THE *AMBRYSUS* STÅL (HETEROPTERA: NAUCORIDAE) OF MEXICO: REVISION OF *AMBRYSUS* (*SYNCOLLUS*) LA RIVERS AND SPECIES GROUPS OF *AMBRYSUS* (*AMBRYSUS*)

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Doctor of Philosophy

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by
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THE *AMBRYSUS* STÅL (HETEROPTERA: NAUCORIDAE) OF MEXICO: REVISION OF *AMBRYSUS* (*SYNCOLLUS*) LA RIVERS AND SPECIES GROUPS OF *AMBRYSUS* (*AMBRYSUS*)

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INTRODUCTION

One of the most fundamental questions in biodiversity research is, how many species are there? It is ironic that in the 21st century this question does not have a concise answer (Mora et al. 2011) or even a consensual estimate. As of August 2015, 1,619,092 described species were listed in the Catalog of Life (Roskov et al. 2015), with Insecta being the most diverse and successful group with close to one million species (Grimaldi & Engel 2005, Mora et al. 2011).

Seventeen countries, mostly in the tropics, collectively harbor close to 70% of the biological diversity on the planet (Mittermeier & Mittermeier 1992, Espinosa et al. 2008). Mexico is one of these megadiverse countries and is among the top five with Brazil, China, Colombia, and Indonesia in known diversity of amphibians, birds, mammals, reptiles, and vascular plants. For each of these groups Mexico contributes almost 10% of the known global biodiversity. Insects, with 47,853 species, has the highest number of known species in the country and represents 5% of the nearly one million insect species described worldwide (Sarukhán et al. 2009).

One of the reasons for such high diversity in Mexico is that the country spans both the Nearctic and Neotropical biogeographic regions. The Nearctic region extends from the north and includes the Baja California peninsula, the Mexican plateau, and Sonora and Tamaulipas states. The Neotropical region includes the tropical lowlands and the Yucatan Peninsula. In addition, a transition zone where Nearctic and Neotropical biotic elements overlap comprises most of the Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, and Trans-Mexican Volcanic Belt (Halffter et al. 2008,

Morrone & Márquez 2008). Also, the country's geologic history and complex topographic relief are important factors influencing its biodiversity (Sarukhán et al. 2009). These aspects allow for a wide range of habitats with particular abiotic conditions (e.g., elevation, climate, temperature) to provide myriad niches where speciation takes place. A direct consequence of this process is the number of endemic species, those only known to occur within the country. Mexico has more endemic species than the majority of countries in the world (Heppner 2002). It has the second highest number of endemic amphibians and reptiles (65% and 57%, respectively) and third highest for vascular plants, just behind China and Indonesia (Sarukhán et al. 2009). Lepidoptera is perhaps the best known insect order in Mexico, with 14,500 described species and 23,750 estimated to occur there (Llorente-Bousquets et al. 2014). Of the described species, 25% are endemic to Mexico (Heppner 2002). Only for a few taxa within the orders Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, Megaloptera, and Odonata is the taxonomy in good condition.

For most of the Mexican insect fauna our taxonomic knowledge is inadequate or lacking entirely. Thus, accurate information regarding the number of species and their distributions, phylogenetic relationships, ecological roles, and economic importance is not available. In particular this applies to the Mexican aquatic and semi-aquatic Heteroptera (Insecta: Hemiptera). This group, considered to be moderately well-collected and with a relatively mature taxonomy (especially for species from Australia, Europe, and North America), represents an important component of the world's aquatic insect biota with 23 families, 343 genera, and 4,810 species (Polhemus & Polhemus 2008). However, in Mexico relatively few works from sporadic and scattered collecting

trips have provided a limited understanding of the taxonomic composition and species distribution of aquatic and semi-aquatic Heteroptera.

The family Naucoridae (Heteroptera: Nepomorpha), commonly known as creeping water bugs or saucer bugs, contains five subfamilies, 39 genera, and 393 species worldwide (Sites, per. comm.). The known fauna of Naucoridae in Mexico is represented by four subfamilies, six genera, and 56 species (La Rivers 1971, 1976; Polhemus & Polhemus 1981, 1983; Davis 1986; Polhemus & Sites 1995; Dinger et al. 2005; Sites et al. 2013; Sites & Reynoso-Velasco 2015). Other than species richness, little reliable information is available regarding species distributions or their ecological roles.

Some species of naucorids have conservation value by acting as umbrella species for aquatic ecosystems where no vertebrates can be similarly designated. For example, *Ambrysus funebris* La Rivers is an umbrella species protecting a spring system in Death Valley National Park, USA (Whiteman & Sites 2008).

Naucorids have the potential to be useful in the biological control of mosquito larvae (Diptera: Culicidae) that transmit viruses and other disease agents (Sites 2000). The creeping water bug *Pelocoris femoratus* (Palisot de Beauvois) feeds on larval *Aedes* Meigen mosquitoes (Hungerford 1927) that transmit viruses causing yellow fever, dengue, and Zika. Also, *Ilyocoris cimicoides* (L.) feeds on mosquito larvae of the genus *Anopheles* Meigen (Eysell 1905, Hamlyn-Harris 1929), a vector of the protists that cause malaria.

Buruli ulcer is a geographically widespread disease (Africa, Australia, Southeast Asia, China, Central and South America, and the Western Pacific) caused by *Mycobacterium ulcerans*, which produces serious necrotizing cutaneous infection in its

victims. This disease is found primarily in rural areas located near wetlands, slow-moving rivers, and in areas prone to flooding. This disease has been reported from Mexico (Merritt et al. 2010); however, there has not been systematic monitoring of this problem in the country. Some authors (e.g., Marsollier et al. 2002) have implicated naucorids as a reservoir of this pathogen where it is maintained in the salivary glands. Although not proven under experimental conditions, it is suspected that naucorids may be able to transmit *Mycobacterium ulcerans* to humans through their bites.

It is important to encourage and support taxonomic projects, especially because delimitation and identification of species is the foundation of biology. Some myopic people consider taxonomy as an archaic activity that is no longer essential; however, any ecological or molecular study using modern techniques makes no sense if the correct name of the basic elements (species) they are working with is not known. Species are the essential units upon which we generate knowledge in biological sciences.

References cited

Davis, J. R. 1986. New distributional records of Naucoridae (Hemiptera) from the United States and Mexico, with morphological and taxonomic notes. The Southwestern Naturalist 31: 535–539.

Dinger, E. C., A. E. Cohen, D. A. Hendrickson & J. C. Marks. 2005. Aquatic invertebrates of Cuatro Ciénegas, Coahuila, México: Natives and exotics. The Southwestern Naturalist 50: 237–281.

Espinosa Organista, D., S. Ocegueda Cruz, C. Aguilar Zúñiga, O. Flores Villela & J. Llorente-Bousquets. 2008. El conocimiento biogeográfico de las especies y su regionalización natural, pp. 33–65. *In*: Capital natural de México, vol. I: Conocimiento actual de la biodiversidad. CONABIO, Mexico.

Eysell, A. 1905. Die Stechmücken, pp. 78–80. *In*: C. Mense (ed.). Handbuch der Tropenkrankheiten, Bd. 2, Barth, Leipzig, Germany.

Grimaldi, D. & M. S. Engel. 2005. Evolution of Insects. Cambridge University Press, New York, USA.

Halffter, G., J. Llorente-Bousquets & J. J. Morrone. 2008. La perspectiva biogeográfica histórica, pp. 67–86. *In*: Capital natural de México, vol. I: Conocimiento actual de la biodiversidad. CONABIO, Mexico.

Hamlyn-Harris, R. 1929. The relative value of larval destructors and the part they play in mosquito control in Queensland. Proceedings of the Royal Society of Queensland 41: 23–38.

Heppner, J. B. 2002. Mexican Lepidoptera biodiversity. Insecta Mundi 16: 171–190.

Hungerford, H. B. 1927. The life history of the creeping water bug, *Pelocoris carolinensis* Bueno (Naucoridae). Bulletin of the Brooklyn Entomological Society 22: 77–83.

La Rivers, I. 1971. Studies of Naucoridae (Hemiptera). Biological Society of Nevada Memoirs 2: 1–120.

La Rivers, I. 1976. Supplement No. 2 to the catalogue of taxa described in the family Naucoridae (Hemiptera) with descriptions of new species. Biological Society of Nevada Occasional Papers 41: 1–17.

Llorente-Bousquets, J., I. Vargas-Fernández, A. Luis-Martínez, M. Trujano-Ortega, B. C. Hernández-Mejía & A. D. Warren. 2014. Biodiversidad de Lepidoptera en México. Revista Mexicana de Biodiversidad, Suplemento 85: 353–371.

Marsollier, L., R. Robert, J. Aubry, J. P. Saint Andre, H. Kouakou, P. Legras, A. Manceau, C. Mahaza & B. Carbonnelle. 2002. Aquatic insects as a vector for *Mycobacterium ulcerans*. Applied and Environmental Biology 68: 4623–4628.

Merritt, R. W., E. D. Walker, P. L. C. Small, J. R. Wallace, P. D. R. Johnson, M. E. Benbow & D. A. Boakye. 2010. Ecology and transmission of Buruli ulcer disease: a systematic review. PLOS Neglected Tropical Diseases 12(4) art. no. e911: 1–15.

Mittermeier, R. A. & C. Mittermeier. 1992. La importancia de la diversidad biológica de México, pp. 63–73. *In*: J. Sarukhán & R. Dirzo (eds.). México frente a los retos de la biodiversidad. CONABIO, Mexico.

Mora, C., D. P. Tittensor, S. Adl, A. G. B. Simpson & B. Worm. 2011. How many species are there on earth and in the ocean? PlosBiology 9: 1–8.

Morrone, J. J. & J. Márquez. 2008. Biodiversity of Mexican terrestrial arthropods (Arachnida and Hexapoda): a biogeographical puzzle. Acta Zoológica Mexicana 24: 15–41.

Polhemus, J. T. & D. A. Polhemus. 1981. Three new species of *Ambrysus* from Mexico (Hemiptera: Naucoridae). The Pan-Pacific Entomologist 57: 397–401.

Polhemus, J. T. & D. A. Polhemus. 1983. Notes on Neotropical Naucoridae II. A new species of *Ambrysus* and review of the genus *Potamocoris* (Hemiptera). The Pan-Pacific Entomologist 58: 326–329.

Polhemus, J. T. & D. A. Polhemus. 2008. Global diversity of true bugs (Hetereptera: Insecta) in fresh water. Hydrobiologia 595: 379–391.

Polhemus, J. T. & R. W. Sites. 1995. The identity of *Pelocoris biimpressus* Montandon and synonymy of *Pelocoris* species in the southwestern United States (Heteroptera: Naucoridae). Proceedings of the Entomological Society of Washington 97: 654–658.

Roskov, Y., L. Abucay, T. Orrell, D. Nicolson, T. Kunze, C. Flann, N, Bailly, P. Kirk, T. Bourgoin, R. E. DeWalt, W. Decock & A. De Wever (eds.). 2015. Species 2000 & ITIS Catalogue of Life, 26th August 2015. Digital resource at www.catalogueoflife.org/col/ [consulted on September 2015].

Sarukhán, J., P. Koleff, J. Carabias, J. Soberón, R. Dirzo, J. Llorente-Bousquets, G. Halffter, R. González, I. March, A. Mohar, S. Anta & J. de la Maza. 2009. Capital natural de México. Síntesis: conocimiento actual, evaluación y perspectivas de sustentabilidad. CONABIO, Mexico.

Sites, R. W. 2000. Creeping water bugs (Naucoridae), pp. 571–576. *In*: C. W. Schaefer & A. R. Panizzi (eds.). Heteroptera of economic importance. CRC Press, Boca Raton, Florida, USA.

Sites, R. W., D. Reynoso-Velasco & R. Novelo-Gutiérrez. 2013. Revision of the Mesoamerican genus *Cataractocoris* Usinger (Hemiptera: Heteroptera: Nepomorpha: Naucoridae). Zootaxa 3682: 475–484.

Sites, R. W. & D. Reynoso-Velasco. 2015. Review of the *Ambrysus stali* La Rivers species complex (Heteroptera: Nepomorpha: Naucoridae) with the description of a new species from Mesoamerica. Zootaxa 4018: 279–291.

Whiteman, N. K. & R. W. Sites. 2008. Aquatic insects as umbrella species or ecosystems protection in Death Valley National Park. Journal of Insect Conservation 12: 499–509.

CHAPTER II

LITERATURE REVIEW

HEMIPTERA

Hemiptera is the fifth largest insect order after Coleoptera, Diptera, Hymenoptera, and Lepidoptera, and the largest nonholometabolous order (Cui et al. 2013). This taxon was established by Linnaeus (1758) based on the wing structure where the first pair of wings have the proximal half coriaceous (*alae superiores semicrustaceae*). Latreille (1810) later recognized the sections Heteroptera and Homoptera in this group, each with three families, and although Kristensen (1981) considered it inappropriate to subdivide Hemiptera into two or more groups, it is now generally accepted that this order comprises the suborders Auchenorrhyncha, Coleorrhyncha, Heteroptera, and Sternorrhyncha (Cryan & Urban 2012). The group is considered monophyletic based on the unique piercing-sucking mouth apparatus in which the mandibles and maxillae are modified into four stylets enclosed within the segmented labial rostrum (Kristensen 1991).

HETEROPTERA

Heteroptera (true bugs) is a group with approximately 40,000 described species (Weirauch & Shuh 2011) with its first appearance in the fossil record approximately 230 million years ago during the Early Mesozoic. Especially important for the study of this group are the Jurassic and Cretaceous periods because of the great number of Heteroptera fossils (Grimaldi & Engel 2005). Heteroptera has been long considered monophyletic based on the characteristic subdivision of the forewings (hemelytra) into a proximal

coriaceous or leathery (corium) and a distal membranous portion. Other synapomorphies are: a) labium inserted anteriorly on the head, b) presence of metathoracic scent glands in adults, c) immatures with dorsal abdominal scent glands, d) open rhabdom of the ommatidium, and e) a four-segmented antenna with two intersegmental sclerites (Weirauch & Shuh 2011).

Singh-Pruthi (1925) provided with a classification of the Heteroptera families and subfamilies based on male genitalic features. His scheme included two main groups, insects of the pentatomoid and reduvioid types, although for both groups the relationships among the great majority of families were unclear. The aquatic and semiaquatic bugs were included with the reduvioid type insects. China (1933) considered that this work overestimated the evolutionary importance of genitalic structures and that the classification was actually just reflecting biological differences in feeding habits, with pentatomoids mainly phytophagous and reduvioids largely predaceous.

The efforts to produce a valid classification of Heteroptera continued and Popov (1971) proposed a new system including the infraorders Cimicomorpha, Enicocephalomorpha (=Dipsocoromorpha), Leptopodomorpha (=Amphibiocorisae), Nepomorpha (=Hydrocorisae), and Pentatomomorpha for the extant taxa; along with Actinoscytinomorpha (Triassocoridomorpha) for the extinct groups.

Štys & Kerzhner (1975) became aware of the different classifications and numerous names for different taxa within Heteroptera and the problems created by such different systems. One particular problem they recognized was the use of old descriptive names, because those were not typified by derivation from a generic name (e.g., *Cryptocerata*) and thus, are not associated with a particular taxon. Instead they favored

the use of compound typified names that would be formed with: a) the grammatical stem of the type-genus of the oldest family-group name in the respective infraorder, b) the appropriate connecting vowel for names derived from Greek ("o"), and c) the ending -*morpha*. The use of the word -*morpha* at the end of the name was previously introduced by Leston et al. (1954) when the terrestrial Heteroptera groups (Geocorisae) were divided into Pentatomomorpha and Cimicomorpha, and had been adopted and used in Heteroptera (Popov 1971), as well as in Diptera and Psocoptera (Štys & Kerzhner 1975).

After reviewing and comparing the available information on the classification of Heteroptera and the relationships among its families, Štys & Kerzhner (1975) presented a new approach to the taxonomy of the group including seven infraorders, all of which were previously proposed by other authors: 1) Cimicomorpha, 2) Dipsocoromorpha, 3) Enicocephalomorpha, 4) Gerromorpha (semiaquatic bugs), 5) Leptopodomorpha, 6) Nepomorpha (aquatic bugs including the riparian Gelastocoridae and Ochteridae), and 7) Pentatomomorpha. In comparison with Popov's classification (1971), this scheme included two more infraorders for the extant taxa, Dipsocoromorpha and Gerromorpha.

Based on original observations and reinterpretation of the information provided by Cobben (1978) on the morphology of the first nymphal instar and adult heteropterans, Schuh (1979) applied cladistic methodology to elucidate the phylogenetic relationships among the seven infraorders and found (Enicocephalomorpha + (Dipsocoromorpha + (Gerromorpha + ((Leptopodomorpha + Nepomorpha) + (Cimicomorpha + Pentatomomorpha))))).

Wheeler et al. (1993) presented a new approach to the phylogeny of Heteroptera based on a total evidence analysis that included 31 morphological characters and 669

base-pairs (bp) of the 18s ribosomal RNA gene (18s rRNA). They found a similar topology to that presented by Schuh (1979) with the exception that Leptodomorpha and Nepomorpha were not recovered as a monophyletic group; instead, Nepomorpha was the sister group of (Leptodomorpha + (Cimicomorpha + Pentatomomorpha)). They also summarized and provided information about the monophyly of each group. In this case, the water bugs (Nepomorpha) were considered monophyletic based on molecular data and the morphological characteristics of the short antenna folded into a groove under the eyes (except Ochteridae) and the structure of the abdominal sternum in females. Another important discovery was the recovery of Corixidae as part of this infraorder, since there had been debate about its position within Heteroptera.

Xie et al. (2008) analyzed the phylogeny of Hemiptera using data from 18s rRNA and found that the group closest to the base of the cladogram was Enicocephalomorpha, the sister group of the clade including (Nepomorpha + (Leptodomorpha + ((Dipsocoromorpha + Gerromorpha) + (Cimicomorpha + Pentatomomorpha)))).

Based on an analysis of a series of papers on the relationships among infraorders in Heteroptera, Cassis & Schuh (2010) constructed a matrix with 78 morphological characters from 43 taxa in Panheteroptera (Cimicomorpha, Leptodomorpha, Nepomorpha and Pentatomomorpha). Their cladistic analysis produced the same topology proposed by Xie et al. (2008), with Nepomorpha as the sister group of the monophyletic (Leptopodomorpha + (Cimicomorpha + Pentatomomorpha)), although Leptodomorpha was paraphyletic in this study.

Li et al. (2012) evaluated the phylogeny of the group using multiple genes and found that the only stable relationships recovered were Nepomorpha at the base of the

cladogram and the sister group relationship of Cimicomorpha and Pentatomomorpha; the latter was a common outcome in other studies.

The most recent study (Wang et al. 2015) on the phylogeny of Heteroptera included molecular data from 10,149 homologous sites (6,416 sites from 18s and 28s rDNA, and 3,733 from the 13 protein-coding genes in mitochondrial genomes) from 77 species in 54 families representing the seven current infraorders. Dipsocoromorpha and Enicocephalomorpha formed a monophyletic group at the base of the cladogram as the sister group of (Gerromorpha + (Nepomorpha + (Leptodomorpha + (Cimicomorpha + Pentatomomorpha)))). The monophyly of the Panheteroptera was previously recovered by Schuh (1979) and Wheeler et al. (1993), as well as the strongly supported Cimicomorpha + Pentatomomorpha. According to this study, the divergence of Gerromorpha, Nepomorpha and Leptodomorpha could have happened within a short time span, from 269 to 246 million years ago, corresponding to a similar pattern shown by aquatic holometabolous insects that were also invading new aquatic niches during Late Permian and Early Triassic.

The study of relationships among infraorders in Heteroptera has a long history that still today is under scrutiny. The different approaches, most based on different sets of data, produced conflicting topologies. With the development and wide use of new molecular techniques, new next-gen studies in the coming years based on molecular data are probable.

NEPOMORPHA

The infraorder Nepomorpha originally was recognized by Latreille (1810) as Hydrocorisae (Schuh & Slater 1995) and given family rank. In his work Latreille (1810) divided Hydrocorisae into two groups. One group included genera *Belostoma* (Belostomatidae), *Galgulus* (Gelastocoridae), and *Pelogonus* (Ochteridae), with the unifying characteristic of the tarsomeres being similar to one another (cylindrical), biarticulated, and possessing pretarsal claws. The second group included *Corixa* (Corixidae), *Naucoris* (Naucoridae), *Nepa* (Nepidae), *Notonecta* (Notonectidae), and *Ranatra* (Nepidae), and was unified by having tarsomeres varying in number, shape, and number of pretarsal claws. The name Nepomorpha was originally established and used by Popov (1968) to refer to the insects in Latreille's Hydrocorisae.

In their work on Helotrephidae, Esaki & China (1927) presented a phylogenetic tree depicting the relationships among families in Nepomorpha (Hydrocorisae at that time). All aquatic and semiaquatic bugs were included except families in Gerroidea, because they considered it to be a group with a distinct origin. The topology of the tree included an early dichotomy in Nepomorpha corresponding to the evolution of Corixidae, with differences in the morphology of the mouthparts adapted to phytophagy. A second dichotomy split the Helotrephidae from the rest of the families and the last major dichotomy was for the groups Hydrobia and Telmatobia. The former was represented by insects adapted for life in water and included the families (Notonectidae +((Aphelocheiridae + Naucoridae) + (Belostomatidae + Nepidae)); and the latter included the families ((Gelastocoridae + Ochteridae) + (Velocipedidae + (Leptopodidae + Saldidae))), which were adapted to life in the riparian zone.

In China's (1955) analysis, Ochteridae represented the earliest diverging clade in the Nepomorpha (Hydrocorisae) phylogeny, which was contrary to his initial concept of Corixidae as the basal group (Esaki & China 1927). Important characters that China (1955) thought were ancestral were the presence of ocelli and the littoral habitat association of the group, which later gave rise to adaptation by early nepomorphans to move underwater. In addition, the reduction of the antenna in ochterids was a required step prior to the colonization of the aquatic habitat. China's (1955) phylogenetic relationships among the families were (Ochteridae + (Gelastocoridae + ((Belostomatidae + Nepidae) + (Corixidae + (Naucoridae + (Helotrephidae + (Notonectidae + Pleidae))))))).

Popov (1971) proposed a new classification for the Nepomorpha based on morphology of the digestive system, reproductive organs, egg structure, embryogenesis, and the location of the antennae. The infraorder was composed of the superfamilies Corixoidea (Corixidae, Shurabellidae), Gelastocoroidea (Ochteridae, Gelastocoridae), Naucoroidea (Naucoridae), Nepoidea (Belostomatidae, Nepidae), and Notonectoidea (Helotrephidae, Mesotrephidae, Notonectidae, Pleidae, Scaphocoridae) and the relationships among them were (Nepoidea + (Corixoidea + (Gelastocoroidea + (Naucoroidea + Notonectoidea)))), with Leptodomorpha (Gerroidea, Leptopodoidea) as the sister taxon. Wang et al. (2015) proposed that the extant superfamilies of Nepomorpha diversified from a common ancestor in the Middle and Late Triassic, and further diversification within each superfamily occurred in the Early Jurassic.

Rieger (1976) used the species *Ochterus marginatus* Latreille as a model in the study of the exoskeleton and musculature of the head and prothorax to clarify if

Gelastocoridae belonged to Nepomorpha. This was the first strict cladistic approach regarding the phylogeny of the Nepomorpha and found that Gelastocoridae was indeed part of this infraorder and was related to Ochteridae, together forming the Telmatobia group. The relationships among families proposed by Rieger (1976) were ((Belostomatidae + Nepidae) + (Gelastocoridae + Ochteridae) + (Corixidae + (Naucoridae + (Aphelocheiridae + (Notonectidae + (Pleidae + Helotrephidae)))))).

Mahner (1993) used a detailed cladistic approach on the Nepomorpha based on morphology. He analyzed the phylogenetic relationships among the families based primarily on the structure of the food pump and related modifications of the anteclypeus. This work also included partial phylogenies for taxa below the family level. Mahner recovered essentially the same cladogram topology to that presented by Popov (1971), although he used the name Ochteroidea instead of Gelastocoroidea, Naucoroidea also included the Aphelocheiridae, and the position of Potamocoridae was not fully resolved, although he stated that the characters present in this family suggested it was related to Naucoroidea and Notonectoidea. The position of Corixidae was still in question because Mahner did not find strong support for its placement in his analysis.

Hebsgaard et al. (2004) reviewed the phylogeny of the families in Nepomorpha using morphological characters and molecular sequences (never previously used in studies of Nepomorpha). They constructed a character matrix that included 65 morphological features and approximately 960 bp from the mitochondrial gene 16s and the nuclear gene 28s. They included 40 species representing all families in Nepomorpha and used species from Gerromorpha and Leptopodomorpha as outgroups. The results were based on the analysis of combined morphological and molecular data and supported

the monophyly of all families and superfamilies in the group, although there was a rearrangement of the families in each superfamily in comparison with Popov (1971). The seven superfamilies recognized by the authors were Aphelocheiroidea (Aphelocheiridae, Potamocoridae), Corixoidea (Corixidae), Naucoroidea (Naucoridae), Nepoidea (Belostomatidae, Nepidae), Notonectoidea (Notonectidae), Ochteroidea (Gelastocoridae, Ochteridae), and Pleoidea (Helotrephidae, Pleidae). The phylogenetic relationships recovered by the analysis of combined data were (Nepoidea + (Corixoidea + (Aphelocheiroidea + (Naucoroidea + (Ochteroidea + (Notonectoidea + Pleoidea)))))).

Hua et al. (2009) presented a phylogenetic analysis of the Nepomorpha (all seven superfamilies represented) based on information from the 37 genes forming the mitochondrial genome (mitogenome) of nine ingroup and six outgroup species. The most notable result from the analysis was that Pleoidea was not included within Nepomorpha, but was the sister group of the clade including Cimicomorpha, Leptodomorpha, Nepomorpha, and Pentatomomorpha. Based on this, Hua et al. (2009) proposed to elevate Pleoidea to infraorder level as Pleomorpha. Another difference found in this analysis (in comparison with Hebsgaard et al. 2004) was that Aphelocheiridae was recovered as the sister group of Naucoridae. Thus, the authors proposed to eliminate the recently created Aphelocheiroidea (Hebsgaard et al. 2004) and include Aphelocheiridae in Naucoroidea. Note that the authors did not include the mitogenome of any species of Potamocoridae, the sister group of Aphelocheiridae (after Hebsgaard et al. 2004). This would have provided more information about the relationships among those two families and Naucoridae. The relationships Hua et al. (2009) found among the superfamilies in Nepomorpha based on the analysis of the mitogenomes were (Corixoidea +

((Naucoroidea + Notonectoidea) + (Ochteroidea + Nepoidea))). This topology supported the concept of Corixidae as an early branch in the phylogeny of Nepomorpha as proposed by Esaki & China (1927), but substantially changed the relationships proposed by Hebsgaard et al. (2004) among Aphelocheiroidea, Naucoroidea, Notonectoidea, and Pleoidea. This work presented a radical change in the phylogeny of the group by removing the Pleoidea from inside Nepomorpha, even stating that Cimicomorpha, Leptopodomorpha, and Pentatomomorpha were more closely related to Nepomorpha than the latter was to Pleidae. Li et al. (2014) considered that the source of these major changes in the phylogeny of Nepomorpha was the small sample size for this project. Although the amount of data is vast (ca. 15,000 bp per mitogenome), the small number of species included in the study could have generated misleading information that affected the authors' conclusions. Specifically, Li et al. (2014) suggested that the study by Hua et al. (2009) could have been affected by long-branch attraction as a result of inadequate taxon sampling and evaluated this hypothesis by removing distant outgroups from the analysis, incorporating closely related outgroups, and including the mitogenome of a second family of Pleoidea. The result was a rejection of a paraphyletic Nepomorpha and the creation of the infraorder Pleomorpha.

Another recent study (Brozek 2014) on the phylogeny of Nepomorpha with 62 species representing all families included a matrix with 48 characters pertaining to the external and internal structures of maxillae and mandibles, the morphology of labial structure, and the distribution of labial sensillae. Brozek (2014) explained the relationships among superfamilies and families in Nepomorpha and compared the results with previously proposed ideas. A preliminary analysis of the presented consensus tree

made clear that the characters used were not sufficiently informative to support some of the formerly recognized clades. In fact, the base of the tree included an unresolved trichotomy (Corixoidea) + (Nepoidea) + (Naucoroidea + Notonectoidea + Ochteroidea). However the Bootstrap resampling technique resolved some of the relationships (clades); Brozek (2014) found the relationships to be (Nepidae + (Belostomatidae + (Corixoidea + (Ochteroidea + (Aphelocheiridae + (Potamocoridae + (Naucoroidea + (Notonectoidea + Pleoidea))))))), with paraphyletic Naucoridae and Notonectidae. An otherwise well-supported and recognized relationship not found in the analysis was Nepoidea (Belostomatidae + Nepidae); instead, Nepidae was a monophyletic group and the earliest branch in the phylogeny.

It is clear as a result of a long history on the study of Nepomorpha phylogeny that some family-groups (superfamilies) can be unequivocally considered to be monophyletic based on their continuous recovery as closely related taxa in different analyses. In particular, the sister group relationships of Belostomatidae + Nepidae (except Brozek 2014) and Gelastocoridae + Ochteridae (except China 1955) are clear. Hebsgaard et al. (2004) also recovered some of the groups that had been proposed to be related in different studies: Naucoroidea (Aphelocheiridae, Naucoridae, Potamocoridae), Nepoidea (Belostomatidae, Nepidae), Ochteroidea (Gelastocoridae, Ochteridae), and Pleoidea (Pleidae, Helotrephidae).

The use of only morphological data, only molecular data, or even combined data can lead to different interpretations about relationships. A clear example is the work by Hebsgaard et al. (2004), where the use of combined morphological and molecular data found the relationships (Nepoidea + (Corixoidea + (Aphelocheiroidea + (Naucoroidea +

(Ochteroidea + (Notonectoidea + Pleoidea)))))). In the same paper using only morphological data the relationships were (Nepoidea + (Corixoidea + (Ochteroidea + (Naucoroidea + (Notonectoidea + Pleoidea))))). Thus, the position of Naucoroidea changed to be more closely related to Notonectoidea + Pleoidea, with Ochteroidea as the sister taxon of this new clade. Also, the families in Aphelocheiroidea (Aphelocheiridae, Potamocoridae) were merged into Naucoroidea. In contrast, the analysis based only on molecular data produced a topology where the relationships were (Aphelocheiroidea + (Naucoroidea + ((Notonectoidea + Pleoidea) + (Nepoidea + (Ochteroidea + Corixoidea))))). The results from the molecular analysis provided an evolutionary scenario substantially different from those resulting from analyses based on morphological and combined data.

