi. In the closely related *Heleocoris spinipes* Montandon, 1897 from Venezeula the anterior tarsi are the same as the Old World *Ctenipocoris*, i. e. not sexually dimorphic, therefore all of the South American species now held in the genus *Heleocoris* are here transferred to *Ctenipocoris* (see nomenclature section), with the exception of *Heleocoris plaumanni* De Carlo, 1968b.

Heleocoris plaumanni cannot be placed with certainty because of a lack of material. DE CARLO'S (1968b) figure of the anterior leg of the male shows the anterior tarsus as robust, with a callosity on the inferior side and with two tiny claws. The anterior tarsi are described as robust, and in the diagrammatic figure appear to be long and single segmented, but unfortunately no specimens are available for examination. This species is certainly very different from any of the other New World species that have been placed in this genus, therefore it is not re-assigned to another genus.

Because he did not recognize the importance of the anterior tarsal segmentation, LA RIVERS (1960) misidentified *Ctenipocoris africanus* as a *Heleocoris* species and proposed it as a new species, *Heleocoris faradjensis* La Rivers, 1960; the latter is placed in synonymy (see below).

On the other hand, *Heleocoris (Interocoris) mexicanus* Usinger, 1935 from Mexico has sexually dimorphic anterior tarsi, typical of most Laccocorinae, but is quite different in other regards, in our view supporting LA RIVERS' (1974) decision to erect a separate genus group taxon for it (see new status below).

The trend toward the use of such unstable characters as a basis for species separation in the Laccocorinae has continued into recent times. For instance, NIESER & CHEN (1992) used only the shape of the posterolateral pronotal angles to separate their new species *Heleocoris floresensis* Nieser & Chen, 1992 from *H. nebulosus* Montandon, 1909 and *H. obscuratus* Montandon, 1897 (said to be rounded in the former, sharp in the latter two). They did not further separate these species on the basis of more stable characters such as the male and female abdominal terminalia and genitalia. Their figure of *H. floresensis* shows the morph with reduced hind wings and produced posterolateral pronotal angles, although narrowly rounded posterolaterally. In spite of the contention that these species should be separable by the shape of the pronotal angles, the specimens of the three taxa they discuss all belong to a single morph that MONTANDON (1897b: 447) characterized as having 'angles latéraux postérieurs du pronotum aigus et légèrement proéminents en arrière' (= lateral posterior angles of the pronotum sharp and slightly prominent behind). The 'sharpness' of the apex of the pronotal angles varies somewhat within each of the species they compared, and even within single populations, although each species possesses a characteristic norm. Apparently Nieser and Chen had before them specimens of *H. floresensis* with produced but narrowly rounded pronotal angles, and specimens of *H. nebulosus* and *H. obscuratus* exhibiting produced and rather sharp pronotal angles. We have in the J. T. Polhemus collection long series of all three of these species, containing individual specimens with reduced hind wings that have essentially the same pronotal shape, with produced but narrowly rounded pronotal angles, and others with produced and rather sharp pronotal angles, thus on this basis alone they are impossible to separate. We also have the long winged morph of each of these species, with truncate and broadly rounded pronotal angles; Nieser and Chen gave no indication that they knew of this morph. Fortunately from the standpoint of nomenclatural stability, *Heleocoris floresensis* seems to be a good species based on an analysis of other more stable characters also mentioned in

NIESER & CHEN (1992), although the comparison to *H. obscuratus* is rather tentative because the type of this latter species has not been located in modern times (LUNDBLAD 1933: 73).

Taxonomy

Laccocoris staudingeri Montandon, 1897

(Figs. 1-2)

Laccocoris staudingeri Montandon, 1897b: 440. Type locality: Brunei (Borneo). Lectotype in BMNH (designated here).

Laccocoris maai La Rivers, 1970: 496, **syn. nov.** Type locality: Sabah (Borneo).

Laccocoris lipogonia La Rivers, 1970: 498, **syn. nov.** Type locality: Sabah (Borneo).

