Taxonomic overview of the family Naucoridae (Heteroptera: Nepomorpha) in Mexico

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ABSTRACT

The state of taxonomy of the Mexican fauna of the family Naucoridae is summarized and is fairly complete as a result of recent research. Currently, 71 species from six genera and four subfamilies have been recorded from the country. Species richness is distributed in the subfamilies Cryphocricinae: Ambrysus Stål (53), Cataractocoris Usinger (3), Cryphocricos Signoret (2); Laccocorinae: Interocoris La Rivers (1); Limnocorinae: Limnocoris Stål (10); and Naucorinae: Pelocoris Stål (2). Recent works have focused on the fauna of the genus Ambrysus. Additionally, studies are required for the genera Cryphocricos and Pelocoris, while a taxonomic revision of the genus Limnocor is close to completion. A key to the subfamilies and genera of Naucoridae from Mexico is provided.

Key words: distribution, aquatic insects, Hemiptera, North America.

RESUMEN

Se resume el conocimiento taxonómico de la fauna mexicana de la familia Naucoridae, el cual es bastante completo debido a estudios recientes. Actualmente se encuentran registradas para el país 71 especies pertenecientes a seis géneros y cuatro subfamilias. La riqueza de especies está distribuida en las subfamilias Cryphocricinae: Ambrysus Stål (53), Cataractocoris Usinger (3), Cryphocricos Signoret (2); Laccocorinae: Interocoris La Rivers (1); Limnocorinae: Limnocoris Stål (10); y Naucorinae: Pelocoris Stål (2). Recientes trabajos han enfocado su atención en el estudio del género Ambrysus. Adicionalmente se requieren estudios de los géneros Cryphocricos y Pelocoris, mientras que la revisión taxonómica del género Limnocor está cerca de ser finalizada. Se proporciona una clave para la identificación de las subfamilias y géneros de Naucoridae de México.

Palabras clave: distribución, insectos acuáticos, Hemiptera, Norteamérica.

Naucoridae Leach is a family of ovate and dorsoventrally flattened aquatic insects in the order Hemiptera (Fig. 1). It is one of the 11 families in the heteropteran infraorder Nepomorpha (Schuh and Slater 1995), which includes approximately 2,400 described species worldwide (Polhemus and Polhemus 2008a). The insects in the family Naucoridae are commonly known as saucer bugs or creeping water bugs. Naucorids are common predators in tropical lentic and lotic habitats worldwide with less representation in temperate regions. These insects grasp their prey with retentorial forelegs while using the piercing-sucking mouthparts to feed upon the predigested prey contents. The type of habitat preferred by saucer bugs is diverse, but they are commonly found associated with marginal submerged vegetation in lentic and lotic situations and among rocks in shallow areas close to the margins of streams. A remarkable environment is that inhabited by species in the genus Cataractocoris Usinger, which prefer the near-vertical rock faces of waterfalls (Fig. 2), waterfall splash zones, and large rocks in fast current. Several Asian genera in the subfamily Laccocorinae also occupy the rock faces of waterfalls.

The currently accepted classification of Naucoridae includes the subfamilies Cheirochelinae, Cryphocricinae, Laccocorinae, Limnocorinae, and Naucorinae (Stys and Jansson 1988). The subfamily Cheirochelinae, which has no representatives in Mexico, is distributed in India, southern China, Southeast Asia, Borneo, and New Guinea; Cryphocricinae is found only in the New World with the highest diversity in North America; Laccocorinae is mainly distributed in the Old World with few representatives in the New World; Limnocorinae is distributed only in the New World with the highest diversity in South America; and Naucorinae is cosmopolitan. The family Naucoridae includes 40 genera and approximately 400 described species, approximately half of which occur in the New World.

For most of the Mexican insect fauna our taxonomic knowledge is inadequate. Thus, accurate information regarding species richness, diversity, biology, distribution, phylogenetic relationships, ecological roles, and economic importance is not available. In particular, this applies to most Mexican aquatic and semi-aquatic Heteroptera, except for Naucoridae, which has been studied in recent years. The aquatic and semi-aquatic Heteroptera (Gerrimorpha, Leptopodomorpha, Nepomorpha) represent an important component of the world’s aquatic insect biota with 23 families, 343 genera, and 4,810 species (Polhemus and Polhemus 2008a). However, in Mexico relatively few works (e.g., Usinger 1946, La Rivers 1953) from sporadic and scattered collecting trips have provided a limited understanding of the taxonomy, species richness, and distribution of these aquatic and semi-aquatic groups.