All studies on the phylogeny of Nepomorpha presented the group Ochteroidea (Gelastocoridae, Ochteridae) as an internal clade; only the work by China (1955) considered Ochteroidea to be the earliest branch in the phylogeny of the water bugs. It makes sense to consider this group as such because these insects occur in a semiaquatic habitat and have ocelli, which all the other aquatic bugs lack, and that could have been inherited from the ancestor of Nepomorpha. In the other hypothesis on the relationships of the group, the Ochteroidea is an internal clade, in which case the unlikely evolutionary scenario would imply that after the aquatic bugs colonized the aquatic environment a group returned to live outside the water and re-developed ocelli. Therefore it is reasonable to consider Ochteroidea the earliest dichotomy in the phylogeny of the group as proposed by China (1955).

In summary, six superfamilies and 11 families constitute Nepomorpha (Schuh & Slater 1995, Hebsgaard et al. 2004): Corixoidea (Corixidae), Naucoroidea (Aphelocheiridae, Naucoridae, Potamocoridae), Nepoidea (Belostomatidae, Nepidae), Notonectoidea (Notonectidae), Ochteroidea (Gelastocoridae, Ochteridae), and Pleoidea (Helotrephidae, Pleidae). The worldwide number of species per family (Polhemus & Polhemus 2008) is: Aphelocheiridae 78, Belostomatidae 169, Corixidae 662, Gelastocoridae 116, Helotrephidae 164, Naucoridae 398, Nepidae 268, Notonectidae 422, Ochteridae 75, Pleidae 44, Potamocoridae 8; for a total of 2,404 species in Nepomorpha.

NAUCORIDAE

The family Naucoridae Leach is a group of aquatic insects commonly known as creeping water bugs or saucer bugs. Leach (1815) first recognized the group as family Naucorida within the *Aquatica* section, in which constituent insects had small antennae (not projected) inserted beneath the eyes. He placed Naucorida in the tribe *Nepides* in which he also included the family Nepida given that both groups presented the fore tarsus fused with the tibiae. The type genus was *Naucoris* Geoffroy with hind legs modified for swimming (fringe of setae) and an ovate depressed body.

Stål (1876) produced a classification of the Naucoridae that included four divisions and nine genera: Aphelocheiraria (*Aphelocheirus* Westwood), Laccocoraria (*Laccocoris* Stål, *Heleocoris* Stål), Limnocoraria (*Borborocoris* Stål, *Limnocoris* Stål), and Naucoraria (*Ilyocoris* Stål, *Macrocoris* Signoret, *Naucoris* Geoffroy, *Pelocoris* Stål). Although Stål also included the genus *Ambrysus* and *Cryptocricus* (posteriorly emended as *Cryphocricos* Signoret) in his "*Enumeratio Naucoridarum*", he did not assigned them

to one of his divisions. This was the first clear definition of the higher groups of Naucoridae (Popov 1970). The divisions Laccocoraria and Limnocoraria were later explicitly assigned to formal taxonomic ranks as subfamilies (Montandon 1897a), while Aphelocheiraria was treated in some cases as a distinct family (Cobben 1968) or a subfamily in Naucoridae (Popov 1970). No study formally assigned Naucoraria to a taxonomic rank, but after the other divisions had their own status Naucoraria was considered a subfamily in Naucoridae and Stål was credited with its creation (see Štys & Jansson 1988, Polhemus & Polhemus 1988).

Montandon (1897b) created the subfamily Cryptocricinae, which he later emended as Cryphocricinae (Montandon 1897c), to include the genera *Ambrysus*, *Cryptocricus* (later emended to *Cryphocricos*), and the therein described genera *Idiocarus* and *Pseudambrysus*. The diagnostic characteristic of the subfamily was the deep concavity on the anterior margin of the pronotum, where the posterior part of the head fits and attaches to the body.

The subfamily Cheirochelinae was established by Montandon (1987d) with *Cheirochela* Hope as the type genus and included the two new species *Cheirochela birmaniensis* and *C. feana*. Also, therein he established the genus *Gestroiella* for the new species *G. limnocoroides*. In the same year Montandon (1897a) elevated Stål's Laccocoraria to subfamily level as Laccocorinae and included the previously established genera *Ctenipocoris* Montandon, *Diaphorocoris* Montandon, *Heleocoris* Stål, and *Laccocoris* Stål; and the newly created *Aneurocoris* and *Temnocoris*. In the same work Montandon elevated the division Limnocoraria to subfamily level as Limnocorinae and

subsequently revised the group (Montandon 1897e) where he synonymized the genus *Borborocoris* Stål under *Limnocoris* Stål.

Hungerford (1941) created the genus *Potamocoris* for the South American species *P. parvus*. Hungerford (1941) noted that this unusual naucorid had slender antenna, shape of the head, beak, and genitalia similar to those of *Aphelocheirus*, suggesting a possible relationship between both groups. Usinger (1941) proposed the creation of the subfamily Potamocorinae in Naucoridae to include Hungerford's newly described species *P. parvus* due to its distinctive features and geographical distribution, which easily set it apart from the other subfamilies. In the same paper Usinger studied species of the genera *Ambrysus* and *Cryphocricos* and based on unique morphological features and the plastral respiration of *Cryphocricos*, this genus was retained as the only representative in the subfamily Cryphocricinae. In the case of *Ambrysus* and *Melloiella*, the latter established by De Carlo (1935) for the species *M. truncaticollis*, Usinger (1941) created a new subfamily that would take the name Ambrysinae, after the genus *Ambrysus,* which he considered the oldest, most widespread, and typical genus of Naucoridae present in the New World. In this work Usinger (1941) also created the genus *Cataractocoris* for the species formerly described as *Cryphocricos macrocephalus* Montandon and the new species *Cataractocoris marginiventris* from central Mexico. Up to this point the family Naucoridae was constituted by eight subfamilies: Ambrysinae, Aphelocheirinae, Cheirochelinae, Cryphocricinae, Laccocorinae, Limnocorinae, Naucorinae, and Potamocorinae. This classification was later followed by other authors (China & Miller 1959).

Popov (1970) conducted a morphological analysis of the structure of the head as well as ventral and dorsal body features of species from 12 genera in Naucoridae, and suggested that the most reliable feature to discriminate among the subfamilies was the degree of development of the rostrum. Based on this, he presented a new classification of Naucoridae with only four subfamilies, the remaining previously recognized subfamilies were downgraded to tribes: Naucorinae (Ambrysini, Cheirochelini, Laccocorini, Limnocorini, Naucorini), Cryphocricinae (Cryphocricini, Cataractocorini), Potamocorinae (Potamocorini, Coleopterocorini), and Aphelocheirinae (Aphelocheirini). This classification was followed by Nieser (1975).

De Carlo (1971) studied and compared the male genitalia from American and European species of Naucoridae and argued that based on the differences in the morphology of the testes and harpagones (parameres), the species from the Old World (including representatives from Asia) could not be considered members of the same family as those from the New World. As a result he considered that species from Europe to be members of the original Naucoridae and species from America should be placed in Pelocoridae (including Potamocorinae). This classification had no impact on the study of Naucoridae and did not prevail. As asserted by Nieser (1975), the study did not have a good representation of all the genera in the family and the major changes in the classification were made based on few characters.

In his work on egg morphology and embryology, Cobben (1968) noted that the differences (micropyles, eclosion split) showed by members of the eight subfamilies in Naucoridae (with special attention to Potamocorinae) could suggest that some of them deserved family rank, but it was not until later that Cobben (1978) formally recognized

Potamocoridae as a distinct family. De Carlo (1971) treated Aphelocheiridae as a distinct family and mentioned that because of the similarity in the external morphology of the genital capsule of the three families (including Naucoridae and Pelocoridae), those should be considered members of the same superfamily, which he called Naucoroidea. Many authors have treated Aphelocheiridae (e.g. De Carlo 1971, Rieger 1976, Štys & Jansson 1988, Mahner 1993, Schuh & Slater 1995) and Potamocoridae (Štys & Jansson 1988, Mahner 1993, Schuh & Slater 1995) as separate families closely related to Naucoridae and this classification scheme is widely accepted.

The family Naucoridae consistently has been retrieved as a monophyletic group closely related to Aphelocheiridae, Potamocoridae, and members of Notonectoidea and Pleoidea, but has not been recovered in close relation to Belostomatidae, which Leach (1815) suggested could be possible based on the general similarity of the groups.

Few studies have considered the phylogenetic relationships among taxa within Naucoridae; in fact, no study focused primarily on this topic. The available information comes from broader studies that present cursory views at possible relationships among the subfamilies. The first study (Popov 1971) suggested that subfamily diversification occurred during Late Triassic and Early Jurassic and the phylogenetic relationships presented were (Potamocorinae + (Naucorinae + (Aphelocheirinae + Cryphocricinae))). Inside Naucorinae the relationships were (Ambrysini + (Cheirochelini + (Naucorini + (Laccocorini + Limnocorini)))). Mahner (1993) with his cladistic analysis of relationships among the families in Nepomorpha (based on the structure of the food pump and the related modifications of the anteclypeus) found the partial relationships (Laccocorinae + (Naucorinae + (Limnocorinae + Cryphocricinae))). This study did not

include representatives from the subfamily Cheirochelinae. The most recent study (Brozek 2014) from which it is possible to get an idea of the phylogeny of Naucoridae is based on the morphology of the mouthparts. This study did not find support for most of the clades in Nepomorpha; instead, it recovered several polytomies suggesting that the features used do not possess the relevant information to reconstruct the phylogenetic relationships. From the strict consensus tree (100 most parsimonious trees found) a sizable polytomy included all Naucoridae and Potamocoridae as the sister taxa of the monophyletic (Notonectidae + (Pleidae + Helotrephidae). What can be gleaned is that inside the polytomy formed by the naucorid species there is a monophyletic group that could be analogous to a recognized naucorid subfamily, although the inclusion of more taxa could result in a different topology. The partially supported subfamily found was Cheirochelinae, with four species from different genera (*Cheirochela, Coptocatus*, *Gestroiella*, *Tanycricos*). Although two species from different genera (*Heleocoris*, *Laccocoris*) in Laccocorinae resulted in a group together, a third species (*Namtokocoris*) from the same family was part of the unsolved polytomy. The same inconsistency occurred with the subfamily Naucorinae, where two species came together (*Ilyocoris*, *Pelocoris*), but three more from different genera (*Macrocoris*, *Naucoris*, *Neomacrocoris*) were placed elsewhere. Even the phylogenetic tree from Bootstrap resampling showed a paraphyletic Naucoridae.

The most currently accepted classification of Naucoridae includes five subfamilies, 39 genera, and 394 species (number of species in parentheses):

CHEIROCHELINAE. Insects in this subfamily can be identified by the labium inserted in a deep excavation posteroventrad from the anterior margin of head, the labrum often greatly reduced, and the anterior margin of the pronotum concave to receive the adjoining posterior part of the head (Schuh & Slater 1995). The species in this subfamily are distributed in Borneo, India, New Guinea, Southeast Asia, and southern China.

Cheirochelini Popov

Cheirochela Hope (7)
Coptocatus Montandon (6)
Gestroiella Montandon (3)

Sagocorini La Rivers

Aptinocoris Montandon (8)
Cavocoris La Rivers (5)
Halmaheria Zettel (1)*
Sagocoris Montandon (7)
Warisia La Rivers (1)

Tanycricini La Rivers

Idiocarus Montandon (7)
Nesocricos La Rivers (5)
Tanycricos La Rivers (8)

* Zettel (2007) stated that *Halmaheria* could be a member of Cheirochelinae or Naucorinae.

CRYPHOCRICINAE. Insects in this subfamily can be identified by the labium inserted near the anterior margin of the head (not in a deep excavation), the labrum well developed, and the anterior margin of the pronotum deeply concave to receive the adjoining posterior part (interocular space) of the head (Schuh & Slater 1995). The species in this subfamily are distributed only in the New World.

Ambrysini Popov

Ambrysus Stål (83)
Carvalhoiella De Carlo (3)
Hygropetrocoris Sites (1)

Cataractocorini Popov

Cataractocoris Usinger (3)

Cryphocricini Popov

Cryphocricos Signoret (13)
Procryphocricos Polhemus (4)

LACCOCORINAE. Insects in this subfamily can be identified by the labium inserted near the anterior margin of the head (not in a deep excavation), the labrum well developed, the anterior margin of the pronotum nearly straight (not concave), and the prothoracic legs with two articulated pretarsal claws (Schuh & Slater 1995; except *Namtokocoris* with just one claw). A distinctive feature in this family is that the front of the head is folded posteroventrally in such way that the labrum is set back from the anterior margin of the head (Mbogho & Sites 2013). Some genera from this subfamily have species distributed in the New World but the greatest diversity occurs in the Old World.

Laccocorini Popov

Aneurocoris Montandon (2)
Ctenipocoris Montandon (8)
Decarloa La Rivers (1)
Diaphorocoris Montandon (4)
Heleocoris Stål (28)
Interocoris La Rivers (1)
Laccocoris Stål (18)
Temnocoris Montandon (8)
Namtokocoris Sites (6)
Pogonocaudina Sites & Zettel (1)

LIMNOCORINAE. Insects in this subfamily can be identified by the labium inserted near the anterior margin of the head (not in a deep excavation), the labrum well developed, the anterior margin of the pronotum nearly straight, forelegs with a single unmovable claw fused to the protarsus, and meso- and metasterna with prominent, broad and laterally expanded median longitudinal carinae (Schuh & Slater 1995). The species

in this subfamily are distributed only in the New World, with the greatest diversity occurring in South America.

Limnocorini Popov

Limnocoris Stål (72)

NAUCORINAE. Insects in this subfamily can be identified by the labium inserted near the anterior margin of the head (not in a deep excavation), the labrum well developed, the anterior margin of the pronotum nearly straight, forelegs with a single unmovable claw fused to the protarsus, meso- and metasterna not prominent and without expanded longitudinal carinae (Schuh & Slater 1995). This subfamily is cosmopolitan.

Naucorini Popov

Asthenocoris Usinger (4)
Ilyocoris Stål (1)
Macrocoris Signoret (9)
Naucoris Geoffroy (20)
Nanonaucoris Zettel (2)
Neomacrocoris Montandon (16)
Pelocoris Stål (14)
Philippinocoris Polhemus & Polhemus (2)
Placomerus La Rivers (2)
Stalocoris La Rivers (8)
Thurselinus Distant (1)

SUBFAMILY CRYPHOCRICINAE

The early history of this subfamily began when Signoret (1850) described the species *Cryphocricos barozzii* based on a male from Brazil, and placed it in Latreille's (1810) Hydrocorisae. Later, Stål (1862) would create, in his work "*Hemiptera Mexicana",* the genus *Ambrysus* and included the species *A. melanopterus*, *A. pudicus*, and *A. signoreti*. In his classification of the Naucoridae Stål (1876) did not assign the genera *Ambrysus* and *Cryphocricos* to one of his four major divisions (Aphelocheiraria, Laccocoraria,

Limnocoraria, and Naucoraria). It was not until 1897 when Montandon (1897b) created the subfamily Cryptocricinae for these two genera and described nine species in *Ambrysus*. In that same year Montandon (1897c) emended the name Cryptocricinae to Cryphocricinae (after Signoret's *Cryphocricos*), transferred *Pseudambrysus* into Naucorinae, and described the species *Cryphocricos macrocephalus* and three more species in *Ambrysus.* In his work on the classification of the Cryphocricinae, Usinger (1947) continued with the firm idea of a monotypic subfamily, a concept that was supported by the exposed prosternum, abdominal sense organs, glabrous abdomen, and alary dimorphism present in species of *Cryphocricos*. In this paper he described four new species, among them were *C. hungerfordi* and *C. mexicanus*, the only two species from this genus that have been reported to occur in Mexico. *Cryphocricos mexicanus* was described from a large series of specimens collected in Temascaltepec during Usinger's well-known trip to central Mexico in the summer of 1933 (Usinger 1972). The species *C. hungerfordi* was described from specimens collected in western Mexico in the state of Veracruz. The distinction between these two species was based on the size of the hemelytra, width of embolia, and total body length. The other two species described in this paper were *C. obscuratus* from Panama and *C. latus* from Costa Rica. A total of 13 nominal species have been described in this genus (La Rivers 1971, 1974, 1976).

The third genus to be included in this subfamily was *Melloiella*. De Carlo (1935) described the species *M. truncaticollis* from Brazil and noted that the new species had more affinity with species of *Ambrysus* due to similar head shape, but could be differentiated because the new species presented reduced membrane and clavus of the hemelytra.

Usinger (1941) considered *Cryphocricos* to be the sole member of the subfamily Cryphocricinae due to its specialized plastral respiration, as opposed to the use of a compressible air-bubble breathing mechanism present in species of *Ambrysus* and *Melloiella*. For these two genera he erected the subfamily Ambrysinae in which he also included his new genus *Cataractocoris* with the species *C. macrocephalus* (Montandon) and the newly described *C. marginiventris* from Temascaltepec in the state of Mexico. This enigmatic Mesoamerican genus *Cataractocoris*, which lives on the vertical wall of waterfalls and on large rocks in fast current was recently revised (Sites et al. 2013). In the revision a third species was described (*C. shepardi*), which is distributed from central Mexico south to Guatemala. It was also reported that the three known species in this genus are able to live sympatrically.

The genus *Carvalhoiella* was established by De Carlo (1963a) for the species *C. beckeri* from Minas Gerais (Brazil). He suggested that the new genus was more closely related to *Cataractocoris* based on the presence of a lateral glabrous area on the ventral side of the abdomen. In contrast, *Ambrysus* and *Melloiella* have the entire ventral side of the abdomen clothed with short, fine setae. Nieser (1975) initially placed this genus in Naucorinae but later (Nieser et al. 1999) moved it into Ambrysinae since the propleural structure was similar to species in this subfamily. The second species to be described in this genus was *C. nitida* (La Rivers 1976). The description was based on a single male from Suriname that could easily be distinguished from *C. beckeri* by its smaller size and glabrous appearance. Nieser et al. (1999) described the species *C. stysi* from three female specimens collected in Minas Gerais (Brazil). The size of this third species was similar

to that of *C. beckeri* but could be distinguished by the posterior margin of the female operculum (subgenital plate) being concave, whereas it is straight in *C. beckeri*.

When Popov (1970) proposed the classification of the Naucoridae with four subfamilies and ten tribes, he contended that the genera *Cataractocoris* and *Cryphocricos* should be placed together in the subfamily Cryphocricinae based on the shared features: a) more dismembered head capsule, b) granular sculpture on the dorsal part of the body, c) strongly developed claws of middle and hind tarsi, d) general structure of genitalia, e) prominent compound eyes, and f) maxillary plates clearly separated and produced forward. This was contrary to what Usinger (1941) had proposed for the monotypic Cryphocricinae. Popov (1970) also mentioned that species of *Ambrysus* had a characteristic short rostrum and strongly developed prothoracic epimera (touching each other), similar to those present in species of *Cataractocoris* and *Cryphocricos*, and because of that the three genera should be placed in the same subfamily but in their own tribe. Opposed to this latter conclusion, Popov (1970) placed the tribe Ambrysini in the subfamily Naucorinae, arguing a closer relationship. It was clear to him that a study including more species (and genera) would help to clarify the relationships among subfamilies and tribes. It was not until Štys & Jansson (1988), that the tribe Ambrysini (with its three genera) was placed back into Cryphocricinae. As Nieser et al. (1999) noted, to this point two differing classifications of the Ambrysinae were held. The European view considered this group as the tribe Ambrysini and placed it in Naucorinae (Popov 1970) or Cryphocricinae (Štys & Jansson 1988). In contrast the American view considered the group as a distinct subfamily (Usinger 1941; La Rivers 1971,1974,1976; Polhemus & Polhemus 1988). The view that remains as the most accepted is that from

Štys & Jansson (1988), in which Ambrysini is part of Cryphocricinae along with the tribes Cataractocorini and Cryphocricini.

In 1991 Polhemus created the genus *Procryphocricos* for the species *P. perplexus*, based on two brachypterous males from the department of Antioquia in northwestern Colombia. This new genus was similar to *Cryphocricos*, however, the new genus possessed (mostly) plesiomorphic features when compared with *Cryphocricos*. Almost 20 years later the female of the species *P. perplexus* was described (Sites & Alvarez-Arango 2010) base on a brachypterous female collected in the same river (topotype) as the holotype. Later, Sites & Camacho (2014) described two more species in this genus from Venezuela. The species *P. macoita* was described from brachypterous and macropterous males and females (brachypterous holotype). Although it is apparent the use of plastral respiration by this species, due to the presence of brachypterous forms (fully developed hemelytra would allow the insect to use an air bubble), the great majority of specimens were collected in fine rootmats (a habitat with stronger current would be expected for plastral respiring insects). The second species was *P. quiu*, described from only brachypterous forms. In this case the apparently preferred habitat for this species was among dead leaves, twigs, and debris along the margin of the river. Although species in this genus appear to be using plastral respiration, an adaptation for living in habitats with turbulent current (riffles), they could be exploiting another niche (rootmats and debris along the margin of the river) to avoid competition with species from the closely related *Cryphocricos*, which is found exclusively in habitats with strong current. The fourth species in this genus was described from brachypterous forms from

Peru (Sites & Shepard 2015). The species *P. pilcopata* was collected from leaf packs and the gravel substrate in a shallow stream in southern Peru.

Nieser et al. (1999) downgraded De Carlo's genus *Melloiella* (*M. truncaticollis*) to subgeneric level and described the species *Ambrysus* (*Melloiella*) *lamprus* from Brazil. Regarding *Melloiella* as a subgenus, they argued that other than the triangular pronotum (straight margins) and the reduced membrane on the hemelytra, the species *Melloiella truncaticollis* had the features reported for other species of *Ambrysus*. Rather than synonymize *Melloiella* under *Ambrysus*, Nieser et al. (1999) followed La Rivers' protocol (1952) in creating subgenera for different species groups in this genus.

The most recent change in Cryphocricinae is the creation of the genus *Hygropetrocoris* for the species *H. guyana* from South America (Sites 2015). This species possesses a series of remarkable features not present in any other member of the subfamily. Two particularly unusual characters in this species are the head oriented almost vertically (with apparent movement independent from that of the prothorax) and the presence of bulbous eyes. Other atypical features include: a) lines and patches of hair on forewings, b) fore femur excavate distally, c) fore tibia with prominent tooth, and d) stout marginal tufts of setae along the dorsum of the body. The author suggested that based on these atypical features (including a mottled color pattern) and the conditions of the site where the specimens were collected (wet rock covered on algae), this insect could inhabit a terrestrial environment (semiaquatic), rather than living under water.

The current classification of Cryphocricinae includes three tribes, six genera, and 107 species:

Cryphocricinae Montandon

Ambrysini Popov

Ambrysus Stål (see section for this genus)

Carvalhoiella De Carlo
C. beckeri De Carlo
C. nitida La Rivers
C. stysi Nieser, Pelli & De Melo

Hygropetrocoris Sites
H. guyana Sites

Cataractocorini Popov

Cataractocoris Usinger
C. macrocephalus (Montandon)
C. marginiventris Usinger
C. shepardi Sites, Reynoso & Novelo

Cryphocricini Popov

Cryphocricos Signoret
C. barozzii Signoret
C. breddini Montandon
C. daguerrei De Carlo
C. fittkaui De Carlo
C. granulosus De Carlo
C. hungerfordi Usinger
C. latus Usinger
C. mexicanus Usinger
C. obscuratus Usinger
C. peruvianus De Carlo
C. rufus De Carlo
C. schubarti De Carlo
C. vianai De Carlo

Procryphocricos Polhemus
P. macoita Sites & Camacho
P. perplexus Polhemus
P. pilcopata Sites & Shepard
P. quiu Sites & Camacho

GENUS *AMBRYSUS* STÅL

The history of this genus is with any doubt the most interesting of all saucer bugs. It is the most species-rich genus in the family with 83 described species, followed by *Limnocoris* with 72 species. In fact, the species richness in this genus alone is greater than that of any other subfamily of Naucoridae. This genus is restricted to the New World and is distributed from the northern United States (La Rivers 1951a) south to Argentina (La Rivers 1971), with the greatest number of species occurring in Mexico, where some species apparently found suitable niches and conditions and underwent diversification. La Rivers (1951a) considered that the group could have originated in South America where we find lower species richness and the fauna seems to be ancestral when compared with that from North America, although a study on the biogeography of the group is in need to find evidence to support this hypothesis.

Stål (1862) created the genus *Ambrysus* for the Mexican species *A. melanopterus*, *A. pudicus*, and *A. signoreti*. He indicated that this genus was similar to *Naucoris* but the main difference was the concavity on the anterior margin of the pronotum in *Ambrysus*, a character later used by Montandon (1897b) as the diagnostic feature for the subfamily Cryphocricinae. The only available data from the specimens examined by Stål was that they were collected in Mexico; no other detailed collection information was provided at the time of the description. Years later Stål (1876) divided Naucoridae into four divisions (Aphelocheiraria, Laccocoraria, Limnocoraria, and Naucoraria) and although he did not place *Ambrysus* in one of the groups, he described two more species in the genus: *A. guttatipennis* based on a single female from Mexico and *A. puncticollis*, with a similar size to that of the former species, based on two specimens (male and female) collected in

Texas (USA). Species descriptions at that time consisted of a few sentences with special attention to gross features such as body length, width, color, and characteristics of the pronotum and hemelytra surface (e.g., punctation, rugosity). Unfortunately, those generalized original descriptions are not useful for identifying species. In most cases it is more useful to examine the type material to look for other features to be certain about the identity of the species.

The next species to be described was *A. fucatus* Berg (1879), described from material collected in the northern provinces of Córdoba and Tucuman in Argentina. This species was distinguished from *A. melanopterus* by its lighter color and more convex and wider body. Almost two decades later Montandon (1897b) established the subfamily Cryphocricinae (Cryptocricinae at the time) where he included *Ambrysus* and described nine species in it. Those descriptions were based on specimens deposited in European museums. Four of the species were from South America: *A. attenuatus* (Brazil), *A. bergi* (Argentina), *A. crenulatus* (Colombia), and *A. oblongulus* (Costa Rica). The other five species were from Central and North America: *A. californicus* (USA), *A. pulchellus* (Guatemala), and the Mexican species *A. hybrida*, *A. mexicanus*, and *A. parviceps*. The specific epithet *hybrida* was later corrected as *hybridus* (Champion 1901). In this work Montandon (1897b) presented a taxonomic key for the species he was describing and included Stål's species, except for *A. pudicus*.

Montandon (1897c) described three new species from specimens deposited in the collection of the National Museum of Natural History in Paris. The two species from South America were: *A. acutangulus* from the province of Corrientes in Argentina and *A. fraternus* from central Brazil. *Ambrysus geayi* was described from southern Panama.

Montandon (1897c) provided a key for the new species that included an extra couplet to serve as a link to his previous key (Montandon 1897b). In the following year, Montandon (1898) described *A. obscuratus* from a single specimen collected in eastern Brazil (Pernambuco) and provided the necessary couplets to incorporate this species into his previous keys. That was the last species described in *Ambrysus* during the 19th century.

Champion (1901) reported in the *Biologia Centrali-Americana* the existence of 19 species of Naucoridae in Mexico and Central America. Ten of those species were in *Ambrysus* and seven were reported from Mexico. During the 39 years since the establishment of the genus *Ambrysus* and the end of the century, a total of 19 species had been described, seven from Mexico. At the time Montandon was the most active entomologist working on the group, with 13 of the known species described by him.

During the first decade of the 20th century Montandon continued actively working on Naucoridae. He published the first taxonomic key (Montandon 1909a) for the 19 species known in *Ambrysus* and five new species. Four of the new species were distributed in South America: *A. colombicus* (Colombia), *A. horvathi* (Peru), *A. ochraceus* (Bolivia), and *A. peruvianus* (Peru). A fifth species, *A. nitidulus,* was described from the western state of Jalisco in central Mexico. This species was later synonymized under *A. pulchellus* (La Rivers 1953a). In the same year Montandon (1909b) described *A. mormon* from St. Georges (sic.) in the western state of Utah (USA), probably from what is now known as the Virgin River or its tributaries. In the following year he continued describing species (Montandon 1910a). *Ambrysus heidemanni* (named after the American hemipterologist Mr. Otto Heidemann) was described from

Yellowstone National Park and he made clear that the species was similar to his *A. mormon* but the new species was smaller. He also described *A. dilatus* from Mexico, which was reported to have the same color pattern on the head and pronotum as that of *A. mormon*. The species was later synonymized under *A. mexicanus* (La Rivers 1958). Also, the subspecies *A. pulchellus pallidulus* was described (Montandon 1910a), which was the first subspecies reported in this genus. The nominate species had been described from Guatemala and the subspecies was described from Texas (USA). It was given this status because of the different color pattern on the head and prothorax. He also made clear that the subspecies was very similar to his *A. nitidulus* from Mexico. The subspecies were later synonymized by La Rivers (1951a). Montandon (1910b) described *A. circumcinctus* from a female specimen collected in Kerrville (Texas), perhaps in the Guadalupe River. This would become the last species described by Montandon in this genus.

The early work by Usinger (1941, 1946) on Naucoridae (especially on *Ambrysus*) was in part a result of his collecting trip to central Mexico during the summer of 1933. As he explained in his autobiography (Usinger 1972), in the spring of 1933 during the time of the great depression, he met entomologist Howard E. Hinton at the University of California (Berkeley), who had grown up in Mexico. Hinton invited Usinger to go to Mexico during the summer and collect insects at the town of Real de Arriba in the state of Mexico, where his father was an engineer working for a British mining company. They spent almost two months collecting mainly in the district of Temascaltepec (Real de Arriba and Tejupilco), considered by Usinger as the "Original home of the Naucoridae" since they were able to collect thousands of specimens. He described his collecting there

as "fantastic", because just in that small area he collected more subfamilies, genera and species than those reported for Central America in the *Biologia Centrali-Americana* (Champion 1901). In his work of 1946, Usinger described a total of 16 new species in *Ambrysus*; of those, ten species were from Mexico, five of them from his trip to the state of Mexico in 1933 (*A. caliginosus*, *A. convexus, A. fuscus*, *A. hintoni*, and *A. infuscatus*). The other five were from other places in Mexico: *A. barberi* (Tamaulipas), *A. hungerfordi*, *A. lundbladi* (Morelos), *A. sonorensis* (Sonora), and *A. vanduzeei* (Baja California). Of the other species, four were from the United States: *A. bohartorum* (California), *A. buenoi* (Texas), *A. lunatus* (Texas), and *A. woodburyi* (Utah); and the other two species were from Central and South America: *A. fossatus* (Ecuador) and *A. variegatus* (Costa Rica). Some of these species were later synonymized (La Rivers 1953a, 1958), some were considered subspecies (La Rivers 1951a, 1953a), but most are still valid species.

The year of 1948 was the beginning of a remarkable career in the study of Naucoridae. In that year Ira La Rivers published a paper describing the species *Ambrysus funebris* from Death Valley in California (USA). This paper would be the first of an important series of contributions by La Rivers over a period of three decades. The new species was described from an unusual habitat; it was found living in Cow Creek, a warm (35.5º - 40ºC) and mineralized stream in the western foothills of the Funeral mountain range.