Type material examined. *Laccocoris staudingeri*: LECTOTYPE: ♂, 'Brunei, 0 Sta. B. H. [handwritten] // Montandon Coll. 1901-233 [printed] // Type [circular label with red ring] // Laccocoris staudingeri Montand., type [handwritten] // LECTOTYPE, Laccocoris staudingeri Montandon 1897, J. T. Polhemus [handwritten on pink card]' (BMNH; here designated). PARALECTOTYPE: ♂, 'Brunei, Borneo, Laccocoris staudingeri Montand., det. Montandon 1908' (JTPC, exchange from Snow Entomological Museum Collection).

Laccocoris maai: PARATYPE: ♀, **BORNEO: MALAYSIA: SABAH:** 'British North Borneo, Sensuron, Jan. 9-11' (CAS).

Laccocoris lipogonia: PARATYPE: ♀, **BORNEO: MALAYSIA: SABAH:** 'British North Borneo, Sensuron, Jan. 9-11 (CAS).

Additional material examined. **BORNEO: MALAYSIA: SABAH:** 1 ♂ 1 ♀, Tawau Hills, Tawau River, 9.-10.vi.1998, J. Kodada & F. Ciampor (NHMW); 1 ♂ 1 ♀, Samalong River, 7 km S. of Ranau, CL 2026, 3.viii.1985, J. T. & D. A. Polhemus (JTPC); 1 ♂ 1 ♀, Liwagu River at Kundesan, CL 2021, 1.viii.1985, J. T. & D. A. Polhemus (JTPC); 1 ♀, Liwagu River, N. of Kundesan, 915 m, 16.viii.1972, G. F. & C. H. Edmunds (JTPC). **SARAWAK:** 2 ♀♀, Kelabit Highland, 1000-1200 m (11), Bareo-Arur Dalam, Bach durch Regenwald [= brook in rain forest], 26.ii.-1.iii.1993, H. Zettel (NHMW); 1 ♂ 4 ♀♀, Kelabit Highland, 5 km E. of Bareo, Pa Ukat, 1000 m, 1.iii.1993, breiter fluss [= wider river], M. Jäch (19) (NHMW, JTPC); 1 ♀, Mulu Nat. Park, 8.-5.iii.1993, M. Jäch (19) (NHMW).

Discussion. According to MONTANDON (1897b) syntypes of *Laccocoris staudingeri* were deposited in the Montandon and Staudinger collections. A male syntype of *Laccocoris staudingeri* Montandon present in the BMNH is here designated as lectotype.

In describing *L. maai*, LA RIVERS (1970) took no notice of *L. staudingeri*, instead comparing his new species only to *L. horvathi* Montandon, 1897, also described from Brunei (type said to be in Budapest), and to *L. hoogstraali* La Rivers, 1970 from the Philippines. We have before us the male lectotype of *L. staudingeri*, a specimen of *L. horvathi* from Brunei determined by Montandon, and paratypes of *L. maai* and *L. lipogonia*, as well as a paratype and additional long series of *L. hoogstraali*. La Rivers' paratypes of *L. maai* match both the description and lectotype of *L. staudingeri*, and *L. maai* is here placed in synonymy. *Laccocoris lipogonia* is simply the long winged morph of *L. maai*, and is also considered a synonym. We have collected series of both *L. staudingeri* and *L. horvathi* in Sabah, which adjoins Brunei to the north.

The key characters we have found useful in separating *Laccocoris* species are the pattern of dark markings on the head and scutellum, the shape of parasternite VI in both males and females, the shape of female subgenital plate (sternite VII), the morphology of the male genitalia, and the shape of the metaxyphus. The form of the interocular space was used by Montandon, and the shape of the labrum and embolium by Poisson, but these are of limited utility and often separate species only into groups. Because Montandon did not recognize the pronotal polymorphism, he divided the *Laccocoris* into two sections based on the shape of the posterolateral pronotal angles (MONTANDON 1897b), an invalid species group character

as pointed out in the preceding discussion.

Laccocoris marginatus Montandon, 1897a is close to *L. staudingeri*, but the male genitalia, parasternites and female subgenital plate are quite different in the two species. His descriptions of these two species are not directly comparable as they were not standardized and not presented in the same paper, but we have studied the types of both species and they are distinct.