Taxonomic History

The first major taxonomic contributions to understanding the Mexican saucer bug fauna were by the French entomologist Arnold L. Montandon, who at the end of the 19th century described a large number of species from North America and Europe.
Figure 1. Female of *Ambrysus signoreti*. (A) dorsal habitus, (B) ventral habitus, (C) frontal view of head, prothoracic legs, and prothorax (D) lateral view of left side.

Figure 2. DRV collecting specimens of the genus *Cataractocoris* at El Arcoiris waterfall in Veracruz, Mexico.
of the 19th century described 10 of the species currently known to be distributed in Mexico, including *Ambrysus mexicanus* Montandon. Later into the 20th century, American entomologists Ira La Rivers and Robert L. Usinger provided description of many new taxa.

In 1946, Usinger published a study in which he described 16 new species in the genus *Ambrysus* Stål; 10 species were from Mexico, five of them collected personally during his two-month collecting trip to central Mexico in 1933. During the trip to the Estado de México, collecting took place around the towns of Tejupilco and Temascaltepec. Usinger (1972) later explained that he collected thousands of specimens and considered the area as “The original home of the Naucoridae.” He described collecting in the area as “fantastic,” because he was able to collect more subfamilies, genera, and species of Naucoridae than those reported by Champion (1901) for Central America in the *Biologia Centrali-Americana* (Usinger 1972).

Although La Rivers published several small works dealing with the Mexican Naucoridae, his most important contribution was the revision of the genus *Ambrysus* of Mexico (La Rivers 1953), which was a complement to his revision of the genus in the United States (La Rivers 1951). An important contribution from these works was the use of structures associated with the terminal abdominal segments of males and females as diagnostic features. Formerly, the species descriptions were based on gross morphological characteristics such as body length, width, color, and features of the pronotum and hemelytra surface. La Rivers was the first to use the shape of the posterior margin of the female seventh mediosternite (subgenital plate) and the shape of the male accessory genital process of the sixth tergum for species determination. These two features are still commonly used to determine and diagnose species (e.g., Sites and Shepard 2015, Sites and Reynoso-Velasco 2015).

La Rivers (e.g., 1951) designated distinct species complexes within the genus *Ambrysus*, but in many cases he did not provide sufficient unifying attributes or define the complexes based on the same features. For example, La Rivers (1957) compared the *A. mexicanus* and *A. signoreti* species complexes using contrasting character states of body shape, embolium width, coloration, and production of posterolateral corners of the abdominal segments. However, the *A. hybridus* species complex was defined based on other features, including the overall similar shape of the male accessory genital process and the female subgenital shape (La Rivers 1957). Furthermore, the presence of strikingly different morphological features led to the establishment of different monotypic species complexes.

Until the end of the 20th Century, the Mexican fauna of Naucoridae was represented by 55 described species in six genera and four subfamilies. Cryptochricinae was the most species-rich subfamily with 42 species in three genera, followed by Limnocrininae with 10 species in its single genus, Naucorinae with 2 species in one genus, and Laccocorinae with a single representative (Hungerford 1936; La Rivers 1971, 1976; Polhemus and Polhemus 1981, 1983; Davis 1986, 1996; Polhemus and Sites 1995).

**Recent Taxonomic Research**

In 2012, we undertook a project to clarify the taxonomy of the family Naucoridae in Mexico. An important aspect of this study was to evaluate the reliability of the diagnostic features used by La Rivers for species identification. Frequently, we were unable to identify specimens using his characters; thus, we were concerned that unrecognized intraspecific variation resulted in species being described more than once. To investigate intraspecific variation, we endeavored to examine as many specimens as possible within and among populations throughout the range of each species.

The first obstacle we encountered was the small number of specimens of Naucoridae deposited in different collections. La Rivers (1951) faced the same problem when trying to revise the entire genus *Ambrysus*. Thus, we examined material from as many collections as possible (including type material) and conducted extensive collecting throughout the country to maximize the opportunity to detect intraspecific variation.