De Carlo (1950) compiled a list of all the species described in Ambrysinae, with special attention to those reported for Argentina. For a time when the main method of communication was postal service, De Carlo was up to date regarding publications on

Ambrysus. His list was only missing *A. funebris*, which was the most recently described species (La Rivers 1948). For the species reported from Argentina, De Carlo provided supplemental descriptions, distributions, and comments. He reported structures associated with the female lobe or genital operculum (subgenital plate) and provided drawings of the subgenital plate shape. For the males he described the shape of the claspers (parameres). Some of those aspects would be relevant in future species descriptions. In this work De Carlo described another species from Argentina, *A. gemignanii* from specimens collected in the northern province of Salta.

The main objective of the American entomologist Ira La Rivers as a graduate student at the University of California (Berkeley) was to conduct a taxonomic revision of *Ambrysus*. Unfortunately it was not possible as originally planned as a consequence of the inaccessibility of some type specimens held in European Museums and that the tropical areas where most of the species were distributed were undercollected with only a few specimens in museum collections. Nevertheless, he produced two important works relying heavily on the material collected by Usinger and specimens housed at the University of Kansas (Lawrence). His revision of the *Ambrysus* in the United States (1951a) was the first comprehensive study that covered different aspects of the group, such as biology, history, geographical distribution, paleontology and taxonomy. In this work he reported 12 species and two subspecies from the country. He also described the species *A. arizonus* and *A. occidentalis* from Arizona. The most important contribution from his work is the use of structures associated with the terminal abdominal segments of males and females as diagnostic features. He was the first to use the shape of the posterior margin of the subgenital plate in females (mediosternite 7) and the shape of the

male accessory process (accessory genitalic process of the sixth tergum) to determine species. These two features are still commonly used to determine and diagnose species (e.g., Sites & Shepard 2015, Sites and Reynoso-Velasco 2015), and in some cases the outline of the subgenital plate is the most useful feature to correctly identify species.

Because the group was still not well known, La Rivers published several individual papers dealing with the fauna of the group, including small papers where he described new species. For example, in one paper he described *A. planus* from Peru and *A. teutonius* from Brazil (La Rivers 1951b), and in another he described *A. usingeri* from Brazil, French Guiana, Guyana, and Suriname (La Rivers 1952). This species was placed in its own subgenus (*Picrops*) due to the presence of four or more rows of small spines on the distal part of the hind tibia as well as the males bearing a short lateral process on the seventh tergum. The remaining species were assigned to the subgenus *Ambrysus* and as opposed to *Picrops*, these species had three or fewer rows spines on the hind tibia and the males lacked the lateral process on the seventh tergum.

The second of La Rivers' most important works on this group was his revision of the fauna of *Ambrysus* from Mexico (1953a), which was largely based on the material on loan from the University of Kansas. This work followed Usinger's work in 1946 in which were descriptions of several new species from Mexico, and it was also a complement to his revision of the group in the United States (1951a). In this paper he described eight new species from the Mexico, four of them from the state of Mexico: *A. abortus*, *A. cosmius*, *A. magniceps*, and *A. pygmaeus*. The remaining species were from other places in Mexico: *A. hydor* (Morelos), *A. inflatus* (Jalisco), *A. portheo* (Coahuila), and *A. scalenus* (Michoacán). He also described four subspecies: *A. hungerfordi triunfo*

(Baja California), *A. hungerfordi angularis* (Guerrero), *A. lunatus menoides* (Puebla), and *A. mormon australis* (Chihuahua). La Rivers (1953a) also presented taxonomic changes. The species *A. nitidulus* Montandon was considered a junior synonym of *A. pulchellus* Montandon, *A. barberi* Usinger was given the status of a subspecies of *A. pudicus* Stål, and *A. caliginosus* Usinger was considered a subspecies of *A. circumcinctus* Montandon. In this work La Rivers provided descriptions or redescriptions of 23 species and five subspecies. He did not have access to the type specimens of *A. hybridus* and *A. mexicanus*; thus, he excluded those species from the study. He also excluded *A. lundbladi* and *A. sonorensis* in the revision because both species were known from only a single specimen each. As in his previous work (La Rivers 1951a), he used the shape of the female subgenital plate and the male accessory process as the main features to diagnose species. This work still remains the primary reference for species identification of specimens collected in Mexico. In the same year and while his work on the *Ambrysus* of Mexico was in press, La Rivers published three more papers where he described four new species and a subspecies. In two of the studies he described two species from the United States: *A. thermarum* collected in hot springs in New Mexico (La Rivers 1953b) and *A. amargosus* collected in Nevada (La Rivers 1953c). Along with the description of *A. thermarum*, he described *A. bispinus* from the western state of Veracruz in central Mexico (La Rivers 1953b). The species *A. dyticus* and the subspecies *A. hungerfordi spicatus* were described from Guatemala (La Rivers 1953d) and the subspecies was also reported to occur in Mexico (Chiapas).

In the next ten years La Rivers was the sole entomologist to describe new species in this genus; he reported seven more new species and a subspecies in small papers from

1954 to 1963. *Ambrysus maldonadus* was described from Venezuela (La Rivers 1954). La Rivers noticed that this species had a pair of posterolaterally produced structures at the base of the male eighth tergum that he called "procts" (pseudoparameres) but considered those structures to have a minor importance to delimitate species. In recent studies within the subfamily Cryphocricinae, specifically in the revision of the genus *Cataractocoris* Usinger (Sites et al. 2013), the pseudoparameres were used to diagnose the three species. Sites (2015) noted that *A. maldonadus* presents features that suggest this species does not belong to *Ambrysus* and a future study will clarify its classification.

La Rivers (1957a) also described the species *A. drakei* from Durango in northern Mexico. In the same year he redescribed the type specimens of *A. signoreti* and *A. mexicanus* (La Rivers 1957b). He had the opportunity to examine the type specimens of those species and provided the information that was missing in his previous work (La Rivers 1953a) and proposed some taxonomic changes (La Rivers 1958). The species *A. dilatus* and *A. hintoni* (both described by Usinger) were considered junior synonyms of *A. mexicanus* Montandon and *A. fuscus* Usinger was a junior synonym of *A. hybridus* Montandon.

In 1962 La Rivers described four new species, two of them from Mexico. *Ambrysus tridentatus*, a species with features similar to those of *A. woodburyi* and representing the southernmost distribution of the *woodburyi* archetype, was described from the state of Puebla (La Rivers 1962a). The species *A. rotundus* (with the specific epithet referring to the rounded and convex appearance) was described from San Luis Potosí (La Rivers 1962b). The species *A. harmodius* was described based on four specimens collected in the Virilla River in Costa Rica (La Rivers 1962c) and *A. stali* was

described from Brazil, French Guiana, Suriname, and Trinidad (La Rivers 1962d). In the following year *A. montandoni* was described from the Amazonian region in Venezuela and the subspecies *A. mormon minor,* a smaller version of the nominal species was described from the United States (La Rivers 1963). Sites (2015) noted that *A. montandoni* (as well as *A. maldonadus*) presents features that distinguish this species from congeners and probably does not belong in this genus.

De Carlo (1963b) described two species from Brazil, *A. siolii* and *A. fittkaui,* the latter would be later synonymized under *A. usingeri* (La Rivers 1974). Five years later he described *A. partridgei* (name that was originally misspelled as *partridgi*, but because it was named after the ornithologist William H. Partridge it should be spelled as *partridgei*, as in the work by Nieser (1975)) and *A. bourquini* from Brazil (De Carlo 1968). The latter species would later be synonymized under *A. stali* La Rivers (La Rivers & Nieser 1972). Although De Carlo had knowledge of the use of the female subgenital plate and the male accessory process as important features to determine species, he did not pay special attention to those features during his descriptions.

La Rivers (1967) described three subspecies: *A. planus plax* was described from Costa Rica based on its smaller size and differences with the nominal species regarding the morphology of the hemelytra and prothorax and *A. circumcinctus concavus* and *A. c. extremus* were described from Mexico and Honduras, respectively. The designation of the subspecies of *A. circumcinctus* was based on the depth of the depression on the posterior margin of the female subgenital plate. La Rivers (1970) described the atypical-appearing naucorid *A. scolius* from Venezuela and reported the species also from Guyana and Trinidad. We recently examined paratypes of this species (Sites & Reynoso-Velasco

2015) and the drawing of the holotype habitus provided in the original description does not resemble the specimens examined. It was also difficult to understand and find the diagnostic feature cited for the female of this species. In the following year, La Rivers (1971) published his work entitled "Studies of Naucoridae (Hemiptera)", which consisted of two parts: a) the Naucoridae of New Guinea and b) the catalogue of taxa described in the family Naucoridae. The second part was a compendium of all the species and subspecies described in this family in the last 156 years since the creation of the family, an incredible effort considering the amount of work that it represented to be up to date regarding all the publications that were produced before him. In this work he reported a total of 273 species described in Naucoridae from which 64 were from the genus *Ambrysus*. In the following year La Rivers & Nieser (1972) published a study on the *Ambrysus* of Suriname in which they described *A. bifidus* and included it in the *oblongulus* species complex. Recent studies (Sites & Reynoso-Velasco 2015) placed the species in the newly denominated *ståli* complex with four other species.

The first supplement (La Rivers 1974) to the catalogue of taxa described in the family Naucoridae included corrections, emendations, additions, and descriptions of new species. Just prior to that a new classification of the Naucoridae had been proposed (Popov 1970); however, La Rivers considered that it needed further evaluation and opted not to follow it. In the supplement *A. tricuspis* was described from Colombia. La Rivers suggested that the species could be related to *A. bifidus*, which the recent study on the species in the *ståli* complex confirmed (Sites & Reynoso-Velasco 2015). In a second supplement, La Rivers (1976) described three new species from Mexico. *Ambrysus lattini* was described from Durango and apparently was related to the species *A. hybridus,*

A. tridentatus, and *A. woodburyi* because all exhibited variation of what La Rivers considered to be a common structure (shape) of the female subgenital plate. The species *A. quadracies* was described from Veracruz and *A. ultimus* was described from an atypical habitat, a crater lake. Based partially on the subgenital plate morphology of *A. ultimus*, this could be a population of a species related to the *hybridus-woodburyi-lattini-tridentatus* species complex that became isolated and evolved under different selective pressures to the point that it is now a distinct species.

The American entomologists John T. Polhemus and Dan A. Polhemus described four species from Mexico during the early 1980s. The first three species were *A. baeus* (from the Greek *baios* meaning small), *A. colimanus* from the state of Colima (western part of the country), and *A. spiculus* (Polhemus & Polhemus 1981), a species closely related to the *hybridus-woodburyi-lattini-tridentatus-ultimus* species complex. The species *A. plautus* was described from specimens collected in the northern state of Durango (Polhemus & Polhemus 1983). In that paper the authors erroneously compared *A. plautus* with *A. drakei* as if they were related. The comparison was based on superficial features and a closer examination of the new species readily reveals that it is related to the *hybridus-woodburyi-lattini-tridentatus-ultimus-spiculus* species complex. Later they described *A. relictus* (Polhemus & Polhemus 1994), an interesting species from hot springs in the Amargosa River system (Mojave Desert, Utah, USA).

De Carlo (1935) created the genus *Melloiella* for the Brazilian species *M. truncaticollis* and placed it in the subfamily Cryphocricinae. Nieser et al. (1999) considered that the characteristics present in De Carlo's species were essentially the same exhibited by species of *Ambrysus* and downgraded *Melloiella* to subgeneric rank, and

also described *A.* (*Melloiella*) *lamprus* from Brazil. In that work they presented a key to the species of *Ambrysus* from Brazil and northern Argentina.

López Ruf (2004) discussed the problems with identifications of species of *Ambrysus* based on features used in the original descriptions. She advocated for the use of the external structure of the egg (chorion) as a diagnostic feature to distinguish species in this genus because she had shown the advantages of using this feature in previous studies. She described *A. kolla* from the northern provinces of Jujuy, Salta, and Tucumán (Argentina) and described the chorion for future reference (López Ruf 2004). Later she described *A. calilegua* (López Ruf 2007) and *A. wichi* (López Ruf 2013) from Calilegua National Park in northern Argentina. She compared the chorion from the three species and found differences supporting her concept of the chorion as a valuable taxonomic character.

Recently, Sites and Shepard (2015) described *A. cayo* from the Cayo district in Belize. This paper represents a step forward in the taxonomy of the group since for the first time it uses two more features related to the male genitalia as diagnostic features. One of those characters is the pseudoparameres, the median lobes of the male eighth tergum, which were recognized by La Rivers (1954) but not considered diagnostic. I have found that these structures provide information to distinguish among species of *Ambrysus*. The other important new feature used by Sites & Shepard (2015) and Sites & Reynoso-Velasco (2015) is the shape of the left and right ventral lobes of the phallosoma, which have proven to be useful for identifying species complexes.

The *oblongulus* species complex originally was part of the *Coalescens* division in the subgenus *Ambrysus* and all of its species were from North America (La Rivers

1951a). La Rivers (1951b) included *A. teutonius* from Brazil and indicated that *A. pygmaeus* was the most distinctive member of the *oblongulus* species complex (La Rivers 1953a). Later La Rivers & Nieser (1972) used the *oblongulus* species complex to include three South American species (*A. bifidus, A. scolius,* and *A. stali*) with *A. oblongulus*. The group no longer included *A. teutonius* or any North American species other than *A. oblongulus* as originally proposed (La Rivers 1951a, 1953a). It was later suggested that *A. tricuspis* belonged to this group as it appeared to be related to *A. bifidus* (La Rivers 1974). During the recent revision of the group (Sites & Reynoso-Velasco 2015) newly discovered features were useful for recognition of group affiliation. The only species that did not share the same features was *A. oblongulus*; thus, Sites & Reynoso-Velasco (2015) removed it from the group and renamed the group *ståli* after the oldest species still in the species complex. They also described the species *A. maya* from specimens collected in Belize, Guatemala, and Mexico and placed it in the *ståli* species complex.

The most recent contribution to the classification of the group is the description of two species from South America (Sites 2015). *Ambrysus brunneus* was described from a single female collected in Guyana. The specimen had a characteristic digitate process on the sixth laterosternite, something never reported for any other species of *Ambrysus*. The second species was *A. shorti*, described from a single male collected in Venezuela. This male specimen presented tentacular setae on the male parameres, also something never reported from any species in this genus.

La Rivers (1952) first mentioned the concept of subgenera in *Ambrysus* in the work in which he described the monotypic subgenus *Picrops* for the South American species *A. usingeri* and placed the remaining species in the subgenus *Ambrysus*. The

feature distinguishing *Picrops* was the presence of four or more distal rows of small spines on the hind tibia as well as the males bearing a short lateral process on the seventh tergum. In his revision of the fauna of *Ambrysus*, La Rivers (1951a) recognized two divisions within the subgenus *Ambrysus*: the *Coalescens* division included species with the prosternum fused to the adjacent propleura and the *Disjunctus* division included those species with the prosternum free from the propleura. In a later paper La Rivers (1965) elevated the former division to subgeneric rank as *Syncollus* (*A. circumcinctus, A. geayi, A. maldonadus, A. montandoni, A. planus, A. pygmaeus, A. teutonius*) and the 52 species originally placed in the *Disjunctus* division were assigned to the subgenus *Ambrysus.* In the same work he also created the monotypic subgenus *Acyttarus* for *A. funebris*, which lacked a costal cell on the hind wings. The last subgenus assigned was *Melloiella* (Nieser et al. 1999), which was downgraded from generic status and contained two species (*A. lamprus*, *A. truncaticollis*).

La Rivers (e.g., 1951a, b; 1953a) made reference to distinct species-groups or species complexes within the subgenus *Ambrysus*, but in many cases did not provide supporting evidence. La Rivers (1951a) discussed the existence of two groups in the *Coalescens* division: a) *planus*, for which the nominal species was not described at that time but was later published (La Rivers 1951b) and b) *oblongulus* with species from North America and with *A. pygmaeus* as the most distinctive member (La Rivers 1953a).

In the *Disjunctus* division La Rivers (1951a) recognized three species-groups from South America, one of them was *ståli*, with three rows of spines on the metatibia and the other two groups, *fossatus* and *fucatus*, with just two rows of spines. He did not

distinguish between the two latter groups. Also, he noted that *A. bergi* and *A. ochraceus* were members of these groups, but did not specify the correct placement for each species.

The taxonomy of the North American fauna of *Ambrysus* was more complicated since eight groups were discussed. The groups *melanopterus* and *puncticollis* were monotypic based on unique morphology of the species that was so different that he could not suggest and relationship with any other group (La Rivers 1951a). The *pudicus* group had several small members (*A. amargosus, A. hungerfordi, A. parviceps, A. pudicus*) with a distinctive pubescence around the body and a characteristic serration on the edge of connexiva IV and V while having a smooth edge on connexiva II and III. Another feature of the group is that the male accessory genitalic process of some species is lost or reduced (La Rivers 1951a, 1953d).

La Rivers (1951a) did not describe any features for the *oblongulus* group and the other four groups were assigned to two poorly supported divisions depending on whether the propleura were fused or touching at the midline (*vanduzeei* and *signoreti*) or the propleura were separated (*pulchellus* and *californicus*).

The *californicus* group had three members, *A. californicus* and its two subspecies. The *vanduzeei* group represented another monotypic group based on the unique tubular female subgenital plate that La Rivers (1953a) suggested could be used to insert eggs into plant tissue or crevices. All remaining species fell into the *signoreti* group, which La Rivers (1951a) considered the most diverse, more complex, and difficult to characterize since the shape of the female subgenital plate and the male accessory process presented great variation among species. The only unmistakable features to La Rivers were the homogeneous shape and coloration.

In the description of *A. drakei*, La Rivers (1957a) reported that some features of the *signoreti* group were: a) broad form, b) wide embolia, c) prominent maculation, and d) pronounced connexival spination. He assigned *A. drakei* to this group but noted that it also presented some characteristic features of the *mexicanus* group. This latter group was distinguished by: a) slimmer form, b) uniformly colored, and c) relatively or entirely spineless along the connexival margins. The *hybridus-woodburyi-tridentatus-ultimus* complex also has been discussed and the relationship among its species was based on the shape of the female subgenital plate (La Rivers 1976).

It is clear and evident that there are species of *Ambrysus* more closely related than others and that those species can form natural supraspecific groups, although we are not confident about the taxonomic rank of such groups at this time. They could be considered at the subgeneric level because even though that category already exists in *Ambrysus*, it seems not to be well supported. The recent study on the *ståli* complex (Sites & Reynoso-Velasco 2015) is an example of the clear existence of those supraspecific groups, which was made evident by using features related to the male genitalia and not those from the female subgenital plate as did La Rivers. In some cases the female subgenital plate can be very informative for species determination; however, it is quite variable and usually does not provide information to clarify relationships among species groups. Future studies on species of this genus should apply the same methodology as that of Sites & Reynoso-Velasco (2015) in order to find stronger support for affiliation with species complexes.

The current classification of the genus *Ambrysus* Stål includes five subgenera, 83 species, and 15 subspecies; 40 species are known from Mexico (marked with an asterisk):

Ambrysus Stål

(*Acyttarus*) La Rivers

A. funebris La Rivers

(*Ambrysus*) Stål

A. abortus La Rivers*
A. acutangulus Montandon
A. amargosus La Rivers
A. arizonus La Rivers
A. attenuatus Montandon
A. bergi Montandon
A. bifidus La Rivers
A. bispinus La Rivers*
A. brunneus Sites
A. buenoi Usinger*
A. californicus Montandon*
A. c. bohartorum Usinger
A. c. californicus Montandon
A. calilegua López Ruf
A. cayo Sites & Shepard
A. colimanus Polhemus & Polhemus*
A. colombicus Montandon
A. convexus Usinger*
A. cosmius La Rivers*
A. crenulatus Montandon
A. drakei La Rivers*
A. dyticus La Rivers
A. fossatus Usinger
A. fraternus Montandon
A. fucatus Berg
A. gemignanii De Carlo
A. guttatipennis Stål*
A. harmodius La Rivers
A. horvathi Montandon
A. hungerfordi Usinger*
A. h. angularis La Rivers*
A. h. hungerfordi Usinger*
A. h. spicatus La Rivers*
A. h. triunfo La Rivers*
A. hybridus Montandon*
synonym *A. fuscus* Usinger
A. hydor La Rivers*
A. inflatus La Rivers*
A. kolla López Ruf

(*Ambrysus*) Stål (cont.)

A. lattini La Rivers*
A. lunatus Usinger*
    A. l. lunatus Usinger
    A. l. menoides La Rivers*
A. lundbladi Usinger 1946*
A. magniceps La Rivers*
A. maya Sites & Reynoso*
A. melanopterus Stål*
A. mexicanus Montandon*
    synonym *A. dilatus* Usinger
    synonym *A. hintoni* Usinger
A. mormon Montandon*
    A. m. australis La Rivers*
    A. m. heidemanni Montandon
    A. m. minor La Rivers
    A. m. mormon Montandon
A. oblongulus Montandon
A. obscuratus Montandon
A. occidentalis La Rivers*
A. ochraceus Montandon
A. parviceps Montandon*
    synonym *A. infuscatus* Usinger
A. peruvianus Montandon
A. plautus Polhemus & Polhemus*
A. portheo La Rivers*
A. pudicus Stål*
    A. p. barberi La Rivers*
    A. p. pudicus Stål
A. pulchellus Montandon*
    A. p. nitidulus Montandon
    A. p. pallidulus Montandon
    A. p. pulchellus Montandon
A. puncticollis Stål*
A. quadracies La Rivers*
A. relictus Polhemus & Polhemus
A. rotundus La Rivers*
A. scalenus La Rivers*
A. scolius La Rivers
A. shorti Sites
A. signoreti Stål*
A. siolii De Carlo
A. sonorensis Usinger*
A. spiculus Polhemus & Polhemus*

(*Ambrysus*) Stål (cont.)

A. stali La Rivers
synonym *A. bourquini* De Carlo
A. thermarum La Rivers
synonym *A. compressicollis* Usinger
A. tricuspis La Rivers
A. tridentatus La Rivers*
A. ultimus La Rivers*
A. vanduzeei Usinger*
A. variegatus Usinger
A. wichi López Ruf
A. woodburyi Usinger

(*Melloiella*) Nieser *et al*.

A. lamprus Nieser, Pelli & de Melo
A. truncaticollis De Carlo

(*Picrops*) La Rivers

A. usingeri La Rivers
synonym *A. fittkaui* De Carlo

(*Syncollus*) La Rivers

A. baeus Polhemus & Polhemus*
A. circumcinctus Montandon*
A. c. circumcinctus Montandon
A. c. caliginosus Usinger*
A. c. concavus La Rivers*
A. c. extremus La Rivers.
A. geayi Montandon
A. maldonadus La Rivers
A. montandoni La Rivers
A. partridgei De Carlo
A. planus La Rivers
A. p. planus La Rivers
A. p. plax La Rivers
A. pygmaeus La Rivers*
A. teutonius La Rivers

References Cited

Berg, C. 1879. Hemiptera Argentina. Buenos Aires & Hamburg, 316 pp.

Brozek, J. 2014. Phylogenetic signal from Nepomorpha (Insecta: Hemiptera: Heteroptera) mouthparts: Stylets bundle, sense organs, and labial segments. The Scientific World Journal Article ID 237854.

Cassis, G. & R. T. Schuh. 2010. Systematic methods, fossils, and relationships within Heteroptera (Insecta). Cladistics 26: 262–280.

Champion, G. C. 1901. Fam. Naucoridae, pp. 354–361. *In*: Godman F. D. & O. Salvino (eds.). Biologia Centrali-Americana Vol. II Rynchota. Hemiptera-Heteroptera. R. H. Porter, London, [1897–1901].

China, W. E. 1933. A new family of Hemiptera-Heteroptera with notes on the phylogeny of the suborder. Annals and Magazine of Natural History 10: 180–196.

China, W. E. 1955. The evolution of the water bugs. Symposium on organic evolution. Bulletin of the National Institute of Sciences in India 7: 91–103.

China, W. E. & N. C. E. Miller. 1959. Check list and keys to the families and subfamilies of the Hemiptera-Heteroptera. Bulletin of the British Museum (Natural History) 8: 1–45.

Cobben, R. H. 1968. Evolutionary trends in Heteroptera. Part I. Eggs, architecture of the shell, gross embriology and eclosion. Agricultural Research Reports 707: 1–475.

Cobben, R. H. 1978. Evolutionary trends in Heteroptera. Part II. Mouthpart-structures and feeding strategies. Mededelingen Landbouwhogeschool, Wageningen, Netherlands.

Cryan, J. R. & J. M. Urban. 2012. Higher-level phylogeny of the insect order Hemiptera: Is Auchenorrhyncha really paraphyletic? Systematic Entomology 37: 7–21.

Cui, Y., Q. Xie, J. Hua, K. Dang, J. Zhou, X. Liu, G. Wang, X. Yu & W. Bu. 2013. Phylogenomics of Hemiptera (Insecta: Paraneoptera) based on mitochondrial genomes. Systematic Entomology 38: 233–245.

De Carlo, J. A. 1935. Hemípteros acuáticos y semiacuáticos: I) Descripción de un nuevo género y una nueva especie de la familia Naucoridae, subfamilia Cryphocricinae; II) Especies no citadas para la Argentina. Revista Argentina de Entomología 1: 1–4.

De Carlo, J. A. 1950. Géneros y especies de la subfamilia Ambrysinae Usinger (Hemiptera-Naucoridae). Anales de la Sociedad Científica Argentina 150: 3–27.

De Carlo, J. A. 1963a. Un nuevo género y una nueva especie de la subfamilia Ambrysinae (Hemiptera-Naucoridae).). Revista de la Sociedad Entomológica Argentina 24: 9–11.

De Carlo, J. A. 1963b. Un nuevo género y una nueva especie de las subfamilias Limnocorinae y Ambrysinae (Hemiptera, Naucoridae). Revista de la Sociedad Entomológica Argentina 28:111–117.

De Carlo, J. A. 1968. Descripción de especies nuevas de los géneros *Ambrysus, Cryphocricos* y *Heleocoris*. Allotypus de *Cryphocricos daguerrei* (Hemiptera - Naucoridae). Revista de la Sociedad Entomológica Argentina 30: 99–104.

De Carlo, J. A. 1971. Valor sistemático del estudio del aparato genital macho en los hemípteros acuáticos y semiacuáticos. División de la familia Naucoridae en dos familias. Características externas en la cápsula genital. Revista de la Sociedad Entomológica Argentina 33: 159–166.

Esaki, T. & W. E. China. 1927. A new family of aquatic Heteroptera. Transactions of the Entomological Society of London 75: 279–295.

Grimaldi, D. & M. S. Engel. 2005. Evolution of the insects. Cambridge University Press, Cambridge, UK.

Hebsgaard, M. B., N. M. Andersen & J. Damgaard. 2004. Phylogeny of the true water bugs (Nepomorpha: Hemiptera-Heteroptera) based on 16s and 28s rDNA and morphology. Systematic Entomology 29: 488–508.

Hua, J., M. Li, P. Dong, Y. Cui, Q. Xie & W. Bu. 2009. Phylogenetic analysis of the true water bugs (Insecta: Hemiptera: Heteroptera: Nepomorpha): Evidence from mitochondrial genomes. BMC Evolutionary Biology 9:134.

Hungerford, H. B. 1941. A remarkable new naucorid water bug (Hemiptera). Annals of the Entomological Society of America 34: 1–4.

Kristensen, N. P. 1981. Phylogeny of insect orders. Annual Review of Entomology 26: 135–157.

Kristensen, N. P. 1991. Phylogeny of extant hexapods, Chapter 5, pp. 125–140. *In*: Insects of Australia, 2nd Edition, CSIRO, Division of Entomology, Cornell University Press, Ithaca, USA.

La Rivers, I. 1948. A new species of *Ambrysus* from Death Valley, with notes on the genus in the United States (Hemiptera: Naucoridae). Bulletin of the Southern California Academy of Sciences 47: 103–110.

La Rivers, I. 1951a. A revision of the genus *Ambrysus* in the United States (Hemiptera: Naucoridae). University of California Publications in Entomology 8: 277–338.

La Rivers, I. 1951b. Two new Ambrysi from South America (Hemiptera, Naucoridae). Proceedings of the Entomological Society of Washington 53: 288–293.

La Rivers, I. 1952. A new subgenus of *Ambrysus* from South America (Hemiptera: Naucoridae). Entomological News 63: 33–39.

La Rivers, I. 1953a. The *Ambrysus* of Mexico (Hemiptera, Naucoridae). The University of Kansas Sciences Bulletin 35: 1279–1349.

La Rivers, I. 1953b. Two new naucorid bugs of the genus *Ambrysus*. Proceedings of the United States National Museum 103: 1–7.

La Rivers, I. 1953c. A new species and subspecies of *Ambrysus* from Guatemala. The Pan-Pacific Entomologist 29: 138–142.

La Rivers, I. 1953d. New gelastocorid and naucorid records and miscellaneous notes, with a description of the new species, *Ambrysus amargosus* (Hemiptera: Naucoridae). The Wasmann Journal of Biology 11: 83–96.

La Rivers, I. 1954. A new Venezuelan *Ambrysus* (Hemiptera: Naucoridae). Entomological News 65: 197–202.

La Rivers, I. 1957a. A new *Ambrysus* from Mexico (Hemiptera, Naucoridae). Entomological News 68: 232–237.

La Rivers, I. 1957b. Re-description of the Stockholm types of *Ambrysus signoreti* and *Ambrysus mexicanus* (Hemiptera: Naucoridae). The Wasmann Journal of Biology 15: 99–106.

La Rivers, I. 1958. New *Ambrysus* records for Mexico (Hemiptera, Naucoridae). Proceedings of the Entomological Society of Washington 60: 71–74.

La Rivers, I. 1962a. A new species of *Ambrysus* from Mexico (Hemiptera: Naucoridae). The Wasmann Journal of Biology 20: 129–133.

La Rivers, I. 1962b. Another Mexican *Ambrysus* (Hemiptera: Naucoridae). Entomological News 73: 152–155.

La Rivers, I. 1962c. A new species of *Ambrysus* from Costa Rica. The Pan-Pacific Entomologist 38: 234–236.

La Rivers, I. 1962d. A new *Ambrysus* from South America. Bulletin of the Southern California Academy of Sciences 61:185–187.

La Rivers, I. 1963. Two new Ambrysi (Hemiptera: Naucoridae). Biological Society of Nevada Occasional Papers 1:1–7.

La Rivers, I. 1965. The subgenera of the genus *Ambrysus*. Biological Society of Nevada Occasional Papers 4: 1–7.

La Rivers, I. 1967. Descriptions of new bugs. Biological Society of Nevada Occasional Papers 14: 1–8.

La Rivers, I. 1970. A new *Ambrysus* from Venezuela (Hemiptera, Naucoridae). The Great Basin Naturalist 30: 1–4.