Asian species of the genera *Heleocoris* and *Laccocoris* are often very difficult to place generically on the basis of the single key generic character currently used, i. e. the possession of an acute versus rounded labrum. As such, we believe that there is considerable doubt as to whether these genera are in fact distinct. We suggest that the African forms currently held in these two genera may need to be combined, but also note that all possess shared character states, such as the chaetotaxy of the mid femur, indicating that they represent a different monophyletic group than the Asian species currently held in this combined assemblage. The type-species of *Laccocoris* is *L. spurcus* Stål, 1856 from Africa, while the type-species of *Heleocoris* is *H. obliquatus* Spinola, 1837 from India, thus it may be that the African species are best assigned to *Laccocoris*, and the Asian species to *Heleocoris*. This question, however, is beyond the scope of the current paper.

***Interocoris* La Rivers, 1974, stat. nov.**

Heleocoris (*Interocoris*) La Rivers, 1974: 11. Type species: *Heleocoris mexicanus* Usinger, 1935, by monotypy.

Discussion. LA RIVERS (1974) proposed three subgenera of *Heleocoris*: the nominate subgenus *Heleocoris*, which includes all Old World species; *Interocoris*, which was proposed to hold *H. mexicanus*; and *Brevocoris* La Rivers, 1974, which was proposed to hold all South American species (see below). The subgenus *Interocoris* is here elevated to generic status. La Rivers separated this genus-group taxon from *Heleocoris* on the basis of the shapes of the metathoracic episternum and connexiva, which we consider valid. See the comparative morphology section above for additional rationale.

***Interocoris mexicanus* (Usinger, 1935), comb. nov.**

Heleocoris mexicanus Usinger, 1935: 133. Type locality: Temascaltepec, Mexico. Holotype in CAS.

Heleocoris (*Interocoris*) *mexicanus*: LA RIVERS (1974): 11.

Material examined. MEXICO: CHIAPAS: 1 ♂, W. of Rizo de Oro, CL 1331, 14.i.1970. GUERRERO: 1 ♀, Terreros, km 31 on Mexico Hwy. 134, NE of Ixtapa, CL 1896, 29.i.1985. JALISCO: 1 ♂, nr. Atentique, CL 740, 12.v.1975; 1 ♂ 3 ♀♀, S. of Mismaloya, CL 733, 9.vi.1975; 1 ♂, S. of Mismaloya, CL 734, 9.vi.1975. NAYARIT: W. of Compostela, CL 730, 8.vi.1975. OAXACA: 7 ♂♂ 8 ♀♀ 5 nymphs, 7 mi. S. of Valle Nacional, CL 508, 5.i.1971, J. T. & M. S. Polhemus. SONORA: 1 ♀, La Aduana, CL 1212, 21.iii.1967; 3 ♂♂ 1 ♀, canyon 17 mi. S. of Bacanora, 25.iv.1982, D. A. Polhemus (all in JTPC, all collected by J. T. Polhemus unless otherwise noted).

Discussion. The original type series was collected from mud along the margins of streams (USINGER 1935). Our specimens were almost all collected from hygropetric habitats, such as cracks in vertical wet rock faces.

***Ctenipocoris* Montandon, 1897**

Ctenipocoris Montandon, 1897c: 373. Type species: *Ctenipocoris asiaticus* Montandon, 1897, by monotypy.

Brevocoris La Rivers, 1974: 11. Nomen nudum.

Discussion. The genus *Ctenipocoris* is construed here to include the species given in the check list below, including two Old World species, and four South American species formerly held in *Heleocoris*. LA RIVERS (1974) proposed the subgenus *Brevocoris* to hold all South American species of *Heleocoris*, however *Brevocoris* is a nomen nudum because no type-species was named.

D. POLHEMUS (1987) transferred the South American *Heleocoris brasiliensis* to *Ctenipocoris*. The remainder of the South American species now held in the genus *Heleocoris* (with the exception of *Heleocoris plaumanni*) are here transferred to *Ctenipocoris* as well.