The museum collections where we examined material or from which we obtained material on loan were: American Museum of Natural History (New York, United States), Bohart Museum of Entomology (Davis, United States), Brigham Young University (Provo, United States), California Academy of Sciences (San Francisco, United States), California State Collection of Arthropods (Sacramento, United States), Carnegie Museum of Natural History (Pittsburgh, United States), Colección Entomológica de la Universidad Autónoma de Querétaro (Juriquilla, Mexico), Colección Entomológica del Instituto de Ecología A.C. (Xalapa, Mexico), Colección Nacional de Insectos, Universidad Nacional Autónoma de México (Mexico City, Mexico), Escuela Agrícola Panamericana, Universidad Zamorano (San Antonio de Oriente, Honduras), Essig Museum of Entomology Collection (Berkeley, United States), Field Museum of Natural History (Chicago, United States), Illinois Natural History Survey (Champaign, United States), Muséum National d’Histoire Naturelle (Paris, France), Natural History Museum of Los Angeles County (Los Angeles, United States), Naturhistorisches Museum (Vienna, Austria), New Mexico State University (Las Cruces, United States), Snow Entomological Museum Collection, University of Kansas (Lawrence, United States), Swedish Museum of Natural History (Stockholm, Sweden), Texas A&M University (College Station, United States), Texas Natural History Collections, Entomology Collection (Austin, United States), The Natural History Museum (London, England), United States National Museum of Natural History (Washington D.C., United States), Universidad del Valle de Guatemala (Guatemala City, Guatemala), University of Idaho Entomological Collection (Moscow, United States), University of Michigan Museum of Zoology (Ann Arbor, United States), University of Missouri (Columbia, United States), Washington State University Collection (Pullman, United States), Zoologisches Museum Hamburg (Hamburg, Germany), Zoologische Staatssammlung (Munich, Germany).

We complemented the information obtained from specimens deposited in the museum collections with the more than 10,000 specimens we collected from 432 localities throughout the country (Fig. 3). To maximize representation of the fauna in Mexico, we collected in all
but three of Mexico’s biogeographic provinces (Morrone 2005). We did not collected in the two provinces in the Baja California Peninsula because of the low overall species richness of the area and because that fauna was well represented in collections from the western United States. We also did not collect in Yucatan Peninsula province due to the small number of surficial waters. Photographs of the collection sites identified as L-numbers are available in a Locality Image Database via a link from the internet site of the Enns Entomology Museum, University of Missouri.

During the still ongoing project, we have found that La Rivers’ diagnostic features (shape of the male accessory genitalic process and female subgenital plate) are informative for species identification. In most cases, the subgenital plate provides the most reliable diagnostic information. We have also found that La Rivers’ diagnostic characteristics exhibit substantial intraspecific variation, which can occur within and/or among populations. This is important because several species and subspecies were described based on only a few specimens from distant populations and the variation of the diagnostic features was not assessed.

A clear example of a species exhibiting intraspecific variation is *Ambrysus circumcinctus* Montandon. Using primarily the shape of the posterior margin of the female subgenital plate, La Rivers (1967) considered this species to be represented by three subspecies: *A. c. extremus* La Rivers from Costa Rica and Honduras, *A. c. concavus* La Rivers from Mexico (Nuevo León and San Luis Potosí), and the nominate *A. c. circumcinctus* from the southern United States (New Mexico and Texas). A fourth subspecies, *A. c. caliginosus* Usinger, was designated by La Rivers but was distinguished from the nominate subspecies based only on size and general coloration. Reynoso-Velasco et al. (2016) found that what La Rivers considered to be a stable and consistent feature instead was an artifact of the small number of specimens and localities used to describe the subspecies. At various localities in the range of *A. circumcinctus*, populations exhibit the characteristics of more than one described subspecies (Reynoso-Velasco et al. 2016), which is contrary to the concept of the subspecies as a geographical variety (Mayr 1982) with morphological uniformity in one or a few diagnostic characters (Wilson and Brown 1953). Reynoso-Velasco et al. (2016) proposed the four subspecies to be synonymized and recognized the presence of a single species, *A. circumcinctus*, with the expected variation in the shape of the subgenital plate throughout its wide range.