La Rivers, I. 1971. Studies of Naucoridae (Hemiptera). Biological Society of Nevada Memoirs 2: 1–120.

La Rivers, I. 1974. Catalogue of taxa described in the family Naucoridae (Hemiptera), Supplement No.1: Corrections, emendations and additions, with descriptions of new species. Biological Society of Nevada Ocassional Papers 38: 1–17.

La Rivers, I. 1976. Supplement No. 2 to the catalogue of taxa described in the family Naucoridae (Hemiptera) with descriptions of new species. Biological Society of Nevada Occasional Papers 41: 1–17.

La Rivers, I. & N. Nieser. 1972. The *Ambrysus* of Surinam, with the description of a new species, *A. bifidus* (Hemiptera, Naucoridae). Biological Society of Nevada Occasional Papers 29: 1–8.

Latreille, P. A. 1810. Considérations générales sur l'ordre naturel des animaux. F. Schoell, Paris.

Leach, W. E. 1815. Hemiptera. *In*: Brewster's Edinburgh Encyclopedia, pp. 57–192. vol. 9. Edinburgh, Scotland.

Leston, D., J. G. Pendergrast & T. R. E. Southwood. 1954. Classification of the terrestrial Heteroptera (Geocorisae). Nature 174: 91–92.

Li, M., Y. Tian, Y. Zhao & W. Bu. 2012. Higher level phylogeny and the first divergence time estimation of Heteroptera (Insecta: Hemiptera) based on multiple genes. PLoS One 7, e32152.

Li, T., J. Hua, A. M. Wright, Y. Cui, Q. Xie, W. Bu & D. M. Hillis. 2014. Long-branch attraction and the phylogeny of true water bugs (Hemiptera: Nepomorpha) as estimated from mitochondrial genomes. BMC Evolutionary Biology 14:99.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th ed. 1 (Animalia). Holmiae, Laurentii Salvii.

López Ruf, M. 2004. Una especie nueva del género *Ambrysus* (Hemiptera Naucoridae). Revista de la Sociedad Entomológica Argentina 63: 97–101.

López Ruf, M. 2007. Nueva especie del género *Ambrysus* (Hemiptera: Naucoridae). Revista de la Sociedad Entomológica Argentina 66: 41–45.

López Ruf, M. 2013. Descripción de una nueva especie del género *Ambrysus* Stål, 1862 (Heteroptera: Naucoridae). Lundiana 11: 43–45.

Mahner, M. 1993. Systema Cryptoceratum Phylogeneticum (Insecta: Heteroptera). Zoologica 143: 1–302.

Mbogho, A. Y. & R. W. Sites. 2013. Naucoridae Leach, 1815 (Hemiptera: Heteroptera) of Tanzania. African Invertebrates 54: 513–542.

Montandon, A. L. 1897a. Hemiptera Cryptocerata. Fam. Naucoridae. Sous-fam. Laccocorinae. Verhandlungen Zoologisch-Botanischen Gesellschaft in Wien 47: 435–454.

Montandon, A. L. 1897b. Hemiptera Cryptocerata. Fam. Naucoridae. Sous-fam. Cryptocricinae. Verhandlungen Zoologisch-Botanischen Gesellschaft in Wien 47: 6–23.

Montandon, A. L. 1897c. Hémiptères nouveaux des collections du Muséum de Paris. Bulletin du Muséum National d'Historie Naturelle (Paris) 3: 124–131.

Montandon, A. L. 1897d. Viaggio di Leonardo Fea in Birmania e Regioni Vicine. LXXV. Hemiptera Cryptocerata. Annali del Museo Civico di Storia Naturale di Genova 17: 365–377.

Montandon, A. L. 1897e. Hemiptera Cryptocerata. Révision de la S. Fa. Limnocorinae. Bollettino del Musei di Zoologia ed Anatomia Comparata della Università di Torino 12: 1–8.

Montandon, A. L. 1898. Hemiptera Cryptocerata, Notes et descriptions d'espèces nouvelles. Bulletin de la Société des Sciences de Bucarest-Roumanie 7: 282–290.

Montandon, A. L. 1909a. Tableau synoptyque des *Ambrysus* et descriptions d'espèces nouvelles. Bulletin de la Société des Sciences de Bucarest-Roumanie 17: 316–330.

Montandon, A. L. 1909b. Naucoridae, descriptions d'espèces nouvelles. Bulletin de la Société des Sciences de Bucarest-Roumanie 18: 43–61.

Montandon A. L. 1910a. Hydrocorises de l'Amerique du Nord. Notes and descriptions d'espèces nouvelles. Bulletin de la Société des Sciences de Bucarest-Roumanie 18: 180–191.

Montandon, A. L. 1910b. Trois espèces nouvelles de la famille Naucoridae. Bulletin de la Société des Sciences de Bucarest-Roumanie 19: 498–444.

Nieser, N. 1975. The water bugs (Heteroptera: Nepomorpha) of the Guyana region, pp. 1–303. *In*: Geilskes, D. C. & P. Wagennar Hummelink (eds.). Studies on the fauna of Suriname and the other Guyanas vol. 16, Utrecht, Netherlands.

Nieser, N., A. Pelli & A. L. de Melo. 1999. Two new Ambrysinae (Heteroptera: Naucoridae) from Minas Gerais, Brazil. Acta Societatis Zoologicae Bohemicae 63: 157–163.

Polhemus, D. A. & J. T. Polhemus. 1988. Family Naucoridae Leach, 1815. The creeping water bugs, pp. 521–527. *In*: Henry, T. J. & R. C. Froeschner (eds.). Catalog of the Heteroptera or true bugs of Canada and the continental United States. E. J. Brill, New York.

Polhemus, J. T. 1991. A new and primitive genus of Cryphocricinae (Heteroptera: Naucoridae). Pan-Pacific Entomologist 67: 119–123.

Polhemus, J. T. & D. A. Polhemus. 1981. Three new species of *Ambrysus* from Mexico (Hemiptera: Naucoridae). The Pan-Pacific Entomologist 57: 397–401.

Polhemus, J. T. & D. A. Polhemus. 1983. Notes on Neotropical Naucoridae II. A new species of *Ambrysus* and review of the genus *Potamocoris* (Hemiptera). The Pan–Pacific Entomologist 58: 326-329.

Polhemus, J. T. & D. A. Polhemus. 1994. A new species of *Ambrysus* Stål from Ash Meadows, Nevada (Heteroptera: Naucoridae). Journal of the New York Entomological Society 102: 261–265.

Polhemus, J. T. & D. A. Polhemus. 2008. Global diversity of true bugs (Hetereptera: Insecta) in fresh water. Hydrobiologia 595: 379–391.

Popov, Y. A. 1968. The origin and basic evolutionary trends of Nepomorpha bugs (Heteroptera). 13th International Congress of Entomology, 2–9 August, Moscow. Abstract of papers.

Popov, Y. A. 1970. Notes on the classification of the recent Naucoridae (Heteroptera: Nepomorpha). Bulletin of the Polish Academy of Sciences (Biological Sciences) Cl. II 18: 93–98.

Popov, Y. A. 1971. Historical development of Hemiptera infraorder Nepomorpha (Heteroptera). Trudy Paleontological Institute, Academy of Sciences, USSR 129: 1–228.

Rieger, C. 1976. Skeleton and musculature of the head and prothorax of *Ochterus marginatus* Latreille: Contribution towards clarification of the phylogenetic relationships of Ochteridae. Zoomorphologie 83: 109–191.

Schuh, R. T. 1979. [Review of] Evolutionary trends in Heteroptera. Part II. Mouthpart-structures and feeding strategies, by R. H. Cobben. Systematic Zoology 28: 653–656.

Schuh, R. T. & J. A. Slater. 1995. True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornel University Press, Ithaca, USA.

Signoret, V. 1850. Description d'un genre nouveau de l'ordre des Hémiptères hétéroptères, et de la section des Hydrocoryses. Revue et magasin de zoologie pure et appliquée 2: 289–291.

Singh-Pruthi, H. 1925. The morphology of the male genitalia in the Rhynchota. Transactions of the Royal Entomological Society of London 73: 127–267.

Sites, R. W. 2015. New taxa of Cryphocricinae (Heteroptera: Naucoridae) from the Guiana shield: *Hygropetrocoris* Sites, n. gen. and two new species of *Ambrysus* Stål. Zootaxa 4033: 427–438.

Sites, R. W. & D. Reynoso-Velasco. 2015. Review of the *Ambrysus stali* La Rivers species complex (Heteroptera: Nepomorpha: Naucoridae) with the description of a new species from Mesoamerica. Zootaxa 4018: 279–291.

Sites, W. R. & J. Camacho. 2014. Neotropical genera of Naucoridae (Hemiptera: Heteroptera: Nepomorpha): New species of *Placomerus* and *Procryphocricos* from Guyana and Venezuela. Zootaxa 3753: 469–482.

Sites, W. R. & L. F. Álvarez-Arango. 2010. Description of the female of *Procryphocricos perplexus* Polhemus (Hemiptera: Heteroptera: Naucoridae). Zootaxa 2562: 66–68.

Sites, W. R. & W. D. Shepard. 2015. Neotropical genera of Naucoridae (Hemiptera: Heteroptera: Nepomorpha): New species of *Ambrysus* and *Procryphocricos* from Belize and Peru. Annals of the Entomological Society of America 108: 613–620.

Sites, R. W., D. Reynoso-Velasco & R. Novelo-Gutiérrez. 2013. Revision of the Mesoamerican genus *Cataractocoris* Usinger (Hemiptera: Heteroptera: Nepomorpha: Naucoridae). Zootaxa 3682: 475–484.

Stål, C. 1862. Hemiptera Mexicana enumeravit speciesque novas descripsit (continuatio). Stettiner Entomologische Zeitung 23: 437–462.

Stål, C. 1876. Enumeratio Hemipterorum. Bidrag till en förteckning öfver alla hittills kända. Hemiptera, jemte systematiska meddelanden. Kongliga Svanska Vetenskaps-Akademiens Handlingar 14: 141–147.

Štys, P. & I. M. Kerzhner. 1975. The rank and nomenclature of higher taxa in recent Heteroptera. Acta Entomologica Bohemoslovaca 72: 65–79.

Štys, P. & A. Jansson. 1988. Check-list of recent family-group and genus-group names of Nepomorpha (Heteroptera) of the world. Acta Entomologica Fennica 50: 1–44.

Usinger, R. L. 1941. Key to the subfamilies of Naucoridae with a generic synopsis of the new subfamily Ambrysinae (Hemiptera). Annals of the Entomological Society of America 34: 5–16.

Usinger, R. L. 1946. Notes and descriptions of *Ambrysus* Stal with an account of the life history of *Ambrysus mormon* Montd. (Hemiptera, Naucoridae). The University of Kansas Sciences Bulletin 31: 185–210.

Usinger, R. L. 1947. Classification of the Cryphocricinae (Hemiptera: Naucoridae). Annals of the Entomological Society of America 40: 329–343.

Usinger, R. L. 1972. Robert Leslie Usinger: Autobiography of an entomologist. Memoires of the Pacific Coast Entomological Society 4: 1–330.

Wang, Y., Y. Cui, D. Rédei, P. Banar, Q. Xie, P. Štys, J. Damgaard, P. Chen, W. Yi, Y. Wang, K. Dang, Ch. Li & W. Bu. 2015. Phylogenetic divergences of the true bugs (Insecta: Hemiptera: Heteroptera), with emphasis on aquatic lineages: The last piece of the aquatic insect jigsaw originated in the Late Permian/Early Triassic. Cladistics 0: 1–16.

Weirauch, C. & R. T. Schuh. 2011. Systematics and evolution of Heteroptera: 25 years of progress. Annual Review of Entomology 56: 487–510.

Wheeler, W. C., R. T. Schuh & R. Bang. 1993. Cladistic relationships among higher groups of Heteroptera: Congruence between morphological and molecular data sets. Entomologica Scandinavica 24: 121–137.

Xie, Q., Y. Tian, L. Zheng & W. Bu. 2008. 18s rRNA hyper-elongation and the phylogeny of Euhemiptera (Insecta: Hemiptera). Molecular Phylogenetics and Evolution 47: 463–471.

Zettel, H. 2007. *Halmaheria skalei* gen.n. et sp.n., eine neue Schwimmwanze (Insecta: Heteroptera: Naucoridae) von der Insel Halmahera, Indonesien. Annalen des Naturhistorischen Museums in Wien 108B: 89–94.

CHAPTER III

THE *AMBRYSUS* STÅL (HETEROPTERA: NAUCORIDAE: CRYPHOCRICINAE) OF MEXICO: REVISION OF THE SUBGENUS *SYNCOLLUS* LA RIVERS

Abstract

The subgenus *Ambrysus* (*Syncollus*) La Rivers is mostly Neotropical and includes nine described species. Features uniting species in this subgenus are related to the position of the propleura with respect to the prosternum in males and females, as well as characteristics of tergum V and the genitalia of males. Three species of *Syncollus* are known from Mexico including *Ambrysus baeus* Polhemus & Polhemus, *A. circumcinctus* Montandon, and *A. pygmaeus* La Rivers. The remaining six species in the subgenus are distributed in Central and South America. Herein we review *Syncollus* and revise the Mexican fauna. More specifically, three new species from Mexico are described: *A. chiapanecus* **n. sp.**, *A. totonacus* **n. sp.**, and *A. xico* **n. sp.** The subspecies *A. circumcinctus caliginosus* Usinger, *A. c. concavus* La Rivers, and *A. c. extremus* La Rivers are proposed as junior synonyms of *A. circumcinctus* Montandon.

Introduction

Mexico is one of 17 countries that collectively harbor close to 70% of the biological diversity on the planet (Mittermeier & Mittermeier 1992, Espinosa et al. 2008). It is among the top five countries with Brazil, China, Colombia, and Indonesia in known diversity of amphibians, birds, mammals, reptiles, and vascular plants. For each of these

groups Mexico contributes almost 10% of the known global biodiversity. Among all major taxa in Mexico, insects are the most diverse and are represented by 47,853 species, which is ca. 5% of the nearly one million insect species described worldwide (Sarukhán et al. 2009).

One of the factors contributing to such high biodiversity is the geographic position of Mexico. The country spans both the Nearctic and Neotropical biogeographical regions and the geological history of the country has produced a complex topographic relief with diverse climatic conditions. These factors in conjunction have promoted the overlapping dispersion of the Nearctic and Neotropical faunas and played a crucial role during the diversification process (Halffter et al. 2008).

The fauna of aquatic and semi-aquatic Heteroptera (Gerromorpha, Leptopodomorpha, Nepomorpha) represents an important component of the world's aquatic insect biota with 23 families, 343 genera, and 4,810 species (Polhemus & Polhemus 2008). Although the taxonomy of the fauna in some areas of the world has been well researched (e.g., Australia, Europe), that of the Mexican fauna is poorly understood and inadequate. Thus, basic information regarding species richness, geographical distributions, phylogenetic relationships, ecological roles, and economic importance can not be treated in a comprehensive manner.

The aquatic insect family Naucoridae, commonly known as creeping water bugs or saucer bugs are common predators in tropical streams worldwide. The family comprises 394 described species in five subfamilies: Cheirochelinae, Cryphocricinae, Laccocorinae, Limnocorinae, and Naucorinae, of which Cheirochelinae has no representatives in Mexico. More specifically, Cheirochelinae is distributed in India,

southern China, Southeast Asia, Borneo, and New Guinea; Cryphocricinae is found 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 in the New World, with the highest diversity in South America; and Naucorinae is cosmopolitan. The Mexican fauna of Naucoridae includes 56 species in six genera and four subfamilies; the subfamily Cryphocricinae has the greatest number of taxa in the country (La Rivers 1971, 1976; Polhemus & Polhemus 1981, 1983; Davis 1986; Polhemus & Sites 1995; Dinger et al. 2005; Sites et al. 2013; Sites & Reynoso-Velasco 2015).

Cryphocricinae comprises 107 species in six genera (*Ambrysus* Stål, *Carvalhoiella* De Carlo, *Cataractocoris* Usinger, *Cryphocricos* Signoret, *Hygropetrocoris* Sites, and *Procryphocricos* Polhemus) and based on the classification by Štys & Jansson (1988) the subfamily is divided into three tribes (Ambrysini, Cataractocorini, and Cryphocricini). The tribe Ambrysini includes the genera *Ambrysus*, *Carvalhoiella*, and *Hygropetrocoris* with 83, 3, and 1 described species, respectively. The genus *Ambrysus* is the most species-rich in Naucoridae, followed by *Limnocoris* Stål (Limnocorinae) with 72 described species. Moreover, the number of species of *Ambrysus* is greater than that of any other subfamily of Naucoridae (Cheirochelinae 58 spp., Laccocorinae 77 spp., and Naucorinae 80 spp.).

Stål (1862) established the genus *Ambrysus* for three Mexican species and indicated it differed from the genus *Naucoris* Geoffroy in having a deep depression on the anterior margin of the pronotum, a character later used by Montandon (1897) as the diagnostic feature for the subfamily Cryphocricinae. *Ambrysus* is distributed in the New

World from the northern United States (La Rivers 1951) south to Argentina (La Rivers 1971), with the greatest number of species in Mexico where 40 species have been reported.

The genus *Ambrysus* includes five subgenera (La Rivers 1952, 1965; Nieser et al. 1999): *Acyttarus*, *Ambrysus*, *Meloiella*, *Picrops*, and *Syncollus*. Only the distinction between *Ambrysus* and *Syncollus* is based on the same morphological feature, the position of the propleura with respect to the prosternum, whereas the other three subgenera were distinguished based on a variety of attributes. The subgenus *Syncollus* includes nine previously described species with the propleura closely appressed to the prosternellum (La Rivers erroneously considered the two structures to be fused): *A. baeus* Polhemus & Polhemus, *A. circumcinctus* Montandon, *A. geayi* Montandon, *A. maldonadus* La Rivers, *A. montandoni* La Rivers, *A. planus* La Rivers, *A. partridgei* De Carlo, *A. pygmaeus* La Rivers, and *A. teutonius* La Rivers. Of these, only *A. baeus*, *A. circumcinctus*, and *A. pygmaeus* occur in Mexico.

Materials and Methods

This work represents the first contribution in a series of papers from a larger project to clarify the taxonomy of species in genus *Ambrysus* from Mexico. As part of the project we collected specimens from 432 localities throughout the country from April 2011 to April 2015. To maximize representation of the fauna of this group in Mexico, we collected in all but two (Baja California and California) of Mexico's biogeographic provinces (Morrone 2005) and complemented that information with collecting records from specimens deposited in museum collections such that all biogeographic provinces

are well-represented. The Yucatan Peninsula has few surficial waters and these habitats are not consistent with that of *Ambrysus*. As a result, our collections did not yield *Ambrysus* from these waterbodies and no specimens from this area were found in museum collections. Thus, *Ambrysus* apparently does not occur in the Yucatan Peninsula.

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. The holotypes were measured for body length and width and major structures, and all measurements are in mm. Body length and width also are given as a mean and range for paratypes. Length of the body is measured from the anterior margin of the head to the posterior margin of the abdomen, and width at the widest point, usually across the embolia. Abdominal segment numbers are expressed as Roman numerals. The male accessory genitalic process of tergum VI in species of *Ambrysus* typically angles to the right at differing degrees. The angle is measured using the basal portion of the process as the axis from which the degree of departure of the distal portion can be measured (Fig. 3B). Images of all species were obtained by use of a Leica MZ16 stereo microscope coupled with the Leica Application Suite V4.4 Extended Depth of Focus module, followed by image preparation with Photoshop CS5 (Adobe Systems Inc., San Jose, California). The margin of the subgenital plate is an important diagnostic character in these species, but it often is difficult to see clearly because of heavy setation and lack of contrast with terminal segments. Thus, we removed the setae (when necessary) and terminal segments to enable a better view of this feature in the figures. Information given in brackets [ ] here did not appear on the labels or was not

provided in publications, but was inferred from available data, or represents corrections to misspellings on the labels. A slash (/) separates data on different labels. Unless otherwise noted, all specimens were collected by Daniel Reynoso-Velasco (DRV) and Pedro Reynoso-Hernández (PRH). Specimens are deposited in the museums corresponding with the following abbreviations.

Museums and Collection Abbreviations

CAS	California Academy of Sciences (San Francisco, United States)
CNIN	Colección Nacional de Insectos (Mexico City, Mexico)
EMEC	Essig Museum of Entomology Collection (Berkeley, United States)
IEXA	Colección Entomológica del Instituto de Ecología A.C. (Xalapa, Mexico)
SEMC	Snow Entomological Collection, University of Kansas (Lawrence, United States)
UAQE	Colección Entomológica de la Universidad Autónoma de Querétaro (Juriquilla, Mexico)
UCDC	Bohart Museum of Entomology (Davis, United States)
UMC	University of Missouri (Columbia, United States)
UMMZ	University of Michigan Museum of Zoology (Ann Arbor, United States)
USNM	United States National Museum of Natural History (Washington D.C., United States)
WSUC	Washington State University Collection (Pullman, United States)

Checklist of Species and Subspecies of *Syncollus*

TAXON	DISTRIBUTION
Ambrysus baeus Polhemus & Polhemus	Belize, Mexico

Ambrysus circumcinctus Montandon	U.S. to Costa Rica
A. circumcinctus caliginosus Usinger **n. syn.**	
A. circumcinctus concavus La Rivers **n. syn.**	
A. circumcinctus extremus La Rivers **n. syn.**	
Ambrysus chiapanecus Reynoso, Sites, & Novelo **n. sp.**	Guatemala, Mexico
Ambrysus geayi Montandon	Panama
Ambrysus maldonadus La Rivers	Venezuela
Ambrysus montandoni La Rivers	Brazil, Venezuela
Ambrysus partridgei De Carlo*	Brazil
Ambrysus planus La Rivers	
A. planus planus La Rivers	Ecuador, Peru
A. planus plax La Rivers	Costa Rica
Ambrysus pygmaeus La Rivers	Mexico
Ambrysus teutonius La Rivers	Brazil
Ambrysus totonacus Reynoso, Sites, & Novelo **n. sp.**	Mexico
Ambrysus xico Reynoso, Sites, & Novelo **n. sp**.	Mexico

*The type specimen of *A. partridgei* is lost; however, we have examined conspecific specimens collected from the type locality. Although La Rivers (1971) placed this species in *Syncollus*, the propleura are not closely appressed to the prosternellum and the posterior margin of male tergum V is not expanded posteriorly to cover the remaining segments. Thus, this species is not a member of *Syncollus* and is transferred to subgenus *Ambrysus*.

Systematics

Genus *Ambrysus* Stål

Ambrysus Stål 1862: Stett. Ent. Zeit. 23: 459. Type species: *Ambrysus signoreti* Stål 1862. Subsequent designation (Kirkaldy 1906).

Discussion: Stål (1862) established the genus *Ambrysus* for the Mexican species *A. melanopterus*, *A. pudicus*, and *A. signoreti*. More recently, La Rivers (1951, 1953) provided detailed descriptions of the genus *Ambrysus*, which includes five subgenera (La Rivers 1952, 1965; Nieser et al. 1999). Of these, *Acyttarus* La Rivers and *Picrops* La Rivers are monotypic (*A. funebris* La Rivers and *A. usingeri* La Rivers, respectively); *Melloiella* De Carlo includes two species [*A. lamprus* Nieser Pelli & de Melo and *A. truncaticollis* (De Carlo)]; *Syncollus* La Rivers comprises nine species, and the remaining 70 species belong to the subgenus *Ambrysus* Stål.

La Rivers (1952) divided *Ambrysus* into two subgenera to accommodate *A. usingeri* with the subgenus *Picrops*. The features distinguishing this subgenus were the presence of four or more rows of small spines on the distal end of the hind tibia and the males bearing a short lateral process on tergum VI. In his revision of the fauna of *Ambrysus* from the United States La Rivers (1951) recognized the divisions *Coalescens* and *Disjunctus* within the subgenus *Ambrysus*, based on the position of the propleura with respect to the prosternum. The former included species with the propleura closely appressed to the adjacent prosternum (prosternellum). In this case the propleura and the anterior part of prosternum (probasisternum) are positioned the same level dorsoventrally. The division *Disjunctus* included species with the propleura detached from the prosternellum; thus, the propleura are at a lower level (further ventrad) than the probasisternum (Fig. 1).

In a later paper La Rivers (1965) created the subgenus *Acyttarus* for the species *A. funebris*, which was the sole species lacking a costal cell on the hind wings. In addition, he elevated the *Coalescens* division to subgeneric rank as *Syncollus* (from Greek *syn*

"together" and Latin *collus* "neck") and the species originally placed in the *Disjunctus* division were assigned to the subgenus *Ambrysus*.

Since La Rivers (1951) first used the shape of the male accessory process of tergum VI and the shape of the female mediosternite VII (subgenital plate) in his revision of the fauna of *Ambrysus* in the United States, these features have been widely used as the two main diagnostic features for distinguishing species of *Ambrysus*. We have examined all species of *Ambrysus* from Mexico including most type specimens, and many thousands of museum and freshly collected specimens. The features used by La Rivers are somewhat instructive, although greater intraspecific variation exists in their expression than was previously considered. In addition to these, we discovered that the medial lobes of male tergum VIII (pseudoparameres) and characteristics of the ventral side of the aedeagus also are important diagnostic features at the species and species complex levels (see Sites & Reynoso-Velasco 2015). Each species complex is best characterized by a certain character or combination of these characters, which differs among complexes. For example, in the *Ambrysus stali* La Rivers complex, the left ventral lobe of the phallosoma is consistent among species, whereas the other three characters are more informative at the species level (Sites & Reynoso-Velasco 2015).

Subgenus *Syncollus* La Rivers

Syncollus La Rivers 1965: Biol. Soc. Nevada Occas. Pap. 4: 4–5. Type species: *Ambrysus circumcinctus* Montandon 1910 (original designation).

Syncollis: Polhemus and Polhemus 1988, Cat. Heteropt., 525. (misspelling).

Discussion: At the time of the establishment of *Syncollus*, La Rivers designated *A. circumcinctus* Montandon as the type species and assigned five of his previously described species to this subgenus (*A. maldonadus*, *A. montandoni*, *A. planus*, *A. pygmaeus*, and *A. teutonius*). Later he included the species *A. geayi* Montandon, *A. partridgei* De Carlo (La Rivers 1971), and *A. stali* La Rivers (La Rivers 1974). In addition, the Mexican species *A. baeus* was assigned to this subgenus (Polhemus & Polhemus 1981). Sites (2015) noted that *A. maldonadus* and *A. montandoni* present features that distinguish them from congeners and will be remove from the genus *Ambrysus* in the near future. The recent review of the *A. stali* species complex (Sites & Reynoso-Velasco 2015) confirmed that *A. stali* is actually a member of the subgenus *Ambrysus*. A revision of the South American species that have been placed in *Syncollus* is needed to clarify their taxonomic status.

In addition to the propleura closely appressed to the adjacent prosternellum (Fig. 1A), we present other diagnostic features of *Syncollus* present in males (1–3) and females (4): 1) phallosoma with only the dorsal side well sclerotized, 2) phallosoma with right and left ventral lobes, and adjacent endosoma membranous and papillose with small, lightly- sclerotized papillae, 3) male tergum V produced posteriorly and nearly completely covering terminal abdominal segments (Fig. 2A), and 4) posteroventrally directed tufts of setae just basad of posterior margin on either side of midline of the female subgenital plate (Figs. 5F, 7F, 9F, 10F).

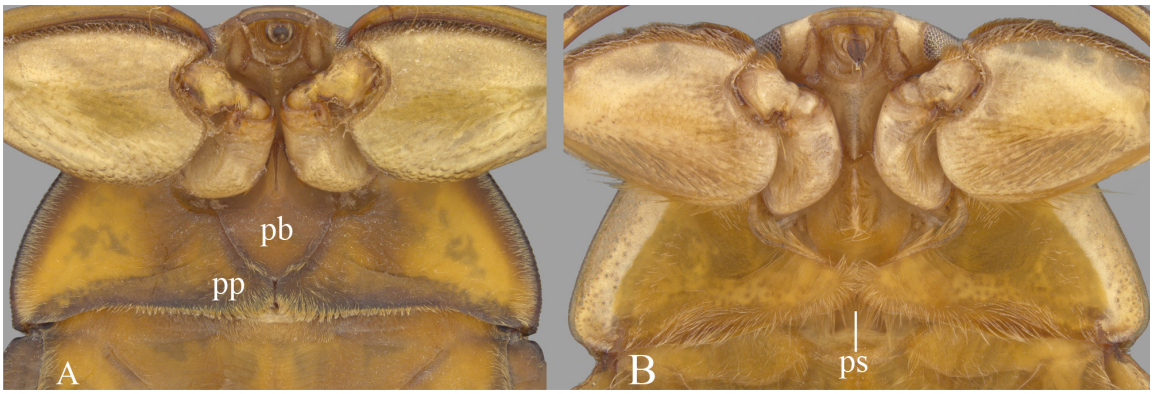

Figure 1. Prothorax (ventral view) of specimens in the subgenera *Syncollus* and *Ambrysus*. (A) *Ambrysus* (*Syncollus*) *circumcinctus*, (B) *Ambrysus* (*Ambrysus*) *inflatus*. pb = probasisternum, pp = propleuron, ps = prosternellum.

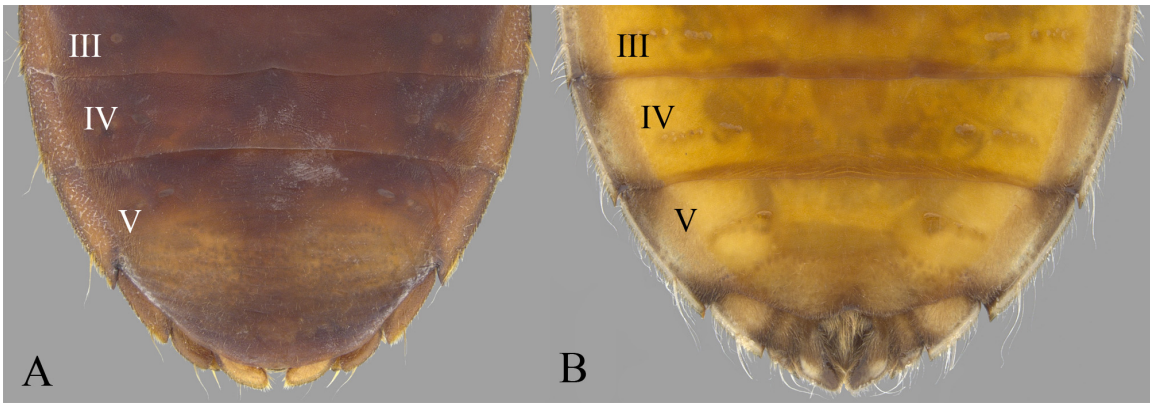

Figure 2. Abdomen (dorsal view) of specimens in the subgenera *Syncollus* La Rivers and *Ambrysus* Stål (wings removed). (A) *Ambrysus* (*Syncollus*) *circumcinctus*, (B) *Ambrysus* (*Ambrysus*) *pudicus*.