LA RIVERS (1960) misidentified *Ctenipocoris africanus* as a *Heleocoris* species and proposed it as a new species, *H. faradjensis* La Rivers, 1960; the latter is transferred to *Ctenipocoris* and synonymized. We have studied the type series from 'Northeastern Belgian Congo', later known as Zaire and recently as Democratic Republic of the Congo.

Checklist of *Ctenipocoris* species

- C. africanus* Poisson, 1948. Democratic Republic of the Congo
= *C. faradjensis* (La Rivers, 1960), **syn. nov.**, **comb. nov.** (from *Heleocoris*)
C. asiaticus Montandon, 1897. Malaysia, Indonesia (Java), Vietnam
C. brasiliensis (De Carlo, 1968) (from *Heleocoris*). Brazil
C. peruvianus (La Rivers, 1974), **comb. nov.** (from *Heleocoris*). Peru
C. schadei (De Carlo, 1940), **comb. nov.** (from *Heleocoris*). Paraguay
C. spinipes (Montandon, 1897), **comb. nov.** (from *Heleocoris*). Brazil, Venezuela

Acknowledgements

This contribution is dedicated to our dear friend and colleague Pavel Štys in recognition of his dedication to the study of Heteroptera.

We are also indebted to the following for the gift, exchange or loan of specimens: G. M. Stonedahl, The Natural History Museum (BMNH); Herbert Zettel, Naturhistorisches Museum Wien (NHMW); David Kavagnagh, California Academy of Sciences, San Francisco (CAS). We further thank Nico Nieser for reviewing drafts of the manuscript.

This research was supported by grants 2698-83, 3053-85, 3398-86, 4092-89 and 4537-91 from the National Geographic Society, which funded field work in South America and tropical Asia, and by grants BSR-9020442 and DEB-9528025 the National Science Foundation Washington, DC. We thank both these organizations for their continued support of research related to the systematics and zoogeography of aquatic Heteroptera.

This research was carried out by JTP as a faculty affiliate of the Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, Colorado, USA.

References

- DE CARLO J. A. 1940: Una nueva especie del género *Heleocoris* Stål (Hemiptera – Naucoridae). *Revista de la Sociedad Entomológica Argentina* **10**: 432-433 + 1 pl.
DE CARLO J. A. 1951: Género *Limnocoris* Stål. (Hem. Naucor.). Usingerina Ira La Rivers igual a *Limnocoris* Stål: Descripción de especies nuevas y datos sobre otras poco conocidas. *Misión de Estudios de Patología Regional Argentina* **22(79)**: 41-51.