Because the *Ambrysus* species complexes were proposed by La Rivers using eclectic rather than homologous features, there is concern that they might not be consistent with phylogeny. At an early stage of our study, we found that the medial lobes of the male eighth tergum (pseudoparameres) and characteristics of the phallosoma could be important diagnostic features at the species and species complex levels. More specifically, features of the phallosoma have been used to better define and circumscribe the species complexes in *Ambrysus* (e.g., Reynoso-Velasco and Sites 2016a, b). The pseudoparameres can sometimes be informative at the species level, as in the case of species in the subgenus *Syncollus* present in Mexico (Reynoso-Velasco et al. 2016), or at the species complex level, as in

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**Figure 3.** The 432 localities where we collected samples for the project on the Mexican fauna of Naucoridae.
the case of the *A. guttatipennis* Stål complex (Reynoso-Velasco and Sites 2016a).

As a result of this ongoing project, we have presented seven papers in which we treated the taxonomy of elements of the Mexican fauna of Naucoridae. We have primarily focused our efforts in studying Cryptocricinae because this subfamily possesses the highest species richness in Naucoridae. Initially, we revised the genus *Cataractocoris* (Sites et al. 2013), then focused our attention on the genus *Ambrysus* (Sites and Reynoso-Velasco 2015; Reynoso-Velasco and Sites 2016a, 2016b, 2018a, 2018b; Reynoso-Velasco et al. 2016), which is the most species-rich genus in this family and comprises more species that do any of the subfamilies of Naucoridae. In addition, the highest species richness of this genus is centered in Mexico.

Based partially on our recent studies, the current list of species present in Mexico includes 71 described species in six genera and four subfamilies. Because we have focused our research on Cryptocricinae, all recent taxonomic changes have taken place in this subfamily, which in Mexico is represented by 58 species in three genera.

**Current State of Taxonomy**

At the present time, the taxonomy of the Mexican fauna of Naucoridae is fairly well understood and nearly complete. Regarding the subfamily Cryptocricinae, the revision of the North American fauna of the most species-rich genus *Ambrysus* is in progress and close to completion. The genus *Cataractocoris* (Fig. 4) has been revised (Sites et al. 2013) and all three recognized species are present in Mexico. However, the genus *Cryptocricos* Signoret (Fig. 5) is in need of a comprehensive taxonomic revision. This genus is more diverse in South America, and in Mexico it has only two representatives. The distinction between the two Mexican species is based on body length, hemelytra mensural features, and characteristics of the posterolateral corners of abdominal segments (Usinger 1947). *Cryptocricos hungerfordi* Usinger is widespread and common in Mexico, whereas *C. mexicanus* Usinger has not been recorded since the type series was collected in 1933. A detailed study using more stable and informative morphological features and molecular data could help to clarify the taxonomy of the genus. The Mexican fauna of this subfamily represents 83% of the total species of Naucoridae known in the country.

The subfamily Limnocorinae currently comprises 73 described species in a single genus and is represented in Mexico by 10 species. Higor D. D. Rodrigues recently completed a taxonomic revision of the genus *Limnocoris* Stål (Fig. 6) as his dissertation research and is preparing it for publication. Several synonymies will be proposed for species reported from Mexico, as well as new records, and the description of at least one new species (H.D.D. Rodrigues, pers. comm.).

The subfamily Laccocorinae is the third most species-rich subfamily and in Mexico it is represented only by the monotypic genus *Interocoris* La Rivers. *Interocoris mexicanus* (Usinger) (Fig. 7) was originally described in the genus *Heleocoris* Stål (Usinger 1935) and was placed in the subgenus *Interocoris* by La Rivers (1974) to distinguish

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*Figure 4.* Staged specimen of *Cataractocoris macrocephalus* (Rio Rana, Oaxaca).
it from the Old World and South American species. Later, the subgenus *Interocoris* was elevated to full generic status (Polhemus and Polhemus 2008b). A more detailed taxonomic study is needed to address the classification of this monotypic taxon and related taxa. The genus *Ctenipocoris* Montandon, also a member of Laccocorinae, is represented in the Neotropics by six species. Five of those are distributed in South America and only one species has been reported as far north as Costa Rica (Herrera 2013). This genus has at least one representative in Mexico; we have examined specimens collected in the southern states of Chiapas and Yucatán. Our understanding of the taxonomy of this genus is poor and the available literature is not sufficient to enable confident identification of the specimens from Mexico.