Key to the subfamilies and genera of the Naucoridae of Mexico

(modified from Usinger 1941, Polhemus 2008, Mbogho & Sites 2013)

1. Front of head folded posteroventrally .....(Laccocorinae) ..... *Interocoris* La Rivers

1'. Front of head not folded posteroventrally 2

2. Anterior margin of pronotum straight or slightly concave behind interocular space 3

2'. Anterior margin of pronotum deeply emarginate behind interocular space .....

..... (Cryphocricinae).....4

3. Inner margin of eyes diverging anteriorly; meso- and metasterna with prominent longitudinal carinae .....(Limnocorinae)..... *Limnocoris* Stål

3'. Inner margins of eyes converging anteriorly; meso- and metasterna without prominent longitudinal carinae .....(Naucorinae)..... *Pelocoris* Stål

4. Propleura extending mesad to cover posterior portion of prosternum (prosternellum) and contiguous or nearly so at midline (Figs. 1A, B); abdominal sternum densely pubescent; fore wing macropterous forms 5

4'. Prosternum exposed, without mesal extensions of propleura; abdominal sternum glabrous; fore wing brachypterous and macropterous forms..... *Cryphocricos* Signoret

5. Body surface covered with scattered granules; eyes distinctly elevated and subglobose; abdominal sternum with wide, lateral glabrous band; meso- and metapretarsal claws large and strongly curved over entire length nearly to semicircle.....*Cataractocoris* Usinger

5'. Body surface without granules; eyes scarcely elevated above surface of head; abdominal sternum almost entirely pubescent, lateral glabrous band narrow; meso- and metapretarsal claws small with curvature mostly in distal half and never to semicircle..... .....*Ambrysus* Stål

Key to subgenera of *Ambrysus* and species of the subgenus *Syncollus* of Mexico

1. Male and female with mesal extensions of propleura closely appressed to posterior part of prosternum (prosternellum), thus propleura and anterior part of prosternum (probasisternum) at same level (Fig. 1A). Male abdominal tergum V expanded posteriorly to cover abdominal segments VI–VIII (Fig. 2A) ..... *Syncollus* La Rivers... 2

1'. Male and female with mesal extensions of propleura detached from prosternellum, thus propleural extensions further ventrad than probasisternum (Fig. 1B). Male abdominal tergum V slightly expanded posteriorly, with central notch, only covering basal part of terminal abdominal segments (Fig. 2B)..... *Ambrysus* Stål

2. Male and female with minute discontinuous tubercles and punctures on hemelytra. Male posterolateral corner of laterotergite V obtuse and not spinose; accessory genitalic process of tergum VI short, curved to right at 45 degree angle, pointed distally (Fig. 12B); medial lobes of tergum VIII (pseudoparameres) long, asymmetrical, with left pseudoparamere slightly longer and narrower (Fig. 12C). Female with posterior margin of mediosternite VII (subgenital plate) broadly excavated with concavity twice as wide as deep, bounded by posterolateral corners (Fig. 12 F) ..... *Ambrysus xico* **n. sp.**

2'. Male and female with tubercles on hemelytra interconnected by continuous sclerotized ridges, giving a polygonal appearance surrounding punctures. Male posterolateral corner of laterotergite V acute; accessory genitalic process of tergum VI long or short, curved to right at ≥ 45 degrees, rounded distally; pseudoparameres long or short, generally symmetrical. Female with posterior margin of subgenital plate not as above, but if central concavity twice as wide as deep then body length ≤ 6.8 mm or concavity occupies only 1/3 of margin (Fig. 5F) 3

3. Male accessory genitalic process of tergum VI long, narrow, parallel-sided, not dilated or pointed distally (Fig. 7B); pseudoparameres long, rounded, asymmetrical, with right pseudoparamere slightly narrower at apex (Fig. 7C). Female with posterior margin of

subgenital plate highly variable (see variation section) but generally with a shallow concavity bearing a central notched lobe (Fig. 7F)..... .....*Ambrysus circumcinctus* Montandon

3'. Male accessory genitalic process of tergum VI short, dilated distally; pseudoparameres generally short and symmetrical, but if long then pseudoparameres asymmetrical, with left pseudoparamere narrower transversely (Fig. 9C). Female with posterior margin of subgenital plate straight and bearing a small central concavity (Fig. 5F), or narrow with an inverted V-shaped notch (Fig. 9F), or large concavity twice as wide as deep (Fig. 3F), or shallow concavity with two central pointed lobes (Fig. 10F)..... 4

4. Male accessory genitalic process of tergum VI curved to right at approximately 45 degree angle, mesal margin evenly curved (Fig. 9B); pseudoparameres asymmetrical, with left pseudoparamere slightly narrower transversely and longer than right (Fig. 9C). Female with subgenital plate narrowed subapically (bottleneck-shape), posterior margin with inverted V-shaped notch (Fig. 9F).....*Ambrysus pygmaeus* La Rivers

4'. Male accessory genitalic process of tergum VI curved to right at ≥ 45 degree angle, if 45 degree then mesal margin roundedly angulated (Fig. 10B); pseudoparameres symmetrical (Figs. 3C, 5C, 10C). Female with posterior margin of subgenital plate straight and bearing a small central concavity (Fig. 5F), or large concavity twice as wide as deep (Fig. 3F), or shallow concavity with two central pointed lobes (Fig. 10F) 5

5. Male accessory genitalic process of tergum VI curved to right at nearly 90 degree angle (Fig. 3B); pseudoparameres with posterior margin straight (Fig. 3C). Female with

posterior margin of subgenital plate with large central concavity almost twice as wide as deep (Fig. 3F)..... *Ambrysus baeus* Polhemus & Polhemus

5'. Male accessory genitalic process of tergum VI curved to right at ≤ 60 degree angle; pseudoparameres with posterior margin straight or slightly convex. Female with posterior margin of subgenital plate straight and bearing a small central concavity (Fig. 5F) or shallow concavity with two central pointed lobes (Fig. 10F).....6

6. Male accessory genitalic process of tergum VI curved to right at nearly 60 degree angle (Fig. 5B); pseudoparameres with posterolateral corners roundedly angled ~45 degrees (Fig. 5C). Female with posterior margin of subgenital plate straight bearing a small central concavity (Fig. 5F) ..... *Ambrysus chiapanecus* **n. sp.**

6'. Male accessory genitalic process of tergum VI curved to right at nearly 45 degree angle (Fig. 10B); pseudoparameres with posterolateral corners narrowly angled nearly 90 degrees (Fig. 10C). Female with posterior margin of subgenital plate with shallow concavity with two central pointed lobes (Fig. 10F) ..... *Ambrysus totonacus* **n. sp.**

Annotated List of Species

***Ambrysus baeus* Polhemus & Polhemus**
(Figs. 3–4)

A. baeus Polhemus & Polhemus 1981: Pan-Pac. Entomol. 57: 399–400 (original description).

Diagnosis. This species can be distinguished from other species in the subgenus based on the overall body size, shape and length of the male accessory genitalic process (AGP),

shape of the medial lobes of tergum VIII (pseudoparameres), and shape of the posterior margin of the female subgenital plate (SGP). Specifically, the body length is ≤ 6.8 mm. The AGP is generally narrow at the base, curving abruptly to right at a nearly 90 degree angle, and is slightly expanded distally (Fig. 3B). The pseudoparameres are short, symmetrical, subrectangular, with the posterior margin nearly straight, the posterolateral corners rounded, and with a pile of scattered fine setae (Fig. 3C). The parameres are rounded with a row of long setae emanating from the middle of the dorsal surface (Fig. 3D). The phallosoma ventral surface is lightly-sclerotized and papillose subapically, which is more evident on the right side (Fig. 3E). The posterior margin of the SGP has a deep, rounded central concavity almost twice as wide as deep (Fig. 3F).

Discussion. This species was described from a series of specimens collected in western Mexico. The authors placed this species in the same subgenus (*Syncollus*) as *A. circumcinctus* and *A. pygmaeus* and indicated that it had a similar color pattern as that of the latter species, but is smaller when compared with both species (Polhemus & Polhemus 1981). The original description listed the length of the holotype at 5.75 mm, but it failed to provide a size range for paratypes. The length of our specimens is 5.20–6.80 mm. This is the smallest known of all species of *Ambrysus* in Mexico. The ground color is brown with the head, prothorax, and lateral corners of the scutellum light brown. The hemelytra are medium brown and patterned with light brown on the anterior 2/3 of the embolia and a conspicuous light brown triangular mark at the base of the posterior margin of the corium. The exposed connexiva are concolorous light brown (Fig. 3A).

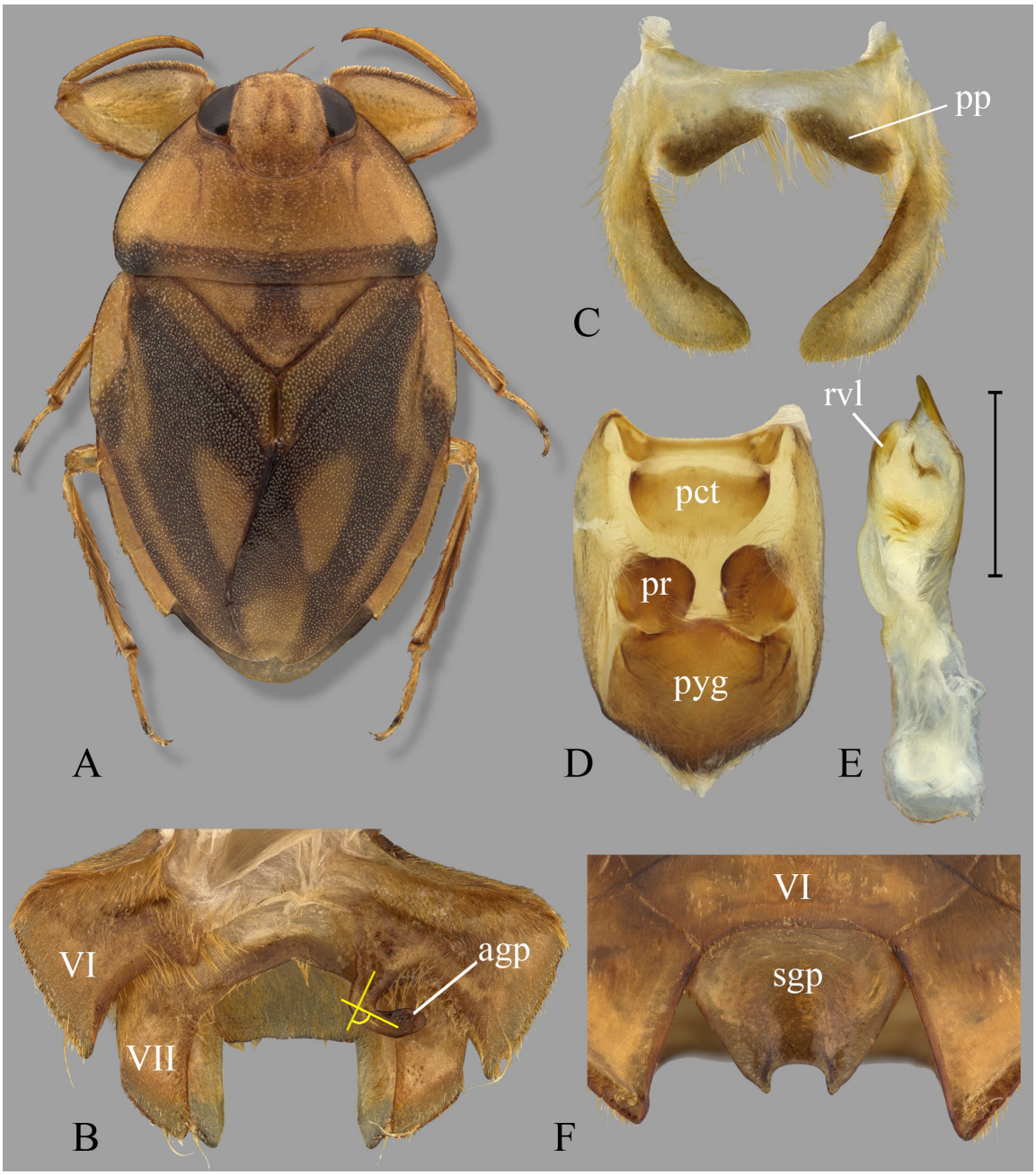

Figure 3. Structures of *Ambrysus baeus*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, angle of curvature of the agp is determined as indicated by yellow lines, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal segments removed). agp = accessory genitalic process, pct = proctiger, pp = pseudoparamere, pr = paramere, pyg = pygophore, sgp = subgenital plate. Size bar = 0.5 mm and applies only to Figs. D and E.

Variation. The color pattern on specimens distributed in southern and eastern Mexico is different from that of western populations. Specimens from southern and western states

(Oaxaca to Nayarit) posses the same color pattern reported in the type series. In general, specimens from southern and eastern Mexico (Chiapas, Oaxaca, San Luis Potosí, Veracruz) present a darker color pattern on the prothorax, with the hemelytra dark brown and a small, inconspicuous light brown triangular mark at the base of the posterior margin of the corium. Also, the exposed connexiva present an alternating brown and light brown checkered appearance. A single population from Michoacán (Mpio. Apatzingán) in the west presented a similar color pattern to that described from eastern populations.

Structure of the AGP is variable; some specimens have a wider base and some have the posterior margin produced posteriorly, giving the impression of less abrupt curvature. Males from eastern Mexico generally present pseudoparameres with posterolateral corners that are more gradually angled as in *A. chiapanecus* **n. sp**. The SGP presents considerable variation in the shape and depth of the posterior margin. Some specimens from Jalisco presented an inverted V-shaped concavity, whereas others from Oaxaca presented a shallow concavity. The posterolateral corners of the SGP are narrow and pointed in the allotype, but we have observed variation from that of the allotype to wide and rounded posterolateral corners.

Type Locality. Mexico: Nayarit: Mpio. San Blas, Aticama.

Repository. Holotype is housed at USNM.

Distribution. This species has been reported from three western states in the Mexican Pacific Coast biogeographic province. Based on our collections, *A. baeus* has a characteristic distribution pattern that includes the tropical lowlands of the Mexican Pacific Coast (Chiapas, Colima, Jalisco, Michoacán, Nayarit, southern Oaxaca) and the

Mexican Gulf (northern Oaxaca, San Luis Potosí, Veracruz) biogeographic provinces. Although we neither collected this species nor found museum specimens that were collected in the state of Guerrero, it is probably present in the coastal and the Balsas Basin regions of Guerrero. We collected *A. baeus* and *A. circumcinctus* syntopically at L-1342, L-1371, L-1488, L-1661, L-1801, L-1802, L-1891, and L-1900.

Published Records. Belize: Cayo (Sites & Shepard 2015). Mexico: Colima, Jalisco, Nayarit (Polhemus & Polhemus 1981).

Figure 4. Distribution of *Ambrysus baeus*, *A. chiapanecus* **n. sp.,** *A. totonacus* **n. sp.,** *A. pygmaeus*, and *A. xico* **n. sp.** in Mexico (topographic map modified from Mexico map relief by Carport and used under CC BY 3.0).

Type Material Examined. HOLOTYPE ♂: **MEX[ICO]: NAY[ARIT]:** [Mpio. San Blas], 5' Aticama, CL727A, VI-7-1975, J. T. Polhemus / HOLOTYPE *Ambrysus baeus* J. T. Polhemus [&] D. A. Polhemus. PARATYPES: 5' Aticama, CL727A, VI-7-1975, J. T.

Polhemus / PARATYPE *Ambrysus baeus* J.T. Polhemus & D. A. Polhemus (4♂, 3♀ CAS; 1♀ CNIN; 1♂, 1♀ EMEC; 2♂, 2♀ USNM).

Material Examined. MÉXICO: CHIAPAS: Mpio. Benemérito de las Américas, Flor de Cacao, tributario del Río Salinas, 16° 09' 24.4" N, 90° 29' 38" W, 140 m, 30-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1891 (1♂, 1♀ UMC); Mpio. Jiquipilas, Rancho Bonito, Pte. Rancho Bonito, 16° 22' 06" N, 93° 52' 04.2" W, 689m, 03-Jun-2014, DRV & PRH colls., L-1814 (1♂ UMC); Mpio. La Concordia, El Altillo, Río El Dorado, 16º 06' 27.5" N, 92º 55' 29.3" W, 524 m, 18-May-2012, DRV & PRH colls., L-1342 (1♀ UMC); [Mpio. Metapa], Metapa, Río Suchiate, 25-III-85, F. Arias (1♂, 3♀ CNIN); same locality information but M. Vertiz (1♀ CNIN); same locality information but H. Velasco (3♂, 2♀ CNIN); [Mpio. Tapachula], Tapachula, Río Huehuetan, 16-III-85, F. Arias (2♀ CNIN); Mpio. Villa Comaltitlán, Chapingo Dos, Pte. Vado Ancho, Río Vado Ancho, 15° 14' 51.8" N, 92° 36' 02.2" W, 57 m, 01-Apr-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1902 (1♀ UMC); Mpio. Villa Comaltitlán, Lázaro Cárdenas, km 238 carr. Huixtla-Mapastepec, 15º 10' 47.4" N, 92º 32' 50.7" W, 16 m, 20-May-2012, DRV & PRH colls., L-1353 (1♀ UMC); Mpio. Villa Comaltitlán, 1.36 km SE of Villa Comaltitlán, 15° 12' 45.8" N, 92° 33' 46.1" W, 48 m, 31-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1900 (1♂ UMC); Mpio. Villa Corzo, Pte. El Carmen, nr. Revolución Mexicana, 16º 07' 51.4" N, 93º 0.2' 00.9" W, 547 m, 08-Jan-2012, DRV coll., L-1318 (1♀ UMC). **COLIMA:** [Mpio. Manzanillo], Pte. El Carrizo at Hwy. 98, 3 rd. km NE [SE] Camotlán, 7 Jan. 2005, C. B. Barr / 19° 13.00' N, 104° 14.66' W, elevation 1250 ft. (1♀ EMEC). **JALISCO:** Las Juntas Verano, 17 I 2005, Río Guapinole / William D. Shepard, leg. (3♂, 1♀ EMEC); Mpio. Cabo Corrientes, Pte. Horcones, 20º 27.548' N, 105º 17.519' W, 330

m, 19-Mar-2014, J. A. Gómez, S. Smith & R. Novelo colls. (11♂, 5♀ UMC); Mpio. Tomatlán, Tomatlán, Río Tomatlán, 19° 56' 41.4" N, 105° 14' 36.1" W, 27 m, 25-Jun-2013, DRV & PRH colls., L-1575 (8♂, 6♀ UMC); Punta Hermanos, 5 I 2005, 980 ft, Río Horcones / William D. Shepard, leg. (1♀ EMEC); Río Cuitzmala, 2.5 km N of Emiliano Zapata, 6 Jan. 2005, C. B. Barr (4♂, 2♀ EMEC); Río Guapinole, 1.3 rd. km E Las Adjuntas Verano/Las Adjuntas del Tuito, 17 Jan. 2005, C. B. Barr / 20° 28.67' N, 105° 16.45' W (1♂ EMEC); Río Los Horcones, 1.1 rd. km W Las Juntas Verano/Las Juntas del Tuito, 5 Jan. 2005, C. B. Barr (3♂, 2♀ EMEC); Río Purificación, 3.7 rd. km NW La Huerta, 8 Jan. 2005, C. B. Barr / 19° 29.50' N, 104° 39.63' W, elevation 740 ft. (1♂, 1♀ EMEC); SE of Chamela, 6 I 2005, 180', Río Cuitzmala / William D. Shepard, leg (1♂, EMEC); 4 km NW la Huerta, 8 I 2005, 740', Río Purificación / William D. Shepard, leg. (2♀ EMEC); 6.6 km SE Villa Purificación, 8 I 2005, Puente El Amborin / William D. Shepard, leg. (1♂, 2♀ EMEC). **MICHOACÁN:** Mpio. Apatzingán, California (arroyo), 21-Feb-2005, R. Novelo & Gómez-Anaya colls. (1♂, 1♀ UMC); Mpio. Aquila, Aquila, Pte. Ramal Aquila, 18º 35' 08.1" N, 103º 30' 51.8" W, 159 m, 25-Dec-2012, DRV & PRH colls., L-1487 (2♂, 4♀ UMC); Mpio. Morelos, La Placita de Morelos, Pte. La Placita, Río Aquila, 18º 32' 19.9" N, 103º 35' 17.9" W, 7 m, 26-Dec-2012, DRV & PRH colls., L-1488 (1♂, 2♀ UMC). **NAYARIT:** Mpio. San Blas, El Palillo, Pte. Palillo, Arroyo Palillo, 21° 38' 27.1" N, 105° 08' 30.8" W, 43 m, 20-Dec-2013, DRV & PRH colls., L-1661 (2♂ UMC). **OAXACA:** Mpio. Ayotzintepec, San José Mano Márques, 17º 47' 26.2" N, 96º 00' 15.3" W, 66 m, 24-May-2012, DRV & PRH colls., L-1371 (1♀ UMC); Mpio. Candelaria Loxicha, Azulillo, Río Candelaria, 15º 53' 29.6" N, 96º 29' 30.8" W, 353 m, 26-May-2012, DRV & PRH colls., L-1377 (8♂, 2♀ UMC); Mpio. Candelaria

Loxicha, km 207 carr. Oaxaca-San Pedro Pochutla, Candelaria Loxicha, Río San Juan, 15º 55' 32.5" N, 96º 29' 12.6" W, 400 m, 25-May-2012, DRV & PRH colls., L-1375 (1♂, 1♀ UMC); same but 02-Apr-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1904 (8♂, 7♀ UMC); Mpio. Candelaria Loxicha, km 206 carr. Oaxaca-San Pedro Pochutla, Candelaria Loxicha, Pte. San Juan, 15º 55' 32.9" N, 96º 29' 25" W, 403 m, 26-May-2012, DRV & PRH colls., L-1376 (2♀ UMC); same but 02-Apr-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1905 (1♂ UMC); Mpio. Mártires de Tacubaya, Mártires de Tacubaya, 16º 34' 41.1" N, 98º 13' 08.7" W, 206 m, 29-May-2012, DRV & PRH colls., L-1390 (15♂, 12♀ UMC); [Mpio. Pluma Hidalgo, El Pacífico] Finca El Pacífico, km 34 carr. Pochutla-Oaxaca, 8-III-1995, 550 msnm, N 15 56 675, W 96 27 892, G. Ortega, E. Barrera (1♀ CNIN); Mpio. San Gabriel Mixtepec, km 194 carr. Puerto Escondido-Oaxaca, San Gabriel Mixtepec, Río Rana, 16º 06' 06.3" N, 97º 03' 52.9" W, 712 m, 27-May-2012, DRV & PRH colls., L-1380 (1♂, 1♀ UMC); same but 03-Apr-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1906 (23♂, 16♀ UMC); Mpio. San Pedro Huamelula, Morro Ayutla, Pte. Río Ayutla, Río Ayutla, 15° 54' 08.7" N, 95° 51' 13.3" W, 29m, 04-Jun-2014, DRV & PRH colls., L-1816 (1♂, 1♀ UMC); km 179 carr. Sta. Maria Zacatepec-Putla, El Rosario, Pte. El Rosario, 16º 51' 34.6" N, 97º 58' 44.7" W, 361 m, 29-May-2012, DRV & PRH colls., L-1394 (4♂, 3♀ UMC); km 201 carr. Mártires de Tacubaya-Santa Maria Zacatepec, ca. 13 km NE of San Pedro Amuzgos, 16º 42' 18.9" N, 98º 00' 52.9" W, 276 m, 29-May-2012, DRV & PRH colls., L-1391 (3♂, 2♀ UMC). **SAN LUIS POTOSÍ:** [Mpio. Huehuetlán], Huichihuayán, (Nacim. Río), 23-Jun-1990, R. Novelo col. (1♂ IEXA). **VERACRUZ:** [Mpio. Chicontepec], Chicontepec, 1-3-76, J. Bueno / *Ambrysus baeus* J. & D. Polhemus, det. J. Polhemus (1♂ CNIN); Mpio. Paso de

Ovejas, Paso de Ovejas, 19° 17' 04.1" N, 96° 26' 03.7" W, 40m, 29-May-2014, DRV & PRH colls., L-1802 (2♀ UMC); Mpio. Puente Nacional, Puente Nacional, Pte. Puente Nacional I, Río La Antigua, 19° 19' 28.5" N, 96° 28' 54.3" W, 67m, 29-May-2014, DRV & PRH colls., L-1801 (1♀ UMC); [Mpio. San Andrés Tuxtla, Los Tuxtlas], Salto [de] Eyipantla, 30-I-84, M. García / Fam: Naucoridae, Gen: *Ambrysus* Det. M. García (1♀ CNIN); same locality information but 01-Apr-2011, R. Novelo coll. (2♂, 3♀ UMC); Mpio. San Rafael, El Faisán, 20° 11' 01.7" N, 97° 05' 38.5" W, 89 m, 12-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1547 (1♂, 1♀ UMC); Mpio. Tlapacoyan, ca. 4 km SW Vista Hermosa, 19º 56.891 N, 97º 07.893 W, 261 m, 8-Nov-2009, Sites, Cervantes & Novelo colls., L-1127 (1♀ UMC); Mpio. Tlapacoyan ca. 4.5 km SW Vista Hermosa, waterfall at Rancho Nuevo, 19º 56.308' N, 97º 07.793 W, 270 m, 8-Nov-2009, Sites, Cervantes & Novelo colls., L-1125 (1♂, 1♀ UMC); Mpio. Tlapacoyan, Ixtacuaco (arroyo), 30-Mar-2003, R. Novelo col. (4♀ UMC); [Mpio. Tlapacoyan], Ixtacuaco, 07-Noviembre-2009, R. Novelo col. (2♂, 1♀ IEXA); [Mpio. Tlapacoyan], Ixtacuaco, 6 IV 2011, 103 m, Río Ixtacuaco, N 20º 02', W 97º 07' / William D. Shepard leg. (1♂, 3♀ UMC); [Mpio.] Tlapacoyan, 1 km antes El Cuajilote (ruinas Filobobos), 8-Nov-2009, R. Novelo col. (2♂, 2♀ IEXA); 10 mi E Xalapa, Dec. 26, 1958, Menke & Stange / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂ CAS).

Ambrysus chiapanecus Reynoso, Sites, & Novelo NEW SPECIES
(Figs. 4–6)

Description. Brachypterous male. HOLOTYPE, length 7.36; maximum width 4.40. Paratypes (n = 7), length 7.12–7.76 (mean = 7.37); maximum width 4.16–4.56 (mean = 4.29). General shape elongate, parallel-sided; widest across embolia (Fig. 5A). Dorsal

coloration of hemelytra brown, with light brown along midline and posterior and lateral margins of corium; head, pronotum, and legs yellowish brown. Dorsal surface coarsely punctate. Ventral coloration of head and thorax yellowish brown, abdomen with dense golden brown pubescence.

Head. Head length 1.44; maximum width 2.04. Mostly yellowish brown with medium brown posteriorly, coarsely punctate. Eyes convergent anteriorly, synthlipsis 0.96; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 11% of head length; posterior margin between eyes strongly convex, extending posteriorly 39% of head length. Labrum width 1.7× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.34 beyond labrum not including extruded stylets. Antennal proportions 2:6:7:7, length 0.48, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color yellowish brown; transverse sulcus marking anterior border of transverse band in posterior 1/4; transverse band pale yellow; ovoid light brown mark on either side of midline at anterior margin; dark submarginal band extending from eye to transverse band; lateral margins dark brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.9× length; length at midline 1.24; maximum width at posterolateral corners 3.60. Prothorax ventrally pruinose throughout; apices of propleura meeting at midline, closely appressed to prosternellum; propleuron yellowish throughout, medial 1/3

of posterior margin with elongate golden setae. Probasisternum with sharp median carina and without row of setae lateral to carina. Prosternellum covered by apices of propleura. Scutellum coarsely punctate, triangular, brown, light brown coloration along margins and midline, width 2.0× length, width 2.52, length 1.26. Hemelytra dark brown, densely punctate, not reaching apex of tergum V, length 5.12 (chord measurement); corium with light brown narrow oblique line at middle and posterior and lateral margins. Clavus with thin yellow stripe at base and apex, length 4.3× width, length 2.80, width 0.64; claval commissure brown, length 0.80. Embolium length 2.20, greatest width 0.54; lateral margin convex, yellow brown in anterior 2/3, becoming darker posteriorly. Oblique suture connecting claval and embolar sutures near bases. Hind wings extending to posterior margin of tergum III. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments yellowish brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third, spines generally single proximally becoming small combs of two to four spines distally; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral, ventromedial, dorsolateral, and dorsomedial rows of stout reddish-brown spines;

ventromedial rows intermixed with combs of two to five spines. Metatibia with ventrolateral, dorsolateral, and dorsomedial rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin, lateral margin without spines at apex to accommodate flexed tarsus. Meso- and metatibiae and metatarsus with long, pale swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.08, tibia 1.72, tarsus 0.40; middle leg, femur 2.04, tibia 1.88, tarsomeres 1–3, 0.16, 0.34, 0.44; hind leg, femur 2.48, tibia 2.84, tarsomeres 1–3, 0.24, 0.46, 0.56.

Abdomen. Dorsally with connexiva III–VIII exposed, laterotergites light brown (Fig. 5A); lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners. Posterolateral corners of II (visible ventrally) – IV narrowly rounded to right angled and not spinose, V–VII bluntly acute. Accessory genitalic process of tergum VI short, curved to right at approximately 60 degrees, dilated distally (Fig. 5B). Medial lobes of tergum VIII (pseudoparameres) short, symmetrical, posterior margin straight to slightly convex, posterolateral corners roundedly angled ca. 45 degrees (Fig. 5C). Ventrally entirely golden brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VII. Phallosoma elongate, linear, constricted basally, sclerotized dorsally; ventral surface lightly-sclerotized and papillose subapically (Fig. 5E). Parameres symmetrical, almost as long as wide, mesal margin straight, row of long dark setae emanating from middle of dorsal surface. Proctiger short, length 0.6× width.

Pygophore with elongate setae sparsely distributed over most of surface, with thick brush of elongate setae on posterior margin (Fig. 5D).

Brachypterous female. Paratypes (n = 8), length 7.68–8.24 (mean = 7.90); maximum width 4.40–4.64 (mean = 4.58). Similar to male in general structure and coloration except as follows: Hemelytra surpassing posterior margin of tergum VI. Mediosternite VII (subgenital plate) width 1.5× length; length at midline 0.84; maximum width 1.30; posterior margin straight with small central concavity; posterolateral corners rounded, slightly produced caudad (Fig. 5F).