- DE CARLO J. A. 1965: Segmentos genitales y contenido de la capsula genital en machos de especies de los generos *Ambrysus*, *Pelocoris*, *Limnocoris*, *Heleocoris* y *Cryphocricos*. (Hemiptera – Naucoridae). *Revista de la Sociedad Entomológica Argentina* **27**: 101-106 + 2 pls.
- DE CARLO J. A. 1968a: Descripción de especies nuevas de los géneros *Ambrysus*, *Cryphocricos* y *Heleocoris*. Allotypus de *Cryphocricos* *deguerri* (Hemiptera – Naucoridae). *Revista de la Sociedad Entomológica Argentina* **30**: 99-104 + 1 pl.
- DE CARLO J. A. 1968b: Tres especies nuevas del género *Coleopterocoris* y una especie nuevas del género *Heleocoris*. (Hemiptera, Naucoridae). *Physis, Revista de la Sociedad Argentina de Ciencias Naturales* **28**: 193-197.
- LA RIVERS I. 1960: *Heleocoris faradajensis*, a new species from the Belgian Congo (Hemiptera: Naucoridae). *Entomological News* **71**: 99-103.
- LA RIVERS I. 1970: Two new species of *Laccocoris* from British North Borneo (Hemiptera: Naucoridae: Laccocorinae). *Proceedings of the Entomological Society of Washington* **72**: 496-499.
- LA RIVERS I. 1974: Catalogue of taxa described in the family Naucoridae: Supplement No. 1: Corrections, emendations and additions, with descriptions of new species. *Biological Society of Nevada Occasional Papers* **38**: 1-17.
- LUNDBLAD O. 1933: Zur Kenntnis der aquatilen und semi aquatilen Hemipteren von Sumatra, Java und Bali. *Archiv für Hydrobiologie, Supplementum* **12** (Tropische Binnengewässer 4): 1-195 + 263-498 pp + pls. i-xxi.
- MAHNER M. 1993: Systema Cryptoceratorum Phylogeneticum (Insecta, Heteroptera). *Zoologica* (Stuttgart) **48**: 1-302.
- MONTANDON A. L. 1897a: Hémiptères-Hétéroptères exotiques. Notes et descriptions. III. *Annales de la Société Entomologique de Belgique* **41**: 50-66.
- MONTANDON A. L. 1897b: Hemiptera cryptocerata. Fam. Naucoridae. Sous-fam. Laccocorinae. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* **47**: 435-454.
- MONTANDON A. L. 1897c: Viaggio di Leonardo Fea in Birmania e regioni vicine. LXXV. Hemiptera Cryptocerata. *Annali del Museo Civico di Storia Naturale di Genova, Serie 2* **17**: 365-377.
- NIESER N. 1975: The water bugs (Heteroptera: Nepomorpha) of the Guyana Region. *Studies on the Fauna of Suriname and Other Guyanas* **16**: 1-310 + 24 pls.
- NIESER N. & CHEN P.-P. 1992: Notes on Indonesian waterbugs (Nepomorpha & Gerromorpha). *Storkia* **1**: 30-40.
- POISSON R. A. 1949: Hémiptères aquatiques. *Parc National Albert, I. Mission G. F. de Witte* **58**: 1-94.
- POLHEMUS D. A. 1986: A review of the genus *Coptocatus* Montandon (Hemiptera: Naucoridae). *Pan-Pacific Entomologist* **62**: 248-256.
- POLHEMUS D. A. 1987: *Heleocoris brasiliensis* DeCarlo is a *Ctenipocoris* (Hemiptera: Naucoridae). *Pan-Pacific Entomologist* **63**: 370.
- POLHEMUS D. A. & POLHEMUS J. T. 1989: The Aphelocheirinae of tropical Asia (Heteroptera: Naucoridae). *Raffles Bulletin of Zoology* **36** (1988): 167-300.
- POLHEMUS J. T. 1985: *Shore Bugs (Heteroptera, Hemiptera; Saldidae). A world overview and taxonomy of Middle American forms*. The Different Drummer, Englewood, Co., v + 252 pp.
- POLHEMUS J. T. 1991: A new and primitive genus of *Cryphocricinae* (Heteroptera: Naucoridae). *Pan-Pacific Entomologist* **67**: 119-123.
- SITES R. W. 1990: Morphological variations in the hemelytra of *Cryphocricos hungerfordi* Usinger (Heteroptera: Naucoridae). *Proceedings of the Entomological Society of Washington* **92**: 111-114.
- SITES R. W. & VITHEEPRADITA. 2007: *Namtokocoris* Sites, a new genus of Naucoridae (Hemiptera: Heteroptera) in waterfalls of Indochina, with descriptions of six new species. *Zootaxa* **1588**: 1-29.
- SLATER J. A. 1975: On the biology and zoogeography of Australian *Lygaeidae* (Hemiptera-Heteroptera) with special reference to the southwest fauna. *Journal of the Australian Entomological Society* **14**: 47-64.
- STÅL C. 1876: Enumeratio Hemipterorum. Bidrag till en förteckning öfver alla hitills kända Hemiptera, jemtes systematica meddelanden. 5. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* **14**(4): 1-162.
- USINGER R. L. 1935: A second American species of the naucoris subfamily Laccocorinae (Hemiptera). *Revista de Entomologia* (Rio de Janeiro) **5**: 133-136.
- USINGER R. L. 1941: Key to the subfamilies of Naucoridae with a generic synopsis of the new subfamily *Ambrysinæ* (Hemiptera). *Annals of the Entomological Society of America* **34**: 5-16