The subfamily Naucorinae, with 11 genera and 80 described species worldwide, is represented in the New World by two genera, one of which occurs in Mexico. *Pelocoris* Stål is most diverse in South America and has been revised for the United States and Canada (Polhemus and Sites 1995, Sites and Polhemus 1995, Sites 2015); however, the fauna of Mexico is uncertain. Currently, two species of *Pelocoris* have been recorded in Mexico, *Pelocoris biimpressus* Montandon (Fig. 8) and *P. femoratus* (Palisot de Beauvois), and we have seen at least one undescribed species in museums. Of these, *Pelocoris biimpressus* is the most common and is widespread. *Pelocoris femoratus* is common throughout the eastern United States and Canada.
and numerous erroneous records are from as far south as Uruguay (Sites et al. 2018). Although *P. femoratus* has been reported from northeastern Mexico (Roback and Nieser 1974), Tamaulipas (Davis 1986), and Yucatán (Hungerford 1936), these records require confirmation because misidentifications in this genus are frequent. Nonetheless, a valid recent record of *P. femoratus* from Belize (Sites et al. 2018) suggests the species also occurs in eastern Mexican lowlands. A comprehensive taxonomic revision of the genus will help to clarify the status of the Mexican fauna of *Pelocoris*.

**SUBFAMILY CRYPHOCRINAE**  
**GENUS Ambrysus Stål**  
**SUBGENUS Ambrysus Stål**  
Species complex *Ambrysus guttatipennis* Stål  
*A. arizonus* La Rivers, 1951  
Distribution: Sonora  
*A. ayoyolin* Reynoso and Sites, 2016  
Distribution: Hidalgo  
*A. bispinus* La Rivers, 1951  
Distribution: Chiapas, Michoacán, Oaxaca, Puebla, Veracruz.  
*A. bowlesi* Reynoso and Sites, 2016  
Distribution: Chihuahua, Durango, Jalisco, Sinaloa.  
*A. contrerasi* Reynoso and Sites, 2016  
Distribution: Estado de México, Guerrero, Jalisco, Michoacán, Morelos, Oaxaca, Puebla.  
*A. drakei* La Rivers, 1957  
Distribution: Durango, Jalisco, San Luis Potosí, Zacatecas.  
*A. guttatipennis* Stål, 1876  
Distribution: Ciudad de México, Guanajuato, Hidalgo, Morelos, Oaxaca, Puebla, Querétaro, San Luis Potosí, Veracruz.  
*A. itsipatsari* Reynoso and Sites, 2016  
Distribution: Michoacán.  
*A. mexicanus* Montandon, 1897  
Distribution: Estado de México, Guerrero, Jalisco, Michoacán, Morelos, Oaxaca, Puebla.  
*A. mormon* Montandon, 1909  
Distribution: Chihuahua, Durango, Sonora.  
*A. noveloi* Reynoso and Sites, 2016  
Distribution: Jalisco.  
*A. veracruzanus* Reynoso and Sites, 2016  
Distribution: Veracruz.  

Species complex *Ambrysus hybridus* Montandon  
*A. convexus* Usinger, 1946  
Distribution: Estado de México, Michoacán, Morelos.  
*A. fuscus* Usinger, 1946  
Distribution: Estado de México, Morelos.  
*A. hybridus* Montandon, 1897  
Distribution: Chihuahua, Durango, Estado de México, Guanajuato, Hidalgo, Nuevo León, Oaxaca, Puebla, Querétaro, Sonora.  
*A. lariversi* Reynoso and Sites, 2016  
Distribution: Durango.  
*A. lattini* La Rivers, 1976  
Distribution: Chihuahua, Durango.  
*A. plautus* Polhemus and Polhemus, 1982  
Distribution: Chihuahua, Durango.  
*A. spiculus* Polhemus and Polhemus, 1981  
Distribution: Chihuahua, Durango, Sinaloa, Sonora, Zacatecas.  
*A. ultimus* La Rivers, 1976  
Distribution: Puebla.  