Macropterous male. Paratypes (n = 2), length 7.76–7.92 (mean = 7.84); maximum width 4.56. Setation, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for brachypterous male. Otherwise head with dark brown stripe at midline becoming wider posteriorly. Scutellum with light brown on anterior corners. Hemelytra solid black, surpassing apex of tergum V, length 5.92 (chord measurement). Clavus without thin, yellow stripe at apex, length 4.3× width, length 2.60, width 0.60; claval commissure length 0.76. Hind wings extending to posterior margin of tergum V. Each laterotergite dark brown in anterior half and light brown posteriorly giving checkered appearance.

Macropterous female. Unknown.

Variation. Some brachypterous specimens from Guatemala and the four localities in Mexico presented a similar dark color pattern to that described for the macropterous male, although one of the dark brachypterous males also exhibited a thin, yellow stripe at the apex of the clavus as in the holotype. The posterolateral corners of the female subgenital plate can be slightly pointed.

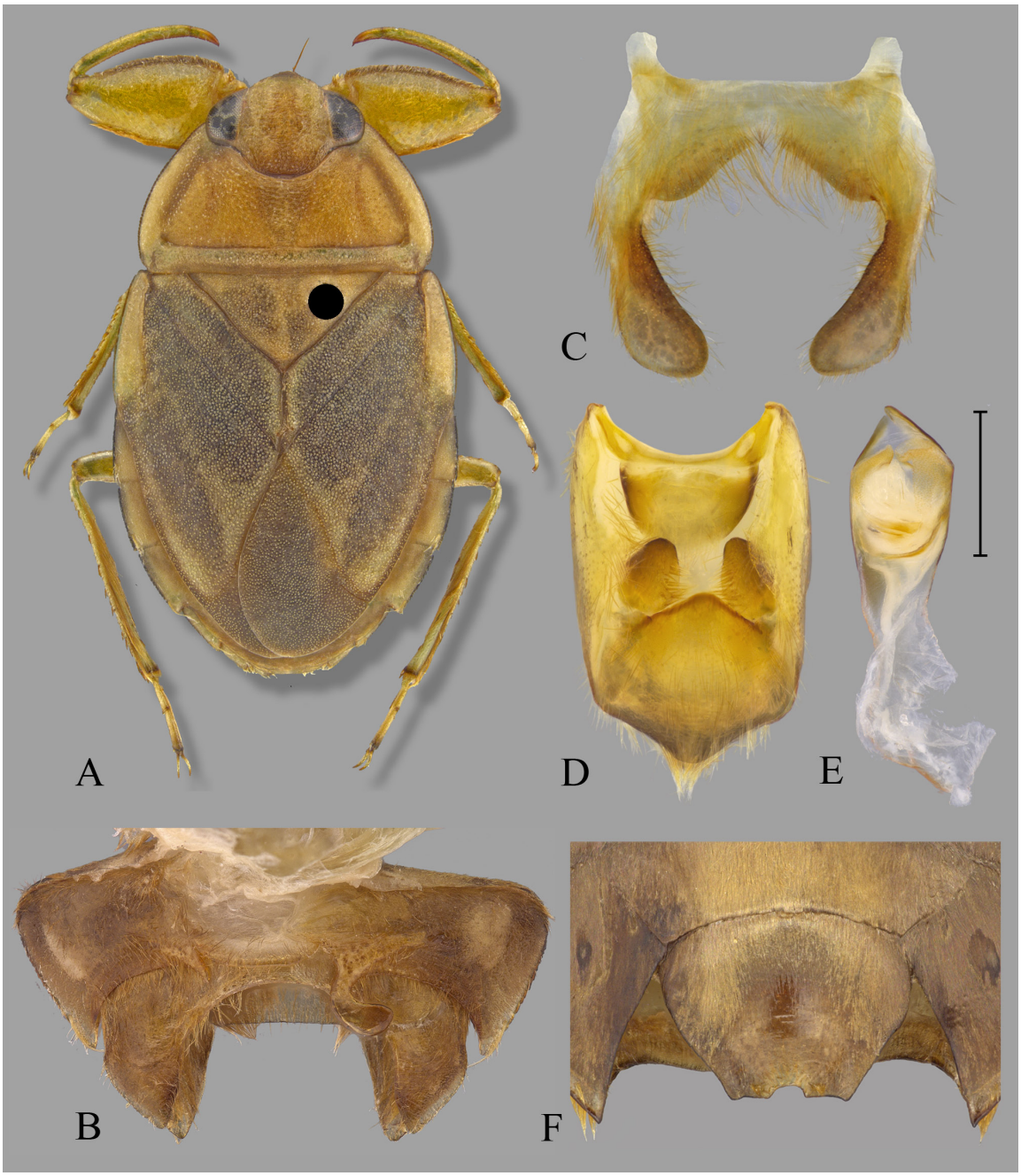

Figure 5. Structures of *Ambrysus chiapanecus* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal segments removed). Size bar = 0.5 mm and applies only to Figs. D and E.

Diagnosis. This species presents a characteristic color pattern on the hemelytra with light brown along the middle and posterior and lateral margins of the corium that is not present

in any other species in the subgenus. The pseudoparameres are noticeably short with the posterolateral corners broadly rounded at a 45 degree angle. The posterior margin of the female subgenital plate has a conspicuous, small, central concavity.

Habitat Description. The source of the Tzaconejá River is in the western mountains in central Chiapas. The river travels southeastward along the Lacantún Basin to drain into the Lacantún River, close to the border with Guatemala. At the type locality the river channel is wide (ca. 20–30 m) with limestone cobble and bedrock (Fig. 6). The collecting was conducted in riffles and in shallow areas with current by disturbing the substrate and holding the net downstream. This method was particularly difficult at the type locality because mineral deposition had cemented cobbles to the bedrock.

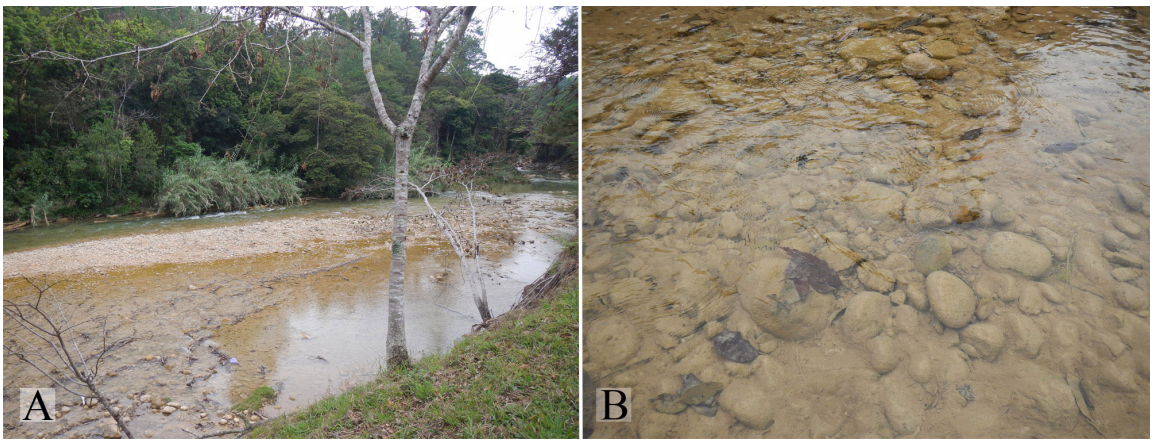

Figure 6. Type locality of *Ambrysus chiapanecus* **n. sp.** at Río Tzaconejá (Chiapas, México). (A) general habitat, (B) specific calcareous habitat.

Distribution. This species was collected from rivers in the highlands and western mountain regions of Chiapas state at elevations above 1000 meters, which are part of the Chiapas biogeographic province. We suspect this species also is present in streams of the western mountains of the Sierra Madre de Chiapas and the easternmost limit (Oaxaca) of the Sierra Madre del Sur biogeographic provinces. In Guatemala the species was

collected in the central mountains of the Sierra de los Cochumatanes (Fig. 4).

Etymology. The specific epithet refers to the southern Mexican state of Chiapas, where we collected this species, an area that harbors great biodiversity.

Repository. The holotype and some paratypes will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the Enns Entomology Museum (University of Missouri), United States National Museum of Natural History (Washington D.C.), and Washington State University (Pullman).

Type Material Examined (brachypterous unless otherwise noted). HOLOTYPE ♂. **MÉXICO: CHIAPAS:** Mpio. Altamirano, Cuauhtemoc, Balneario Tzaconejá, Río Tzaconejá, 28-Mar-20015, 1172 m, L-1886 / 16º 41' 17.5" N, 92º 01' 03.0" W, Reynoso, Sites, Shepard, Barr & Reynoso-Hdez. colls. PARATYPES: same data as holotype (1♂ macropterous, 1♂, 4♀); [Mpio. Bochil], 5 mi N of Bochil, CL1090, 4 May 1964, J. T. & M. S. Polhemus (1♂ macropterous, 2♀); same but / *Ambrysus pygmaeus* La R. det. J. T. Polhemus (1♂); Mpio. Ixtapa, Pte. Río Lajas, Río Lajas, 17-May-2012, 1020 m, L-1340 / 16º 50' 42.6" N, 92º 54' 01.7" W, Reynoso-Velasco & Reynoso-Hernández colls. (1♀); same locality information but 28-Mar-2015, L-1885 / Reynoso, Sites, Shepard, Barr & Reynoso-Hdez. colls (3♂). **GUATEMALA: BAJA VERAPAZ:** Rio Quilila, Rt 5, old rd to Salama from CA-14, 1355 m, N 15º 13.913', W 90º 17.662', 15 Sept 2009, R. S. Zack & J. Monzon collectors (1♂, 1♀ WSUC).

Ambrysus circumcinctus **Montandon**

(Figs. 7–8)

A. circumcinctus Montandon 1910: Bull. Soc. Stiinte 19: 442–444 (original description).

A. circumcinctus: Hungerford 1919, Univ. Kans. Sci. Bull. 21: 201–202 (translation of the original description).

A. circumcinctus: La Rivers 1951, Univ. Calif. Publ. Entomol. 8: 292–295 (supplemental description).

A. caliginosus Usinger 1946: Univ. Kans. Sci. Bull. 31: 190–191 (original description).

A. circumcinctus caliginosus Usinger: La Rivers 1953, Univ. Kans. Sci. Bull. 35: 1290–1292 (considered a subspecies and description of the subspecies), (**new synonym**).

A. circumcinctus concavus La Rivers 1967: Biol. Soc. Nevada Occas. Pap. 14: 3–4 (subspecies description), (**new synonym**).

A. circumcinctus extremus La Rivers 1967: Biol. Soc. Nevada Occas. Pap. 14: 3 (subspecies description), (**new synonym**).

Diagnosis. This species can be distinguished from congeners based on the shape and length of the AGP, as well as the shape of the pseudoparameres. In general the AGP presents the characteristics described by La Rivers (1951): moderately long, parallel-sided, noncapitate, blunt at tip, and uniformly curved to the right at approximately 45 degree angle (Fig. 7B). The pseudoparameres are long, rounded and slightly asymmetrical, with the right pseudoparamere moderately narrower toward the apex; with a pile of fine setae mostly on the mesal margins (Fig. 7C). The parameres are symmetrical, longer than wide, with the mesal margin straight, and with a row of long setae emanating from the middle of the dorsal surface (Fig. 7D). The phallosoma ventral surface is lightly-sclerotized and papillose subapically, which is more evident on the left side (Fig. 7E). The posterior margin of the SGP is highly variable, but in general it has a

shallow concavity with a central notched lobe, and rounded to squared posterolateral corners (Fig. 7F).

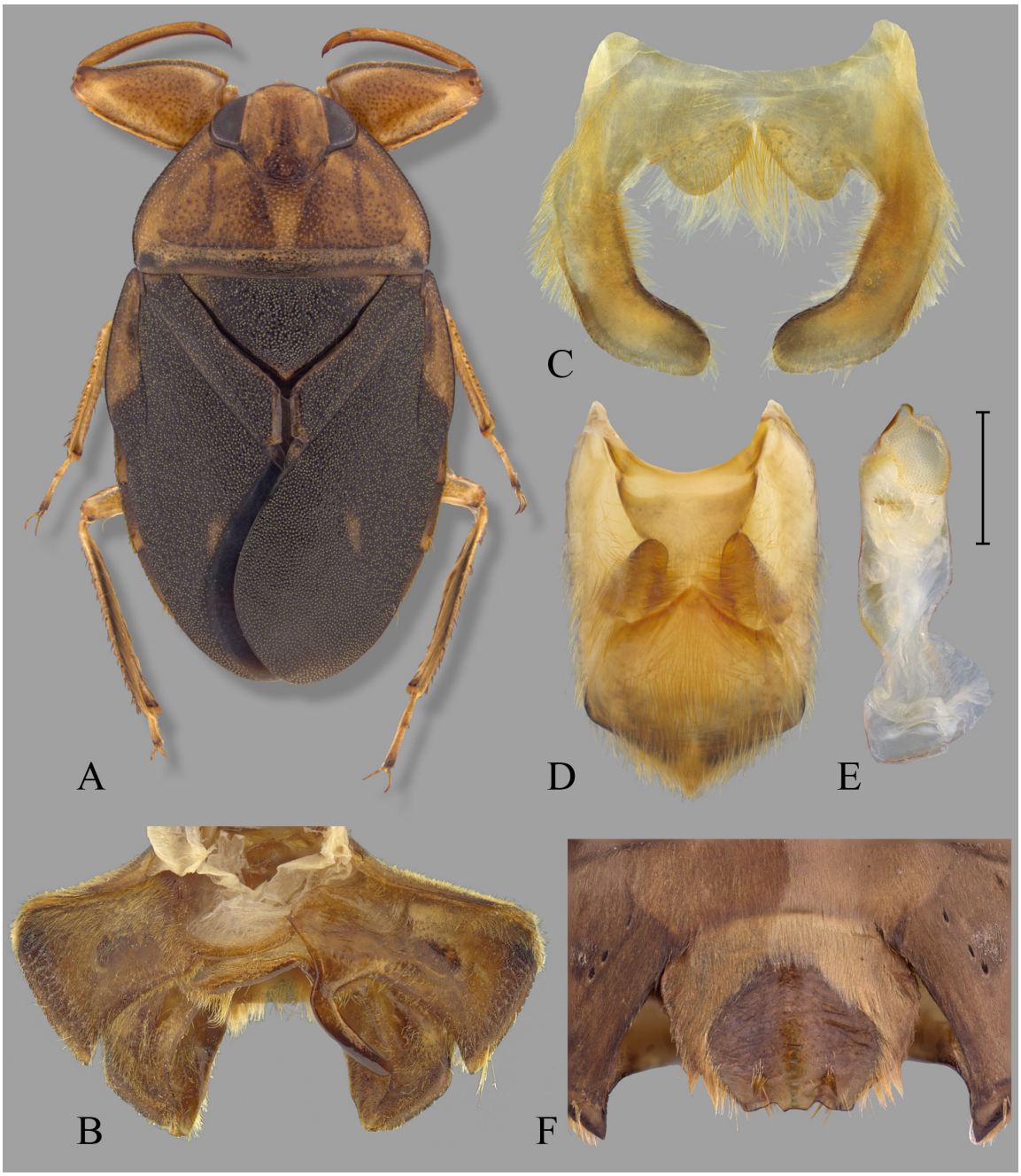

Figure 7. Structures of *Ambrysus circumcinctus* collected in southern Mexico (L-1901). (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal segments removed). Size bar = 0.5 mm and applies only to Figs. D and E.

Discussion. This species originally was described (Montandon 1910) from a single female specimen from Kerrville (Texas) and later assigned as the type species of the subgenus *Syncollus* La Rivers (1965). Usinger (1946) described the species *A. caliginosus* from central Mexico, which was later considered by La Rivers (1953) to be a subspecies of *A. circumcinctus* based on the relatively larger size and darker coloration. Later, La Rivers (1967) described two more subspecies: *Ambrysus c. extremus* from Honduras and Costa Rica with the diagnostic feature of the median lobe in the center of the posterior margin of the SGP conspicuously produced beyond the base of the concavity; and *A. c. concavus*, described from central Mexico with a deeper concavity in the posterior margin of the SGP and the median lobe barely visible. In contrast, the nominal subspecies had a nearly straight posterior margin of the SGP with a short median lobe. The characteristics of the AGP reported for A. *circumcinctus* (La Rivers 1951) were the same reported to be present in *A. c. concavus* and *A. c. caliginosus*, whereas *A. c. extremus* had a distally expanded AGP (La Rivers 1967).

Considering that a subspecies is a geographical variety (Mayr 1982) with morphological uniformity in one or a few diagnostic characters (Wilson & Brown 1953), the four subspecies of *A. circumcinctus* should be identifiable and associated to a particular geographic area based on the shape of the posterior margin of the subgenital plate (La Rivers 1967). This is not the case in part because the subspecies described by La Rivers were based on few specimens from disparate localities and he was not able to assess the variation in subgenital plate shape. We have studied ca. 3,000 specimens from approximately 300 localities from the U.S. to Honduras; thus, this massive amount of material has enabled us to assess intraspecific phenotypic plasticity of this feature. What

La Rivers considered a stable and consistent feature 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. In one example of many, at site L-1350 in Chiapas (southern Mexico) variation in subgenital plate shape includes individuals consistent with that of both *A. c. extremus* and *A. c. circumcinctus.* The latter subspecies purportedly occurs only in the United States and northern Mexico. Because we have examples of more than one subspecific morphological form occurring in various populations and occurrence of the morphological forms does not conform to the latitudinal geographic organization suggested by La Rivers (1967), we consider these subspecies to be consubspecific. As such, we propose *A. c. caliginosus, A. c. concavus*, and *A. c. extremus* to be junior synonyms of *A. c. circumcinctus.*

Variation. The coloration of the hemelytra reported for *A. circumcinctus* was uniformly brownish black with embolia predominantly light yellow, and dark only posteriorly (La Rivers 1951). This coloration of specimens collected in the southern United States was lighter when compared with specimens from central Mexico (La Rivers 1953) and present a conspicuous, light brown triangular mark at the base of the posterior margin of the corium. The coloration of the hemelytra of specimens collected throughout Mexico is solid dark brown with the triangular mark inconspicuous and light brown to reddish brown (Fig. 7A), although some specimens collected in Jalisco, Michoacán, and Nayarit posses a conspicuous triangular mark similar to that present in specimens the from southern United States. A similar mark also is present in specimens of *A. baeus* distributed in western Mexico. Minor variation on the length of the AGP also was

observed. The posterior margin of the SGP showed a high degree of phenotypic plasticity that included the posterior margin with a: a) shallow concavity with central notched lobe, b) shallow concavity with basally constricted central notched lobe, c) deeper concavity with inconspicuous central notched lobe, and d) posterior margin almost straight (without concavity) with inconspicuous central notched lobe.

Type Locality. United States: Texas: Kerr Co., Kerrville.

Repository. Holotype is housed at USNM.

Distribution. This species has the largest range among species in this subgenus in North America. It is distributed from the southern United States south to Costa Rica. In Mexico it is widely distributed with representatives in most of the biogeographic provinces from the Nearctic and Neotropical regions, except the Californian and Baja Californian provinces where the species most likely does not occur (Fig. 8). It is also present in the provinces of the Mexican Transition Zone; however, at high elevations it is replaced by other closely related species. We found *A. circumcinctus* and *A. baeus* occupying the same habitat at different localities within the ranges of both species (L-1342, L-1371, L-1488, L-1661, L-1801, L-1802, L-1891, L-1900), and with *A. totonacus* **n. sp.** in the states of Hidalgo (L-1522) and Veracruz (L-1290, L-1296, L-1549).

Published Records. Belize: Cayo, Orange Walk (Sites & Reynoso-Velasco 2015, Sites & Shepard 2015). Costa Rica: San José (La Rivers 1967, 1971; Herrera 2013). Guatemala (Herrera 2013). Honduras: Atlántida, El Paraíso, Olancho (La Rivers 1967, 1971; Herrera 2013). Mexico: Chiapas, Estado de México, Nuevo León, San Luis Potosí, Sinaloa (La Rivers 1953, 1965, 1967, 1971; Davis 1986; Lee 1991; Herrera 2013).

United States: Arizona, New Mexico, Texas (Montandon 1910; La Rivers 1951, 1953, 1965, 1967, 1971; Davis 1986; Herrera 2013).

Type Material Examined. HOLOTYPE ♀: **UNITED STATES:** [**TEXAS**: Kerr Co.], Kerrville, vi.19.07 TX / F. C. Pratt Collector / From Coll. U.S.N.M. / 052 / *Ambrysus circumcinctus* Montandon Type 1909 / type No. 54270 U.S.N.M. PARATYPES: **MÉXICO: MÉXICO:** Tejupilco, Mex., Temescaltepec [Temascaltepec], VI 18 33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus caliginosus* R. L. Usinger (4♀ EMEC); same but / *Ambrysus circumcinctus caliginosus* determined by Ira La Rivers '50 (1♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI 21 33 / H. E. Hinton, R. L. Usinger / PARATYPE *Ambrysus caliginosus* R. L. Usinger (1♂ EMEC).

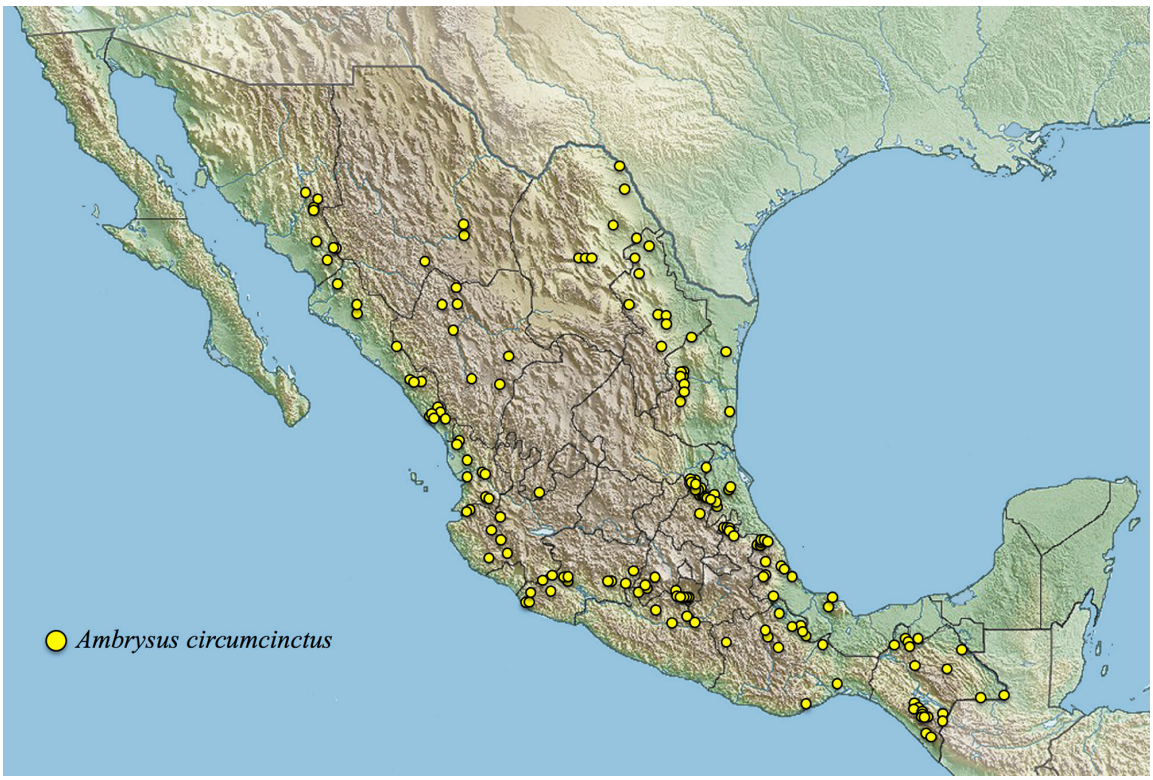

Figure 8. Distribution of *Ambrysus circumcinctus* in Mexico (topographic map modified from Mexico map relief by Carport and used under CC BY 3.0).

Material Examined. MÉXICO: CHIAPAS: Mpio. Amatengo de la Frontera, Barrio Sabinalito, Río Agua Caliente, 15° 25' 0.1" N, 92° 08' 33.7" W, 942 m, 31-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1898 (1♀ UMC); Mpio. Ángel Albino Corzo, Jaltenango, Río Jaltenango (Río Lagartero), 15º 52' 33.7" N, 92º 43' 53.4" W, 605 m, 06-Jan-2012, DRV coll., L-1313 (24♂, 20♀ UMC); same but 07-Jan-2012, L-1314 (46♂, 45♀ UMC); Mpio. Ángel Albino Corzo, km 30 carr. Jaltenango-Siltepec, Plan de Ayutla, Río El Plan de Ayutla, 15º 42' 23.6" N, 92º 34' 43.7" W, 846 m, 19-May-2012, DRV & PRH colls., L-1346 (5♂, 4♀ UMC); Mpio. Ángel Albino Corzo, 1 km S of Finca Prusia, Río Prusia, 15º 43' 23.3" N, 92º 47' 46.5" W, 1010 m, 18-May-2012, DRV & PRH colls., L-1345 (1♂ UMC); Mpio. Benemérito de las Américas, Flor de Cacao, tributario del Río Salinas, 16° 09' 24.4" N, 90° 29' 38" W, 140 m, 30-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1891 (♂1 UMC); Mpio. Frontera Comalapa, El Caracol, 8 km S of Frontera Comalapa, Río Grijalva, 15° 36' 07.0" N, 92° 09' 14.5" W, 677 m, 31- Mar - 2015, DRV, Sites, Shepard, Barr & PRH colls., L-1897 (1♂, 1♀ UMC); Mpio. Huixtla, Huixtla, Río Huixtla, 15° 08' 59.9" N, 92° 27' 04.6" W, 67 m, 31-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1899 (1♂, 4♀ UMC); same but 01-Apr-2015, L-1901 (6♂, 3♀ UMC); Mpio. Ixtapa, Ixtapa, 16º 48' 43.7" N, 92º 54' 30" W, 1030 m, 17-May-2012, DRV & PRH colls., L-1341 (1♀ UMC); Mpio. La Concordia, El Altillo, Río El Dorado, 16º 06' 27.5" N, 92º 55' 29.3" W, 524 m, 18-May-2012, DRV & PRH colls., L-1342 (1♀ UMC); Mpio. La Concordia, Pte. Independencia, 16º 04' 25.2" N, 92º 49' 45.3" W, 547 m, 07-Jan-2012, DRV coll., L-1317 (43♂, 32♀ UMC); Mpio. Maravilla Tenejapa, Ixcán, Pte. Ixcán, Río Ixcán, 16° 04' 33.6" N, 91° 04' 12.8" W, 175 m, 30-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1896 (7♂, 9♀ UMC); [Mpio. Metapa],

Metapa [de Domínguez], Río Suchiate, 25-III-85, M. Vértiz (1♀, CNIN); same but / *Ambrysus circumcinctus* Montd. R. W. Sites det. (1♀ CNIN); Mpio. Monte Cristo de Guerrero, El Paraíso, 15º 39' 28.1" N, 92º 36' 18.7 " W, 864 m, 19-May-2012, DRV & PRH colls., L-1347 (1♂ UMC); Mpio. Ocosingo, Balneario Jataté, Río Jataté, 16° 52' 20.1" N, 92° 02' 18.9" W, 861 m, 28-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1887 (1♀ UMC); Mpio. Palenque, Ángel Albino Corzo, Balneario, Río Chocolja, 17° 17' 32" N, 91° 37' 49.5" W, 119 m, 29-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1888 (17♂, 13♀ UMC); Mpio. Pichucalco, Pte. Rosita, 4 km S of Pichucalco and 800 m S of Río de Janeiro, 17° 29' 07.2" N, 93° 06' 13.5" W, 44 m, 27-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls. L-1883 (2♀ UMC); Mpio. Siltepec, km 72 carr. Jaltenango-Siltepec, nr. Nuevo Galeana, 15º 35' 54.9" N, 92º 32' 28.9" W, 933 m, 19-May-2012, DRV & PRH colls., L-1349 (36♂, 25♀ UMC); Mpio. Siltepec, km 92 carr. Jaltenango-Siltepec, Campo Aéreo, Río Bravo, 15º 35' 17.9" N, 92º 28' 02.3" W, 1068 m, 19-May-2012, DRV & PRH colls., L-1350 (32♂, 31♀ UMC); Mpio. Solosuchiapa, El Beneficio, Río La Sierra, 17° 21' 01.1" N, 93° 00' 21.1" W, 303 m, 27-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1884 (1♂, 3♀ UMC); Mpio. Solosuchiapa, Solosuchiapa, Río La Sierra, 17º 25' 40.5" N, 93º 01' 35.7" W, 122 m, 17-May-2012, DRV & PRH colls., L-1339 (2♂ UMC); [Mpio. Tapachula], Tapachula, Puente Colorado, 31-VIII-85, H. Velasco (1♀ CNIN); [Mpio. Tecpatán], Chintul [El Progreso], 6-III-'88, R. Barba, E. Barrera, A. Cadena (4♂, 2♀ CNIN); same but / *A. c. circumcinctus* Montandon det. R. W. Sites (1♂, 1♀ CNIN); Mpio. Villa Comaltitlán, 1.36 km SE of Villa Comaltitlán, 15° 12' 45.8" N, 92° 33' 46.1" W, 48 m, 31-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1900 (8♂, 8♀ UMC); same locality information but /

William D. Shepard leg. (3♂, 4♀ UMC). **CHIHUAHUA:** Mpio. Balleza, Balleza, Río de Balleza, 26° 55' 20.8" N, 106° 19' 50.1" W, 1574 m, 30-Dec-2013, DRV & PRH colls., L-1703 (15♂, 21♀ UMC); [Mpio. Camargo], Camargo, Río Conchos, 17 August 1952, J. D. Lattin Cal. Acad. Sci. Coll. / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (♂21, 15♀ CAS); [Mpio. Camargo], Camargo, CL1005, 19 April 1964, J. T. & M. S. Polhemus (1♂ SEMC); same but / *Ambrysus circumcinctus* Mont. Det. J.T. Polhemus (1♀ SEMC); [Mpio. Meoqui], Meoqui, Río San Pedro, 20 August 1952, J. D. Lattin Cal. Acad. Sci. Coll. / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (3♂, 3♀ CAS). **COAHUILA:** Mpio. Cuatrociénegas, La Poza Azul, Arroyo La Puerta Colorada, 26° 55' 48.3" N, 102° 07' 41.5" W, 738m, 16-May-2014, DRV & PRH colls., L-1763 (2♂, 1♀ UMC); Mpio. Cuatrociénegas, San Juan de Boquillas, 26° 59' 58.0" N, 101° 53' 35.8" W, 697m, 17-May-2014, DRV & PRH colls., L-1764 (6♂, 1♀ UMC); [Mpio. Jimenez], Río San Francisco, 27 km S of Cd. Acuña, April 01, 1974, R. R. & F. M. Miller (1♂ UMMZ); Mpio. Sabinas, Sabinas (at El Vado), Río Sabinas, 27° 50' 19.5" N, 101° 07' 20.2" W, 340m, 17-May-2014, DRV & PRH colls., L-1765 (1♂, 2♀ UMC); Mpio. Villa de Juaréz, Sección Veintidos Cero, Río Salado, 27° 26' 36.0" N, 100° 28' 38.9" W, 226m, 18-May-2014, DRV & PRH colls., L-1768 (32♂, 21♀ UMC); Mpio. Zaragoza, 25 km N of Zaragoza, Pte. Río San Rodrigo, Río San Rodrigo, 28° 43' 50.5" N, 100° 54' 45.4" W, 329m, 17-May-2014, DRV & PRH colls., L-1766 (11♂, 24♀ UMC); Río Salado de Los Nadadores, at El Carino, 5-IV-1961, R. R. Miller et al., UMMZ Fish M61-43 (1♀ UMMZ). **DURANGO:** Mpio. Guanaceví, El Potrero Viejo, Río Sextín, 25° 56' 28.7" N, 105° 49' 43.0" W, 1931 m, 02-Jan-2014, DRV & PRH colls., L-1713 (3♀ UMC); Mpio.

Nombre de Dios, km 239 carr. Vicente Guerrero-Durango, jct to El Venado, Pte. Melones, Río Mezquital (Río Durango), 23° 52' 17.3" N, 104° 16' 04.7" W, 1731 m, 29-Jun-2013, DRV & PRH colls., L-1591 (3♂, 4♀ UMC); same but 04-Jan-2014, L-1721 (4♂, 8♀ UMC); [Mpio. Peñón Blanco], Peñón Blanco (Belem), 10-VII-85, E. Barrera (1♂, 1♀ CNIN); [Mpio. Peñón Blanco], Peñón Blanco, 10-VII-85, J. Bueno (7♂, 3♀ CNIN); same but / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (2♂, 1♀ CNIN); Mpio. San Bernardo, San Bernardo, Río Sextín (Río Nazas), 26° 00' 05.0" N, 105° 30' 17.6" W, 1607 m, 01-Jan-2014, DRV & PRH colls., L-1711 (13♂, 9♀ UMC); Mpio. Santa Maria de Tepehuanes, Los Corrales, 25° 12' 13.4" N, 105° 34' 22.6" W, 1726 m, 03-Jan-2014, DRV & PRH colls., L-1717 (20♂, 26♀ UMC); Mpio. Villa de Ocampo, Villa de Ocampo, Río Florido, 26° 26' 07.2" N, 105° 30' 24.3" W, 1719 m, 01-Jan-2014, DRV & PRH colls., L-1710 (1♂, 1♀ UMC); 33 mi W Otinapa, Río Arenales, 12 July 1952, J. D. Lattin Cal. Acad. Sci. Coll. / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (2♂ CAS). **GUERRERO:** Mpio. Atenango del Río, Atenango del Río, Río Amacuzac, 18º 06' 01.5" N, 99º 06' 27.8" W, 631 m, 30-Dec-2012, DRV & PRH colls., L-1499 (5♂, 7♀ UMC); Mpio. Copalillo, Papalutla, Río Balsas (Río Papalutla), 18º 01' 27" N, 98º 54' 09.3" W, 627 m, 30-Dec-2012, DRV & PRH colls., L-1500 (11♂, 6♀ UMC); Mpio. Teloloapan, Oxtotitlán, Río Oxtotitlán, 18º 11' 35.7" N, 99º 56' 24.3" W, 1009 m, 29-Dec-2012, DRV & PRH colls., L-1498 (1♀ UMC); [Mpio. Tepecoacuilco de Trujano], Apan, near San Agustín Oapan, at Balsas River, 15 November 2008 / 17º 56' 43" N, 99º 26' 09 W, 505 m, J. D. Amit & A. Domínguez (3♂, 4♀ UMC); [Mpio. Tepecoacuilco de Trujano], 17º 57' 14" N, 99º 26' 22" W, Balsas River, S[an] Ag[ustín] Oapan, 1650 ft, 6 June 2006, #302, coll. J. Amith

(2♂ UMC). **HIDALGO:** Mpio. Atlapexco, Atlaltipa Huitzotlaco, Pte. Atlaltipa, 21° 02' 12.3" N, 98° 22' 24.7" W, 158m, 27-May-2014, DRV & PRH colls., L-1796 (1♀ UMC); Mpio. Huejutla de Reyes, Huitzquilititla, 21° 06' 39.9" N, 98° 27' 24.4" W, 203m, 27-May-2014, DRV & PRH colls., L-1795 (2♀ UMC); Mpio. Molango Escamilla, Malila, Río Malila, 20° 43' 43.8" N, 98° 43' 14.2" W, 1386 m, 05-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1518 (1♀ UMC); Mpio. San Felipe Orizatlán, Huextetitla, 21° 09' 44.4" N, 98° 33' 26.6" W, 154 m, 07-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1525 (1♀ UMC); Mpio. San Felipe Orizatlán, Orizatlán, Pte. Tuntitlán, Río Tuntitlán, 21° 10' 03.4" N, 98° 36' 58.4" W, 175 m, 07-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1527 (2♂ UMC); Mpio. San Felipe Orizatlán, San Felipe Orizatlán, Río San Pedro, 21° 10' 13.6" N, 98° 35' 46.8" W, 173 m, 07-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1526 (18♂, 27♀ UMC); Mpio. Tlanchinol, 3.4 km W of Chalchocotipa, road to Santa Maria Catzotipan (west of Hwy 105, km 3+400), 21° 02' 36.4" N, 98º 36' 00.8" W, 528 m, 06-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1522 (2♂, 5♀ UMC); Mpio. Xochiatipan, Nuevo Acatepec, Pte. Garces Principal, Río El Encinal, 20° 56' 23.7" N, 98° 16' 54.9" W, 201m, 27-May-2014, DRV & PRH colls., L-1797 (7♂, 4♀ UMC). **JALISCO:** Estanzuela, Puente La Estanzuela, W of Ameca, 13 Jan. 2005, C. B. Barr / 20º 31.49' N, 104º 20.16' W, elevation 4580 ft. (1♀ EMEC); Estanzuela, 13 I 2005, 4580', unnamed stream / William D. Shepard, leg. (1♀ EMEC); Hwy 200 @ km 84.5 6 I 2005, 100', Río San Nicolas / William D. Shepard, leg. (1♀ EMEC); Mpio. Atenguillo, Los Volcanes, Río Atenguillo, 20° 19' 16.5" N, 104° 31' 41.1" W, 1459 m, 27-Jun-2013, DRV & PRH colls., L-1582 (5♂, 5♀ UMC); [Mpio. La Huerta], SE of Chamela, 6 I 2005, 180', Río Cuitzmala / William D. Shepard, leg. (1♀ EMEC); Mpio. Puerto Vallarta, Las

Palmas, 235 m, 20º 49.515' N, 105º 05.367' W, 16 March 2014, colls: J. A. Gómez,S. Smith & R. Novelo (1♂ IEXA); Mpio. San Sebastian del Oeste, Pte. Los Arrayanes, Arroyo Los Arrayanes, 20° 49' 44.5" N, 105° 00' 45.1" W, 337 m, 26-Jun-2013, DRV & PRH colls., L-1579 (1♂, 1♀ UMC); [Mpio. Villa Purificación], Río El Amborín, 6.6 rd, km SE Villa Purificación, 19º 38.81' N, 104º 33.92' W, 8 Jan. 2005, C. B. Barr (2♀ UMC; 1♂, 1♀ EMEC); [Mpio. Villa Purificación], 6.6 km SE Villa Purificación, 8 I 2005, Puente El Amborin / William D. Shepard leg. (9♂, 5♀ EMEC); Río de Tepospisaloya, ca. 6 km N Unión de Tula, 9.2 km W Tacotán, 10 Jan. 2005, C. B. Barr / 20º 03.86' N, 104º 20.91' W, elevation 1250 ft. (1♂, 1♀ EMEC); Pte. San Buenaventura at Rd. 513, 8.5 rd. km W of Tonaya, [Río Ferreria], 11 Jan. 2005, coll. C. B. Barr / 19º 47.12' N, 104º 02.71' W, elevation 2360 ft. (1♀ EMEC); 2.4 km SE Purificación, 8 I 2005, 1280', Río Purificación / William D. Shepard leg. (1♂ EMEC); 8.5 km W Tonaya, 11 I 2005, 2360', Puente San Buenavista [San Buenaventura], [Río Ferreria] / William D. Shepard leg. (5♂, 4♀ EMEC); 9.2 km W Tacotán, 10 I 2005, 1250', Río de Tepospisaloya / William D. Shepard leg. (1♂, 2♀ EMEC). **MÉXICO:** Mpio. Amatepec, Las Adjuntas, Río Sn. Felipe, 05-May-2008, R. Novelo & K. Cuevas cols. (1♀ IEXA); [Mpio.] Amatepec, Sn. Felipe de Jesús (1000m), 20-Abril-2004, R. Novelo col. (1♂, 1♀ IEXA); [Mpio. Tejupilco], Bejucos, Río Bejucos, 30-Jan-2008, R. Novelo col. (1♀ IEXA); same but 22-Abril-2004, 700 m (15♂, 8♀ IEXA); [Mpio. Tejupilco], Bejucos, Río Bejucos, 08-Dic-2008, J. Curiel col. (1♀ IEXA); [Mpio. Tejupilco], Bejucos, 22 IV 2004, 1950', Río Bejucos / William D. Shepard, leg. (3♂, 4♀ EMEC); Mpio. Tejupilco, Paso de Vigas, 18º 53' 32.6" N, 100º 13' 57.0" W, 1107 m, 19-Dec-2012, DRV & PRH colls., L-1459 (3♂, 2♀ UMC); San Felipe de Jesus, 20 IV 2004, 3280', Río San Felipe /

William D. Shepard, leg. (1♂ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-18-1933 / H. E. Hinton, R. L. Usinger (3♀ EMEC); same but VI-19-1933 (9♂, 3♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VII-[no day] 1934 / H. E. Hinton (2♂, 4♀ EMEC); Temescaltepec [Temascaltepec], VII-[no day] 1934 / H. E. Hinton (1♂ EMEC). **MICHOACÁN:** [Mpio. Aguililla], Aguililla, 03-Abril-2005, R. Novelo col. (2♂, 2♀ IEXA); [Mpio. Apatzingán], Apatzingán, Pte. El Orejón, 12-Marzo-2004, R. Novelo col. (2♂, 3♀ IEXA); [Mpio.] Apatzingán, California (arroyo), 21-Feb-2005, R. Novelo & J. A. Gómez cols., *Ambrysus circumcinctus* R. Novelo det. (1♂ IEXA); Mpio. Aquila, Aquila, Pte. Ramal Aquila, 18º 35' 08.1" N, 103º 30' 51.8" W, 159 m, 25-Dec-2012, DRV & PRH colls., L-1487 (1♂, 3♀ UMC); Mpio. Carácuaro, Carácuaro, Río San Diego, 19º 01' 04.8" N, 101º 07' 33.2" W, 519 m, 22-Dec-2012, DRV & PRH colls., L-1473 (2♂, 1♀ UMC); [Mpio. Chinicuila], Villa Victoria, 3-Junio-2005, R. Novelo Col. (1♀ IEXA); Mpio. Morelos, La Placita de Morelos, Pte. La Placita, Río Aquila, 18º 32' 19.9" N, 103º 35' 17.9" W, 7 m, 26-Dec-2012, DRV & PRH colls., L-1488 (6♂, 1♀ UMC); Mpio. Nocupétaro, San Antonio de la Huerta, under bridge, 19º 02' 04.4" N, 101º 15' 07.9" W, 624 m, 22-Dec-2012, DRV & PRH colls., L-1475 (5♂, 1♀ UMC); Mpio. Parácuaro, Las Yeguas, Río Tepalcatepec, 18º 53' 42.1" N, 102º 17' 00.3" W, 189 m, 24-Dec-2012, DRV & PRH colls., L-1480 (1♂, 6♀ UMC); Mpio. Tepalcatepec, Los Horcones, km 31 carr. Tepalcatepec-Coalcomán, Pte. Pinolapa, 19º 00' 31.3" N, 103º 01' 25.6" W, 554 m, 25-Dec-2012, DRV & PRH colls., L-1484 (1♀ UMC); Mpio. Tepalcatepec, Río Pinolapa, 10-Jul-2006, R. Novelo, col. (1♂, 2♀ IEXA); Mpio. Tepalcatepec, Tepalcatepec, 19º 11' 47.3" N, 102º 50' 44.9" W, 371 m, 24-Dec-2012, DRV & PRH colls., L-1483 (1♂ UMC); Mpio. Tiquicheo, Piedra China, Pte. Tiquicheo,

Río Purengueo, 18º 53' 37.8" N, 100º 45' 49" W, 363 m, 22-Dec-2012, DRV & PRH colls., L-1472 (6♂, 6♀ UMC); Mpio. Tuzantla, Tuzantla, Río Tuzantla, 19º 13' 18.1" N, 100º 34' 05.5" W, 593 m, 21-Dec-2012, DRV & PRH colls., L-1470 (4♂, 6♀ UMC); Río Pinolapa, 30-May-2005, (4♂ IEXA); S de Coalcomán, Aguililla, 11-Julio-2005, R. Novelo col. (4♂, 9♀ IEXA). **MORELOS:** [Mpio. Amacuzac], Huajintlán, Río Amacuzac, 28 Mayo 1983, [no collector] (1♀ CNIN); same but D. Porras, L. Castrejón [colls.] (2♂ CNIN); same but / *A. c. circumcinctus* Montandon det. R. W. Sites (1♂ CNIN); same locality information but / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♂, 2♀ CNIN); [Mpio. Jojutla], San Rafael Vicente Aranda, 15-Mar-1983, R. Novelo col. (3♂, 4♀ IEXA); [Mpio. Jojutla], S. Rafael A., 13-VII-82, M. Espinosa, (10♂, 7♀ CNIN); same but / *A. c. circumcinctus* Montandon det. R. W. Sites (3♂, 1♀ CNIN); same locality information but / *A. circumcinctus* Mont. det. R. W. Sites 2009 (1♀ CNIN); same locality information but / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♂ CNIN); [Mpio. Jojutla], S. Rafael A., 17-VI-82, M. Espinosa (15♂, 11♀ CNIN); same but / *A. c. circumcinctus* Montandon det. R. W. Sites (1♂, 4♀ CNIN); Mpio. Jojutla, Tehuixtla, Río Amacuzac, 18º 32' 47.9" N, 99º 16' 03.6" W, 854 m, 28-Apr-2011, DRV coll., L-1309 (11♂, 7♀ UMC); Mpio. Jojutla, Tehuixtla, Río Amacuzac, 18º 33' 45.2" N, 99º 16' 51.3" W, 853 m, 28-Apr-2011, DRV coll., L-1308 (3♂, 3♀ UMC); [Mpio.] Jojutla, Vicente Aranda, Río Amacuzac (900m), 11-Diciembre-1982, P. Liljehult col. (1♂, 1♀ IEXA); [Mpio.] Jojutla, Vicente Aranda, Río Amacuzac (900m), 12-Feb-1983, V. García col. (27♂, 40♀ IEXA); same locality information but C. Valencia col. (22♂, 17♀ IEXA); [Mpio.] Jojutla, Vicente Aranda, Río Amacuzac, 27-Marzo-1983, G. Cardoso col. (12♂, 14♀ IEXA); [Mpio.] Jojutla, Vicente

Aranda, Río Amacuzac, 7-Mayo-1983, S. Ibáñez col. (7♂, 7♀ IEXA); [Mpio. Jojutla], Vicente Aranda (900msnm), 16-Marzo-2001, R. Novelo col. (4♂, 7♀ IEXA); [Mpio. Jojutla], Vicente Aranda, Río Amacuzac, 04-Abril-2002, R. Novelo col. (4♂, 10♀ IEXA); [Mpio. Tetecala], Tetecala, (900m), 02-Diciembre-2000, R. Novelo col. (1♀ IEXA); [Mpio.] Tlaquiltenango, El Astillero [La Mezquitera], Río Cuautla (dentro del río c/corriente), 5-Feb-1983, I. Oliva col. (4♂, 4♀ IEXA); [Mpio. Yautepec], Yautepec, Río Yautepec (1,203m), 17-Enero-1983, I. Oliva col. (2♀ IEXA). **NAYARIT:** Las Adjuntas, Río Huaynamota, II 3-VII-92, S. Santiago, R. Barba (1♀ CNIN); Los Sabinos, Río Huaynamota, 10-IV-91 R. Barba, E. Barrera (1♂ CNIN); same but 23-5-1991 (4♂, 1♀ CNIN); same but / *A. c. circumcinctus* Montandon det. R. W. Sites (1♀ CNIN); Mpio. Acaponeta, El Recodo, Río Acaponeta, 22° 31' 31.9" N, 105° 20' 37.3" W, 34 m, 01-Jul-2013, DRV & PRH colls., L-1601 (1♀ UMC); Mpio. Acaponeta, La Guásima, Río Acaponeta, 22° 24' 26.6" N, 105° 23' 48.9" W, 26 m, 02-Jul-2013, DRV & PRH colls., L-1602 (20♂, 17♀ UMC); Mpio. Ahuacatlán, Ejido Tetitlán, Río Tetitlán, 21° 07' 51.3" N, 104° 37' 10.1" W, 747 m, 02-Jul-2013, DRV & PRH colls., L-1606 (10♂, 11♀ UMC); Mpio. Ahuacatlán, Puerta del Río, Balneario El Paraiso, Río Tetitlán, 21° 10' 59.3" N, 104° 38' 32.9" W, 859 m, 18-Dec-2013, DRV & PRH colls., L-1651 (1♂, 1♀ UMC); Mpio. El Nayar, Playa Golondrinas, Río Santiago, 26/5/1991, R. Barba, E. Barrera / *A. c. circumcinctus* Montandon det. R. W. Sites (1♂ CNIN); Mpio. Ruíz, San Lorenzo, Río San Pedro, 21° 57' 04.1" N, 105° 04' 28.3" W, 23 m, 20-Dec-2013, DRV & PRH colls., L-1662 (1♂, 4♀ UMC); Mpio. San Blas, El Palillo, Pte. Palillo, Arroyo Palillo, 21° 38' 27.1" N, 105° 08' 30.8" W, 43 m, 20-Dec-2013, DRV & PRH colls., L-1661 (4♂, 4♀ UMC); Mpio. Tepic, Colorado de la Mora, 232 msnm, 12-IV-91, E. Barrera, J. León (1♂

CNIN). **NUEVO LEÓN:** Mpio. Cadereyta Jiménez, San Juan, Río San Juan, 25° 31' 55.1" N, 99° 50' 39.1" W, 266m, 19-May-2014, DRV & PRH colls., L-1773 (15♂, 23♀ UMC); Mpio. Cd. Anáhuac, Cd. Anáhuac, Río Salado, 27° 14' 09.0" N, 100° 08' 24.1" W, 187m, 18-May-2014, DRV & PRH colls., L-1769 (6♂, 11♀ UMC); Mpio. García, Río Pesquerías, 8-XI-85, H. Rivas (1♂ CNIN); same locality information but R. Barba / *A. c. circumcinctus* Montandon det. R. W. Sites (1♀ CNIN); same locality information but S. Tufinio / *A. c. circumcinctus* Montandon det. R. W. Sites (1♀ CNIN); Mpio. General Terán, La Barreta, Río Conchos, 25° 04' 25.9" N, 98° 58' 55.9" W, 124m, 20-May-2014, DRV & PRH colls., L-1776 (8♂, 8♀ UMC); Mpio. General Terán, La Unión, Río El Pilón, 25° 20' 27.2" N, 99° 34' 57.5" W, 243m, 19-May-2014, DRV & PRH colls., L-1775 (1♀ UMC); Mpio. Lampazos de Naranjo, El Ancón, Río Candela, 27° 02' 33.5" N, 100° 32' 13.5" W, 293m, 18-May-2014, DRV & PRH colls., L-1770 (1♂ UMC); Mpio. Los Ramones, 1 km N of Hacienda El Carrizo, Río San Juan, 25° 31' 40.5" N, 99° 37' 20.9" W, 206m, 19-May-2014, DRV & PRH colls., L-1774 (24♂, 23♀ UMC); [Mpio. Villaldama], Villa Aldama, [Villaldama], [Arroyo] La Coyota, 13-XI-85, R. Barba (3♀ CNIN); Pilon R. at unnamed road, across from General Terán (town), off St. Hwy 35 / 15 May 1995, DB 95-10, colls: D. E. Baumgardner & B. C. Henry (2♂, 3♀ UMC); 17.5 mi. W Linares, V-25-1981, J. T. Doyen, J. K. Liebherr (1♀ EMEC). **OAXACA:** Dominguillo, 7-XI-1988, E. Barrera, R. Barba, L. Cervantes (1♂ CNIN); Mpio. Ayotzintepec, San José Mano Márques, 17º 47' 26.2" N, 96º 00' 15.3" W, 66 m, 24-May-2012, DRV & PRH colls., L-1371 (1♂, 1♀ UMC); Mpio. Guelatao de Juárez, carr. Tuxtepec-Oaxaca, 6 km W of Guelatao, Pte. Xia, 17º 18' 18.3" N 96º 31' 33.8" W, 1497 m, 24-May-2012, DRV & PRH colls., L-1373 (11♂, 1♀ UMC); [Mpio. Ixtepec], Río

Perros, just above Ixtepec, III-27-1957, Elev. 340 ft, R. R. Miller (7♂, 15♀ UMMZ); Mpio. Jalapa de Díaz, Sto. Domingo, Río Sto Domingo, 18° 02' 15.9" N, 96° 32' 57.2" W, 100 M, 25-Mar-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1881 (2♂ UMC); [Mpio. San Juan Bautista Cuicatlán], Santiago Dominguillo, Río Las Huertas, 12-VII-1996, R. Barba, A. Rojas / *A. c. circumcinctus* Montandon det. R. W. Sites (2♀ CNIN); Mpio. San Juan Bautista Cuicatlán, Santiago Dominguillo, 17º 38' 46" N, 96º 54' 36.7" W, 726 m, 01-Jun-2012, DRV & PRH colls., L-1405 (4♂, 2♀ UMC); Mpio. San Juan Cotzocón, Arroyo Carrizal, km 110 carr. Palomares-Tuxtepec, 17º 26' 55.6" N, 95º 26' 39.1" W, 94 m, 22-May-2012, DRV & PRH colls., L-1365 (3♂, 7♀ UMC); Mpio. San Miguel del Puerto, Copalita, Pte. Copalita, Río Copalita, 15° 49' 12.2" N, 96° 03' 57.6" W, 28m, 04-Jun-2014, DRV & PRH colls., L-1818 (3♂, 4♀ UMC); Mpio. San Sebastian Tecomaxthahuaca, Tecomaxthahuaca, Laguna Encantadac [in lateral channel], 17º 21' 57.5" N, 98º 01' 13.3" W, 1662 m, 30-May-2012, DRV & PRH colls., L-1399 (1♂, 2♀ UMC); Mpio. Santiago Jocotepec, nr. San José Río Manso, 17º 38' 44.3" N, 95º 52' 02.1" W, 61 m, 23-May-2012, DRV & PRH colls., L-1368 (5♂, 2♀ UMC); Mpio. Santiago Jocotepec, San Jose Río Manso, Centro Ecoturístico Cerro Chango, 17º 42' 06.6" N, 95º 54' 01.6" W, 54 m, 23-May-2012, DRV & PRH colls., L-1367 (12♂, 3♀ UMC); Mpio. Santo Domingo Zanatepec, carr. Arriaga-Santo Domingo Tehuantepec, Colonia Río Ostula, Pte. Ostula, 16º 29' 59.5" N, 94º 26' 00.5" W, 40 m, 22-May-2012, DRV & PRH colls., L-1360 (1♂, 4♀ UMC); Mpio. Valerio Trujano, km 124 carr. Tehuacán-San Francisco Telixtlahuaca, jct to Tomellín, Pte. El Grande, Río Grande, 17º 45' 25" N, 96º 56' 59.1" W, 607 m, 01-Jun-2012, DRV & PRH colls., L-1406 (4♂, 3♀ UMC); Mpio. Valle Nacional, San Mateo Yetla, 12-X-1990, E. Ramírez, E. Barrera, A. Cadena (1♀

CNIN); km 21 desviación San Miguel Chimalapa, 210msnm, 22-III-1990, E. Barrera, A. Cadena (1♀ CNIN); km 116 carr. Tuxtepec-Palomares, 22-XI-1990, A. Cadena, E. Barrera (1♀ CNIN). **PUEBLA:** [Mpio. Jopala], Patla, 23-VII-75, H. Brailovsky A. col., noct. (1♂, 1♀ CNIN); same but / *Ambrysus circumcinctus* Montandon (Ira La Rivers) (1♀ CNIN); Mpio. Tlacuilotepec, carr. Plan de Ayala-Tlaxco, 2 km E of Papaloctipan, 20º 25' 22.4" N, 97º 56' 38.2" W, 310 m, 05-Jun-2012, DRV & PRH colls., L-1417 (10♂, 8♀ UMC); Mpio. Tlacuilotepec, Río San Marcos, km 1 carr. A. Camacho-Petlacotla, 24-Julio-1987, R. Novelo col. (5♂, 4♀ IEXA); Mpio. Tlaxco, carr. Tlaxco-Cuaxtla, ca. 2 km S of Acalman, Río Los Cajones, 20º 24' 26.8" N, 98º 03' 51.5" W, 785 m, 05-Jun-2012, DRV & PRH colls., L- 1418 (1♀ UMC); Mpio. Xicotepec, carr. Huauchinango-Poza Rica, Miguel Ávila Camacho (La Ceiba), Pte. San Marcos, Río San Marcos, 20º 23' 40" N, 97º 52' 39.1" W, 239 m, 05-Jun-2012, DRV & PRH colls., L-1416 (4♂, 6♀ UMC); [Mpio. Xicotepec], Villa Ávila Camacho, [La Ceiba], Río San Marcos, 17-Julio-1990, R. Novelo col. (1♀ IEXA); same but 30-Abril-1991 (1♂, 1♀ IEXA). **SAN LUIS POTOSÍ:** Mpio. Axtla de Terrazas, Cómoca, Río Tancuilín, 21º 25' 03.8" N, 98º 53' 43.3" W, 75m, 22-Apr-2011, DRV coll., L-1307 (20♂, 13♀ UMC); same but 19-Jul-2011, L-1311 (1♀ UMC); Mpio. Axtla de Terrazas, Cómoca, Río Tancuilín, 21° 25' 02.9" N, 98° 53' 42.8" W, 86 m, 08-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1532 (1♂, 5♀ UMC); Mpio. Huehuetlán, El Nacimiento de Huichihuayán (spring), 21° 27' 35.3" N, 98° 58' 38.8" W, 96 m, 08-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1533 (1♂, 1♀ UMC); Mpio. Matlapa, Los Manantiales, Río Tancuilín, 21° 20' 45.5" N, 98° 51' 45.8" W, 113 m, 07-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1530 (24♂, 21♀ UMC); Mpio. San Vicente Tancuayalab, Ejido El Álamo, Río Moctezuma, 21° 43' 10.9" N, 98° 33' 16.7" W,

32 m, 10-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1540 (17♂, 16♀ UMC); Mpio. Tamazunchale, Vega Larga, 21º 15' 27.3" N, 98º 50' 36.8" W, 161m, 17-Jul-2011, DRV coll., L-1310 (1♂, 1♀ UMC); Mpio. Tamazunchale, Tamazunchale, Río Moctezuma, 21° 15' 27.6" N, 98° 48' 20.6" W, 128 m, 07-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1529 (3♂, 2♀ UMC); Mpio. Tamazunchale, Zacatipan, Río Amajac, ca. 2 km SE of Tamazunchale, 21° 14' 38.1" N, 98° 46' 19.7" W, 111 m, 07-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1528 (2♂, 1♀ UMC); Mpio. Xilitla, ca. 1 km E of Xilitla, unnamed creek from Las Pozas, 21° 23' 30.6" N, 98° 59' 23.3" W, 534 m, 08-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1531 (1♂ UMC); [Mpio. Xilitla], Xilitla, 600 msnm, 24-Jul-1998, R. Novelo col. (1♂ IEXA); Puente Palitla [Palictla], 28-Junio-1990, R. Novelo col. (2♂, 1♀ IEXA); 34 Km antes Tamazunchale, 20-V-78, J. Bueno / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♂, 1♀ CNIN).

SINALOA: Mpio. Concordia, Chupaderos, Río Pánuco, 23° 21' 49.2" N, 105° 57' 10.3" W, 244 m, 30-Jun-2013, DRV & PRH colls., L-1597 (2♂, 2♀ UMC); [Mpio. Concordia], Río Pánuco, 38 mi E Mazatlan, Sin. Mex. VIII-28-52, J. D. Lattin / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂, CAS); [Mpio. Culiacán], Los Mayos, 24 July 1952, John D. Lattin, Cal. Acad. Sci. Coll. / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (2♂, CAS); [Mpio. El Fuerte], El Fuerte, Río Fuerte, 26º 24' N, 108º 37' W, April 2002, W. Trimble (2♂, 1♀ UMC); Mpio. Elota, Pte. Los Barriles, Arroyo El Japuino, 24° 03' 36.7" N, 106° 48' 03.6" W, 83 m, 22-Dec-2013, DRV & PRH colls., L-1670 (27♂, 29♀ UMC); Mpio. Elota, Pte. Río Elota, Río Elota, 23° 57' 20.7" N, 106° 42' 53.4" W, 46 m, 22-Dec-2013, DRV & PRH colls., L-1669 (27♂, 28♀ UMC); [Mpio. Mazatlán], Mazatlán, Mex., V-25-26-1934

/ H. E. Hinton (1♀ EMEC); same but / *Ambrysus pygmaeus* La Rivers PARATYPE (1♀ EMEC); Mpio. Mazatlán, Siqueiros, Siqueiros (Dam), Río Presidio, 23° 20' 47.0" N, 106° 14' 35.3" W, 42 m, 21-Dec-2013, DRV & PRH colls., L-1664 (4♂, 4♀ UMC); Mpio. Mazatlán, Villa Unión, Pte. Presidio, Río Presidio, 23° 11' 32.3" N, 106° 13' 26.3" W, 10 m, 01-Jul-2013, DRV & PRH colls., L-1598 (10♂, 10♀ UMC); Mpio. Mocorito, Mocorito, Río Evora, 25° 28' 55.1" N, 107° 54' 37.6" W, 75 m, 23-Dec-2013, DRV & PRH colls., L-1674 (12♂, 13♀ UMC); Mpio. Rosario, Matatán, 16 km W of El Rosario, Río Los Cedros, 23° 01' 54.1" N, 105° 43' 52.0" W, 55 m, 21-Dec-2013, DRV & PRH colls., L-1663 (3♂ UMC); Mpio. San Ignacio, San Ignacio, Río Piaxtla, 23° 56' 06.3" N, 106° 25' 41.0" W, 127 m, 21-Dec-2013, DRV & PRH colls., L-1666 (1♂ UMC); Mpio. Sinaloa de Leyva, Burague, Río Sinaloa, 25° 49' 25.4" N, 107° 57' 49.4" W, 140 m, 24-Dec-2013, DRV & PRH colls., L-1678 (34♂, 23♀ UMC). **SONORA:** [Mpio. Álamos], Arroyo Cuchujaqui, 7 mi. SE Álamos, Son., Mex., VI-19-63 / J. Doyen Collector (1♀ EMEC); Mpio. Álamos, El Naranjo, Arroyo El Taymuco, 27° 14' 43.3" N, 108° 45' 27.8" W, 462 m, 25-Dec-2013, DRV & PRH colls., L-1682 (5♂, 3♀ UMC); Mpio. Álamos, Taymuco (El Vado), Arroyo La Vinatería, 27° 14' 39.7" N, 108° 43' 17.3" W, 537 m, 25-Dec-2013, DRV & PRH colls., L-1683 (1♂, 2♀ UMC); [Mpio. Álamos], 8 mi S Álamos, 12 Sept 79 / Arroyo Cucyacho in River, C. Y. Kitayama (1♂, 3♀ EMEC); Mpio. Onavas, Tepoca, Arroyo Tepoca, 28° 25' 50.3" N, 109° 15' 26.0" W, 564 m, 27-Dec-2013, DRV & PRH colls., L-1691 (25♂, 9♀ UMC); Mpio. Quiriego, Tepahui, 27° 23' 27.3" N, 109° 11' 03.6" W, 137 m, 26-Dec-2013, DRV & PRH colls., L-1687 (1♀ UMC); Mpio. Rosario de Tesopaco, Nuri, Arroyo Nuri, 28° 06' 39.0" N, 109° 19' 15.5" W, 357 m, 27-Dec-2013, DRV & PRH colls., L-1688 (7♂, 15♀ UMC); Mpio. Rosario de Tesopaco, ca.