Species complex *Ambrysus pudicus* Stål  
Subcomplex *subpilosus*  
*A. pardinus* Stål, 1862  
Distribution: Chiapas, Coahuila, Estado de México, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz.  

Subcomplex *pilosus*  
*A. abortus* La Rivers, 1953  
Distribution: Chiapas, Coahuila, Estado de México, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa.  
*A. angularis* La Rivers, 1953  
Distribution: Guerrero, Jalisco, Michoacán, Oaxaca.  
*A. chinanteco* Reynoso and Sites, 2018  
Distribution: Oaxaca.  
*A. hungerfordi* Usinger, 1946  
Distribution: Chihuahua, Durango, Guanajuato, Jalisco, Michoacán, Nayarit, Querétaro, San Luis Potosí, Sinaloa, Sonora.
Primero en línea

*A. parviceps* Montandon, 1897  
Distribution: Chiapas, Colima, Estado de México, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, San Luis Potosí.

*A. spicatus* La Rivers, 1953  
Distribution: Chiapas, Oaxaca.

*A. triunfo* La Rivers, 1953  
Distribution: Baja California Sur.

Species complex *Ambrysus pulchellus* Montandon

*A. buenoi* Usinger, 1946  
Distribution: Chihuahua.

*A. pulchellus* Montandon, 1897  
Distribution: Chiapas, Coahuila, Colima, Estado de México, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Veracruz, Zacatecas.

*A. pygmaeus* La Rivers, 1953  
Distribution: Durango, Estado de México, Morelos, Oaxaca.

*A. totonacus* Reynoso, Sites, and Novelo, 2016  
Distribution: Hidalgo, Puebla, Veracruz.

*A. xico* Reynoso, Sites, and Novelo, 2016  
Distribution: Chiapas, Jalisco, Nayarit, Oaxaca, Veracruz.

**GENUS Cataractocoris** Usinger

*Cataractocoris macrocephalus* (Montandon), 1897  
Distribution: Chiapas, Estado de México, Jalisco, Morelos, Veracruz.

*C. marginiventris* Usinger, 1941  
Distribution: Chiapas, Estado de México, Guerrero, Jalisco, Michoacán, Oaxaca, Puebla, Veracruz.

*C. shepardi* Sites, Reynoso, and Novelo, 2013  
Distribution: Chiapas, Jalisco, Nayarit, Oaxaca, Veracruz.

**GENUS Cryphocricos** Signoret

*Cryphocricos hungerfordi* Usinger, 1947  
Distribution: Coahuila, Veracruz.

*C. mexicanus* Usinger, 1947  
Distribution: Estado de México.

**SUBFAMILY LACCOCORINAE**

**GENUS Interocoris** La Rivers

*Interocoris mexicanus* Usinger, 1935  
Distribution: Chiapas, Estado de México, Guerrero, Jalisco, Nayarit, Oaxaca, Sonora.

**SUBFAMILY LIMNOCORINAE**

**GENUS Limnocoris** Stål

*Limnocoris borellii* Montandon, 1897  
Distribution: México (not a specific locality).

*L. braillovsky* La Rivers, 1976  
Distribution: Jalisco.

*L. hintoni* La Rivers, 1970  
Distribution: Estado de Mexico, Jalisco, Puebla.

*L. laucki* La Rivers, 1970  
Distribution: Nayarit.

*L. lutzi* La Rivers, 1957  
Distribution: Coahuila, Oaxaca, San Luis Potosí, Veracruz.

*L. profundus* (Say), 1832  
Distribution: México (not a specific locality).

*L. pygmaeus* La Rivers, 1956  
Distribution: Guerrerco, Jalisco, Sinaloa, Sonora.

*L. signoreti* Montandon, 1897  
Distribution: México (not a specific locality).

*L. solenoides* La Rivers, 1970  
Distribution: Oaxaca.
We encourage colleagues worldwide to contact us if they are interested in establishing collaborations to study aquatic and semi-aquatic Heteroptera.

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