6 km N of Nuri, Arroyo Cajón de Amador, 28° 09' 50.0" N, 109° 19' 37.7" W, 324 m, 27-Dec-2013, DRV & PRH colls., L-1689 (11♂, 13♀ UMC); Mpio. Soyopa, ca. 15 km E of Barranca, Río Yaqui, 28° 34' 21.2" N, 109° 33' 11.6" W, 173 m, 27-Dec-2013, DRV & PRH colls., L-1690 (1♀ UMC); 10 miles so[uth] Alamos, VI 13 1961 / F. D. Parker (1♂, 2♀ UCDC). **TABASCO:** Mpio. Tlacotalpa, [Tapijulapa], Río de la Sierra, 29/III/1998, 17º 28' 04" N, 92º 46' 52" W, J. Bueno. R. Barba (2♂, 2♀ CNIN). **TAMAULIPAS:** Mpio. Aldama, Las Nubes, Pte. San Rafael, 23° 09' 56.4" N, 97° 57' 14.2" W, 37m, 23-May-2014, DRV & PRH colls., L-1789 (1♂, 1♀ UMC); Mpio. Güemes, ca. 6 km W of Estación Santa Engracia, Río Corona, 24° 00' 31.4" N, 99° 10' 04.1" W, 216m, 21-May-2014, DRV & PRH colls., L-1782 (5♂, 11♀ UMC); Mpio. Güemes, La Gloria, Río Corona, 24° 00' 30.5" N, 99° 09' 24.0" W, 214m, 21-May-2014, DRV & PRH colls., L-1781 (17♂, 6♀ UMC); Mpio. Juamave [Jaumave], Los Nogales, 2-xi-99, R. Jones, matorral (1♀ UAQE); Mpio. Padilla, El Barretal, Pte. Purificación Poniente, Río Purificación, 24° 04' 43.4" N, 99° 07' 23.9" W, 194m, 21-May-2014, DRV & PRH colls., L-1779 (12♂, 7♀ UMC); Mpio. Padilla, El Barretal, Río Purificación, 24° 04' 40.5" N, 99° 08' 31.3" W, 205m, 21-May-2014, DRV & PRH colls., L-1780 (9♂, 7♀ UMC); Mpio. San Fernando, Las Norias, Arroyo Chorreras, 24° 36' 30.0" N, 98° 17' 54.6" W, 70m, 21-May-2014, DRV & PRH colls., L-1777 (36♂, 40♀ UMC); 15 km N of C. Victoria, 18 March 1983, coll. M. S. Davis (1♂, UMC). **VERACRUZ:** La Palma, 6/V/81, G. Ortega L. (1♂, CNIN); same but / *A. c. circumcinctus* Montandon det. R. W. Sites (1♀ CNIN); Las Palmas, 13-V-83, G. Ortega / *Ambrysus hybridus* det. M. G. Ortega / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♂, 1♀ CNIN); Las Palmas, 13-V-83, G. Ortega / *Ambrysus hybridus* det. M. G. Ortega / *A. c.*

circumcinctus Montandon det. R. W. Sites (1♂ CNIN); same but 18-V-83 (1♂ CNIN); Los Tuxtlas, La Palma, 13-V-83 G. Ortega L. / *Ambrysus hybridus* M. G. Ortega / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♀ CNIN); [Mpio. Atzalán], Tomata, Pte. Tomata, Río Alseseca, 06-Abril-2011, V. Amaya col. (1♀ IEXA); Mpio. Atzalán, Pte. Tomata, Río Alseseca, 19º 55.335' N, 97º 13.385' W, 500 m, 6-Apr-2011, Sites, Shepard, Amaya, Novelo colls., gravel riffles, L-1296 (2♀ UMC): Mpio. Atzalán, Pte. Tomata, Río Alseseca, 19° 55' 15.7" N, 97° 13' 28.2" W, 514 m, 13-Jun-2013, DRV, Sites, Shepard, Novelo & PRH colls., L-1549 (6♂, 2♀ UMC); [Mpio. Atzalán], W of Tlapacoyan, El Filo, Río Filobobos, 08-Noviembre-2009, R. Novelo col., *Ambrysus circumcinctus* R. Novelo det. (33♂, 50♀ IEXA); Mpio. Catemaco, Arroyo a 3 km Margaritas, 11-V-2012, J. L. Villalobos (3♂, 1♀ CNIN); [Mpio. Chicontepec], Chicontepec, 14-IV-75, H. Brailovsky / *Ambrysus circumcinctus* Montandon (Ira La Rivers) (1♂ CNIN); Mpio. Citlaltepec, Citlaltepec, 21°19' 47.7" N, 97° 53' 00.1" W, 194 m, 11-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1544 (2♂, 1♀ UMC); Mpio. Coatepec, Agua Alegre, Río Huehueyapan, 18º [19º] 26.884' N, 96° 58.867' W, 1198 m, 4 IV 2011 / William D. Shepard leg., L-1290 (2♂ UMC); [Mpio. Coatepec], Coatepec, Río Huehueyapan, 04-Abr-2011, R. Novelo Col. (1♀ IEXA); [Mpio. Coscomatepec], Coscomatepec, 29-I-84, L. Becerra (1♀ CNIN); [Mpio. Huatusco]: Huatusco, Río Jamapa (rápidos), 16-Agosto-1986, M. Calvillo Col. (1♀ IEXA); Mpio. Ixhuatlán de Madero, Naranjo Dulce, Río Vinazco, 20° 49' 24.9" N, 97° 55' 19.2" W, 86m, 27-May-2014, DRV & PRH colls., L-1798 (3♀ UMC); [Mpio. Jamapa], Jamapa, 1200 mts, 1-V-1954, C. Bolivar (2♀ CNIN); same but / *A. c. circumcinctus* Montandon det. R. W. Sites (1♂ CNIN); Mpio. Misantla, Libertad, Río Kilate, 20º 03' 06.2" N, 96º 58' 39.4" W, 61

m, 14-Jun-2013, DRV, Sites, Shepard, Novelo & PRH colls., L-1552 (47♂, 47♀ UMC); Mpio. Misantla, Pte. Chapachapa, Río Chapachapa, 19° 58' 12.5" N, 96° 53' 07.6" W, 121m, 14-Jun-2013, DRV, Sites, Shepard, Novelo & PRH colls., L-1554 (1♂, 5♀ UMC); Mpio. Paso de Ovejas, Paso de Ovejas, 19° 17' 04.1" N, 96° 26' 03.7" W, 40m, 29-May-2014, DRV & PRH colls., L-1802 (1♀ UMC); Mpio. Puente Nacional, Puente Nacional, Pte. Puente Nacional I, Río La Antigua, 19° 19' 28.5" N, 96° 28' 54.3" W, 67m, 29-May-2014, DRV & PRH colls., L-1801 (1♂, 1♀ UMC); [Mpio. San Andrés Tuxtla], Est. Biol. Los Tuxtlas, 20-I-86, col. F. Arias & C. Mayorga (3♂, 3♀ CNIN); [Mpio. San Andrés Tuxtla], Estación de Biología Los Tuxtlas, 28-IV-1991, G. Ortega, C. Mayorga / *A. c. circumcinctus* Montandon det. R. W. Sites (1♂, 1♀ CNIN); [Mpio. San Andrés Tuxtla], Los Tuxtlas, El Salto de Eyipantla, 6-5-81, M. García, (1♀ CNIN); same locality information but R. Novelo / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♂ CNIN); same locality information but R. Arce (1♂ CNIN); same but / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♀ CNIN); [Mpio. San Andrés Tuxtla], Los Tuxtlas, L[aguna] Escondida, 5-XII-75, J. Bueno / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] / *Ambrysus circumcinctus caliginosus* Usinger det. R. Sites 2009 (1♀ CNIN); [Mpio. San Andrés Tuxtla], Tuxtlas, L[aguna] Escondida, 8-XII-75, J. Bueno (1♀ CNIN); same but / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♂ CNIN); [Mpio. San Andrés Tuxtla], Los Tuxtlas, Río La Palma, Ver., 7-V-81, R. Novelo / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♀ CNIN); same locality information but 02-Abril-2011, R. Novelo col. (3♂ IEXA); [Mpio. San Andrés Tuxtla], Los Tuxtlas, Río Máquinas, 14-[VII or VIII, unclear]-79, J. Bueno / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus

19[??] (2♂ CNIN); [Mpio. San Andrés Tuxtla], Los Tuxtlas, Río Máquinas, 5-V-81, R. Novelo (1♂ CNIN); same locality information but 5-5-81, M. García (2♀ CNIN); [Mpio. San Andrés Tuxtla], Los Tuxtlas, Río Máquinas, 11-V-81, Herández / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♀ CNIN); [Mpio. San Andrés Tuxtla], Los Tuxtlas, Río Máquinas, 12-5-83, G. Ortega / *Ambrysus hybridus* det. G. Ortega (1♀ CNIN); [Mpio. San Andrés Tuxtla], Los Tuxtlas, Río Máquinas, 02-Abril-2011, R. Novelo col. (2♂, 2♀ IEXA); Mpio. Sta. Maria, E of Ixcatepec, 21° 17' 25.8" N, 97° 54' 56.8" W, 223 m, 11-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1543 (4♂, 7♀ UMC); Mpio. Tantoyuca, N of Platon Sánchez, El Remanzo, Río Calabazo, 21° 17' 08.2" N, 98° 22' 38.6" W, 41 m, 06-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1524 (6♂, 6♀ UMC); [Mpio.] Tlapacoyan, El Encanto, Río Filobobos, 104 msnm, 8-XI-2009, 19º 59' 01" N, 97º 10' 08" W, L. Cervantes, R. Sites, R. Novelo (1♂, 1♀ CNIN); [Mpio.] Tlapacoyan, El Encanto, Río Filobobos, 08-Nov-2009, R. Novelo col. (4♂, 11♀ IEXA); [Mpio.] Tlapacoyan, Ixtacuaco, 30-Marzo-2003, R. Novelo col. (1♀, IEXA); Mpio. Tlapacoyan, Río Bobos, 19º 55' 39.8" N, 97º 09' 45.5" W, 281 m, 14-Jun-2013, DRV, Sites, Shepard, Novelo & PRH colls., L-1551 (97♂, 121♀ UMC); Mpio. Tlapacoyan, Río Filobobos, El Encanto, 8 November 2009, L-1123 / 19º 59.022' N, 97º 10.149' W, 178 m, Sites, Cervantes, Novelo (1♂ UMC); Mpio. Tlapacoyan, Río Filobobos, 19º 55.662' N, 97º 09.764' W, 267 m, 8 Nov 2009, Sites, Cervantes, Novelo colls., L-1124 (16♂, 34♀ UMC); Mpio. Tlapacoyan, Rojo Gómez, Río Filobobos, 20° 02' 41.7" N, 97° 05' 38.5" W, 89 m, 12-Jun-2013, DRV, Sites, Shepard & PRH colls., L-1548 (11♂, 8♀ UMC); [Mpio.] Tlapacoyan, Ruinas El Cuajilote (Filobobos) 08-Nov-2009, R. Novelo col. (5♂, 2♀ IEXA); [Mpio. Tlapacoyan], Tlapacoyan, El Muro (arroyo) 900 msnm, 13-Apr-2004,

R. Novelo col. (1♂ IEXA); [Mpio. Tlapacoyan], Tlapacoyan, Río Tomata, 25/V/1985, J. Bueno, R. Barba (2♀ CNIN); [Mpio. Tlapacoyan], Tlapacoyan, 28-Marzo-1984, H. Velasco col. (1♀ IEXA); [Mpio. Zongolica], Zongolica, 11-VIII-74, J. Bueno (1♂ CNIN); same but / *Ambrysus circumcinctus* Montandon (Ira La Rivers) [det.] (1♂ CNIN); [Mpio. Zongolica], Zongolica, 11-VIII-74, J. Bueno / H. Brailovsky A. det. *Ambrysus circumcinctus* Montandon (1♀ CNIN); San Andrés Tuxtla, 30-VII-76, J. Bueno / *Ambrysus circumcinctus* Montandon det. J.T. Polhemus 19[??] (1♂ CNIN). **ZACATECAS:** [Mpio. Moyahua de Estrada], Moyahua, 13 I 2005, 3610', Río Juchipila / William D. Shepard, leg. (8♂, 7♀ EMEC); [Mpio. Moyahua de Estrada], Río Juchipila at Moyahua, 13 Jan. 2005, C. B. Barr / 21º 16.29' N, 103º 10.33' W, elevation ~ 3850 ft. (1♂, 2♀ EMEC); [Mpio. Moyahua de Estrada], Río Juchipila, 9.1 rd. km S of Moyahua, 13 Jan. 2005, C. B. Barr / 21º 12.63' N, 103º 10.84' W, elevation ~ 3800 ft. (1♂, 2♀ EMEC); [Mpio. Moyahua de Estrada], 9.1 km S Moyahua, 13 I 2005, 3610', Río Juchipila / William D. Shepard, leg. (1♂, 6♀ EMEC).

Ambrysus pygmaeus **La Rivers**
(Figs. 4, 9)

A. pygmaeus La Rivers 1953: Univ. Kans. Sci. Bull. 35: 1289–1290 (original description).

Diagnosis. This species can be distinguished from others in this subgenus based on the shorter AGP that slightly curves to right at approximately 45 degrees and is slightly dilated distally (Fig. 9B). The pseudoparameres are short, subrectangular, and asymmetrical with the left pseudoparamere slightly longer, with posterior margins

straight, posterolateral corners rounded, and scattered fine setae (Fig. 9C). The parameres are symmetrical, longer than wide, with the mesal margin straight, and a row of long setae emanating from the middle of the dorsal surface (Fig. 9D). The ventral surface of the phallosoma is lightly-sclerotized and papillose subapically (Fig. 9E). The lateral margins of the SGP are narrowed subapically, giving it a characteristic bottleneck outline with an inverted V-shaped notch; the notch has two small pointed lobes (Fig. 9F).

Discussion. This species was described based mainly on specimens collected in central Mexico. La Rivers (1951) noticed the prominent bulging eyes on the specimens of the type series and considered this feature diagnostic; however, this character is not particularly different from that exhibited by any other species in this subgenus in Mexico. La Rivers (1951) considered *A. pygmaeus* to be the most distinctive member of the *oblongulus* species complex, which he proposed but did not define. Later La Rivers and Nieser (1972) included four Central and South American species (*A. bifidus, A. oblongulus, A. scolius,* and *A. stali*) in the *oblongulus* species complex, but did not include *A. pygmaeus* as originally proposed (La Rivers 1951, 1953). The taxonomic status of the *oblongulus* species complex recently has been reviewed (Sites & Reynoso-Velasco 2015). *Ambrysus pygmaeus* was included in the subgenus *Syncollus* when the former division *Coalescens* was elevated to subgeneric rank (La Rivers 1965). The color pattern on this species is similar to *A. circumcinctus* with the hemelytra solid dark brown and embolia light yellow anteriorly (Fig. 9A). The small triangular mark at the base of posterior margin of the corium is small and light brown to reddish brown.

Variation. La Rivers considered this a small species ranging from 7.0 to 7.5 mm in length, which is probably why he used *pygmaeus* as the specific epithet. Some specimens

from southern Mexico (Oaxaca) are up to 8.4 mm in length. The small triangular mark at the base of posterior margin of corium is sometimes absent (Fig. 9A). The two small pointed lobes in the notch on the posterior margin of the SGP can be inconspicuous.

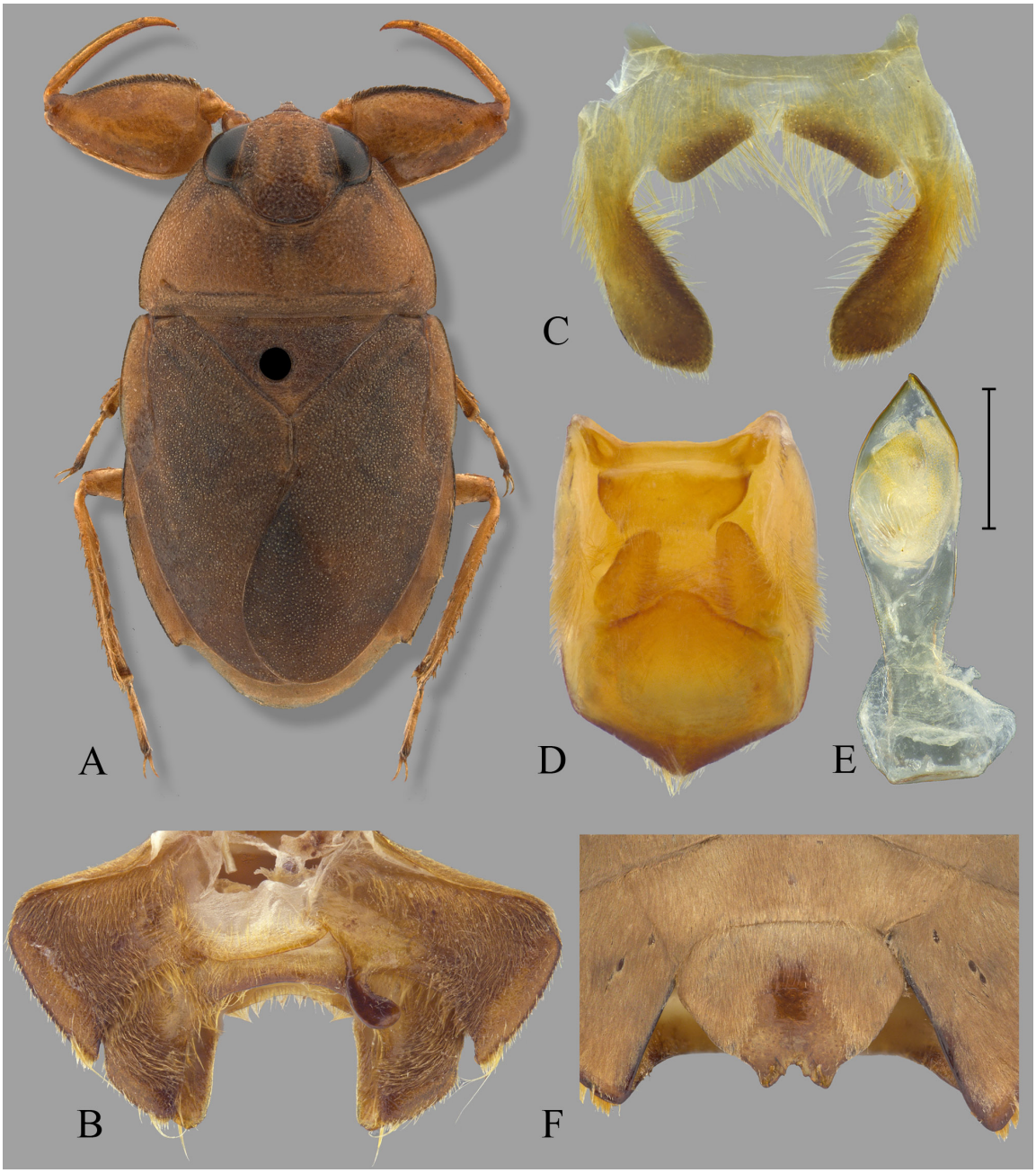

Figure 9. Structures of *Ambrysus pygmaeus*. (A) dorsal habitus of male paratype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal segments removed). Size bar = 0.5 mm and applies only to Figs. D and E.

Type Locality. Mexico: Mexico: Mpio. Temascaltepec, Temascaltepec.

Repository. Holotype is housed at CAS.

Distribution. This species is distributed through the montane areas of the Mexican Transition Zone that includes the Sierra Madre Occidental (Durango), Sierra Madre del Sur (Oaxaca), and Transmexican Volcanic Belt (Mexico) biogeographic provinces. It is also present on the border of the Transmexican Volcanic Belt and the Balsas Basin (Morelos) biogeographic provinces. All the examined specimens were collected at elevations above 1500 meters, except those from Oaxaca (L-1396, L-1397; Fig. 4), which were 711 and 767 m, respectively.

Published Records. Mexico: Mexico (La Rivers, 1953, 1965, 1971)

Type Material Examined. HOLOTYPE ♂: **[MÉXICO: MÉXICO:** Mpio.**]** Temescaltepec [Temascaltepec], Mex. VI-5-33 / H. E. Hinton, R. L. Usinger Collectors / *Ambrysus pygmaeus* La Rivers HOLOTYPE / *Ambrysus pygmaeus* La Rivers determined by Ira La Rivers 1948 / California Academy of Sciences Type No. 10058. PARATYPES: Temescaltepec [Temascaltepec], Mex. VI-5-33 / H. E. Hinton, R. L. Usinger Collectors / *Ambrysus pygmaeus* La Rivers Paratype (2♂, 2♀ EMEC); same but determined by Ira La Rivers '50 (1♂ EMEC); Temescaltepec [Temascaltepec], Mex. VI-5-33 / H. E. Hinton, R. L. Usinger Collectors / *Ambrysus pygmaeus* La Rivers Paratype / 79 [without terminal abdominal segments] (1♂ EMEC); same but 80 [without terminal abdominal segments] (1♂ EMEC). **MORELOS:** Cuernavaca, Mex, 1934 / H. E. Hinton / *Ambrysus pygmaeus* La Rivers PARATYPE (3♂ EMEC; 1♂, 1♀ SEMC)

Material Examined. MÉXICO: DURANGO: La Michilía, Arroyo El Temazcal, 10-Diciembre-1987. R. Novelo col. (4♂, 1♀ UMC); Res. Biósfera de Michilía, Arroyo el

Temascal, 1-VII-1985, 2260 msnm, C. Castillo, P. Reyes (1♂, 2♀ CNIN); Res. Biósfera de Michilía, Est. Piedra Herrada, 1-VII-1985, 2350 msnm, C. Castillo, P. Reyes (1♀ CNIN); same but 2-VII-1985, 2260 msnm (1♀ CNIN). **MÉXICO:** Real de Arriba, Temescaltepec [Temascaltepec], Mex., VI-5-1933 / H. E. Hinton, R. L. Usinger Collectors / *Ambrysus pygmaeus* La Rivers 1953 (Ira La Rivers) (1♂ CNIN). **MORELOS:** Cuernavaca, Mex, 1934 / H. E. Hinton (2♀ EMEC); Cuernavaca, VI-1934 Mex / H. E. Hinton Collector (1♀ EMEC). **OAXACA:** km 72 carr. Putla-Tlaxiaco, 16 km SW of Tlaxiaco, Pte. Los Pinos 17º 11' 11.3" N, 97º 45' 10.6" W, 2083 m, 31-May-2012, DRV & PRH colls., L-1401 (1♀ UMC); Mpio. Putla Villa de Guerrero, Putla de Guerrero, Pte. La Cuchara, 17º 01' 06.7" N, 97º 55' 11.8" W, 711 m, 30-May-2012, DRV & PRH colls., L-1396 (2♂, 2♀ UMC); Mpio. Putla Villa de Guerrero, Pluta de Guerrero, 17º 02' 21.5" N, 97º 54' 42.9" W, 767 m, 30-May-2012, DRV & PRH colls., L-1397 (2♂ UMC); Mpio. Tlaxiaco, km 81 carr. Putla-Tlaxiaco, San Juan del Río [Río de Ocotepec], Río Ocotepec, 17º 10' 27" N, 97º 46' 17.8" W, 1967 m, 31-May-2012, DRV & PRH colls., L-1400 (1♂ UMC).

Ambrysus totonacus Reynoso, Sites, & Novelo NEW SPECIES
(Figs. 4, 10–11)

Description. Brachypterous male. HOLOTYPE, length 7.76; maximum width 4.76. Paratypes (n = 10), length 7.04–8.32 (mean = 7.69); maximum width 4.08–4.88 (mean = 4.45). General shape elongate, parallel-sided; widest across embolia (Fig. 10A). Dorsal coloration of hemelytra dark brown; head, pronotum, and legs yellowish brown. Dorsal surface coarsely punctate. Ventral coloration of head and thorax medium brown, abdomen with dense golden brown pubescence.

Head. Head length 1.52; maximum width 2.08. Mostly yellowish brown with dark brown stripe at midline becoming wider posteriorly, coarsely punctate. Eyes convergent anteriorly, synthlipsis 0.96; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 9% of head length; posterior margin between eyes strongly convex, extending posteriorly 38% of head length. Labrum width 2.1× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.42 beyond labrum not including extruded stylets. Antennal proportions 2:5:10:10, length 0.56, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color yellowish brown; transverse sulcus marking anterior border of transverse band in posterior 1/4; transverse band pale yellow with color extending anteriorly on midline as elongate, pointed marking; ovoid dark brown mark on either side of midline at anterior margin; dark, broad, submarginal band extending from eye to transverse band; lateral margins dark brown, convergent, posterior half convex, anterior half mostly straight, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 3.1× length; length at midline 1.28; maximum width at posterolateral corners 4.0. Prothorax ventrally pruinose throughout; apices of propleura meeting at midline, closely appressed to prosternellum; propleuron brown throughout, medial 2/3 of posterior margin with elongate golden setae. Probasisternum with sharp medial carina and without row of setae lateral to carina. Prosternellum covered by apices of propleura. Scutellum coarsely punctate, triangular,

entirely brown with narrow light brown coloration along margins and midline, width 2.0× length, width 2.68, length 1.32. Hemelytra densely punctate, dark brown, not reaching apex of tergum V, length 5.36 (chord measurement). Clavus with thin, yellow transverse stripe at base, length 4.5× width, length 2.92, width 0.64; claval commissure dark brown, length 0.72. Embolium length 2.28, greatest width 0.54; lateral margin convex, yellow brown in anterior 2/3, becoming darker posteriorly. Oblique suture connecting claval and embolar sutures near bases. Hind wings extending to middle of tergum IV. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments yellowish green. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third, spines generally single proximally becoming small combs of two to five spines distally; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral, ventromedial, dorsolateral, and dorsomedial rows of stout reddish-brown spines; ventromedial rows intermixed with combs of two to six spines. Metatibia with ventrolateral, dorsolateral, and dorsomedial rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb

rows of stout spines near apex of ventral margin, lateral margin without spines at apex to accommodate flexed tarsus. Meso- and metatibiae and metatarsus with long, pale swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.2, tibia 1.88, tarsus 0.40; middle leg, femur 2.2, tibia 1.96, tarsomeres 1–3, 0.24, 0.32, 0.48; hind leg, femur 2.60, tibia 2.88, tarsomeres 1–3, 0.20, 0.52, 0.56.

Abdomen. Dorsally with connexiva III–VIII exposed, each laterotergite brown in anterior half and yellow in posterior half giving checkered appearance (Fig. 10A); lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners. Posterolateral corners of II (visible ventrally) –IV narrowly rounded to right angled and not spinose, V–VII bluntly acute. Accessory genitalic process of tergum VI short, curved to right beyond base at approximately 80 degrees, dilated distally (Fig. 10B). Medial lobes of tergum VIII (pseudoparameres) short, wide, subrectangular, symmetrical, posterior margin straight; posterolateral corners more heavily sclerotized, nearly right-angled, slightly deflexed ventrally (Fig. 10C). Ventrally entirely golden brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VII. Phallosoma elongate, linear, constricted basally, sclerotized dorsally; ventral surface lightly-sclerotized and papillose subapically (Fig. 10E). Parameres symmetrical, longer than wide, mesal margin straight, narrowly rounded anteriorly, row of long dark setae emanating from middle of dorsal surface. Proctiger short, length 0.6× width. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush of elongate

setae on posterior margin (Fig. 10D).

Brachypterous female. Paratypes (n = 10), length 7.84–9.04 (mean = 8.22); maximum width 4.40–5.28 (mean = 4.76). Similar to male in general structure and coloration except as follows: Hemelytra surpassing posterior margin of tergum VI. Mediosternite VII (subgenital plate) width 1.2× length; length at midline 1.02; maximum width 1.30; posterior margin concave; two short, pointed lobes near center of concavity; posterolateral corners rounded, produced posteriorly further than medial lobes (Fig. 10F).

Macropterous male. Unknown.

Macropterous female. Paratype (n = 1), length 8.48; maximum width 4.80. Coloration, setation, pronotum proportions, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for brachypterous female. Otherwise clavus and claval commissure correspondingly longer: Clavus length 6.33× width, length 3.08, width 0.60; claval commissure length 0.80. Hind wings extending to posterior margin of tergum VI.

Variation. The green coloration reported here is seen only in live specimens or specimens that were dry-killed, pinned soon thereafter, and kept in darkness (Fig. 10A). Otherwise, the green coloration appears yellowish brown. Specimens can present the transverse band on the pronotum with pale yellow coloration in the anterior half and brown posteriorly. The posterolateral corners of the subgenital plate can be slightly pointed.

Diagnosis. This species presents a characteristic color pattern on the prothorax with two dark, broad, submarginal bands. The flat and subrectangular shape of the male pseudoparameres is different from that of any other species in this subgenus in Mexico.

Although the subgenital plate is similar to that in some females of *A. circumcinctus*, the pointed central lobes are distinctive for this species.

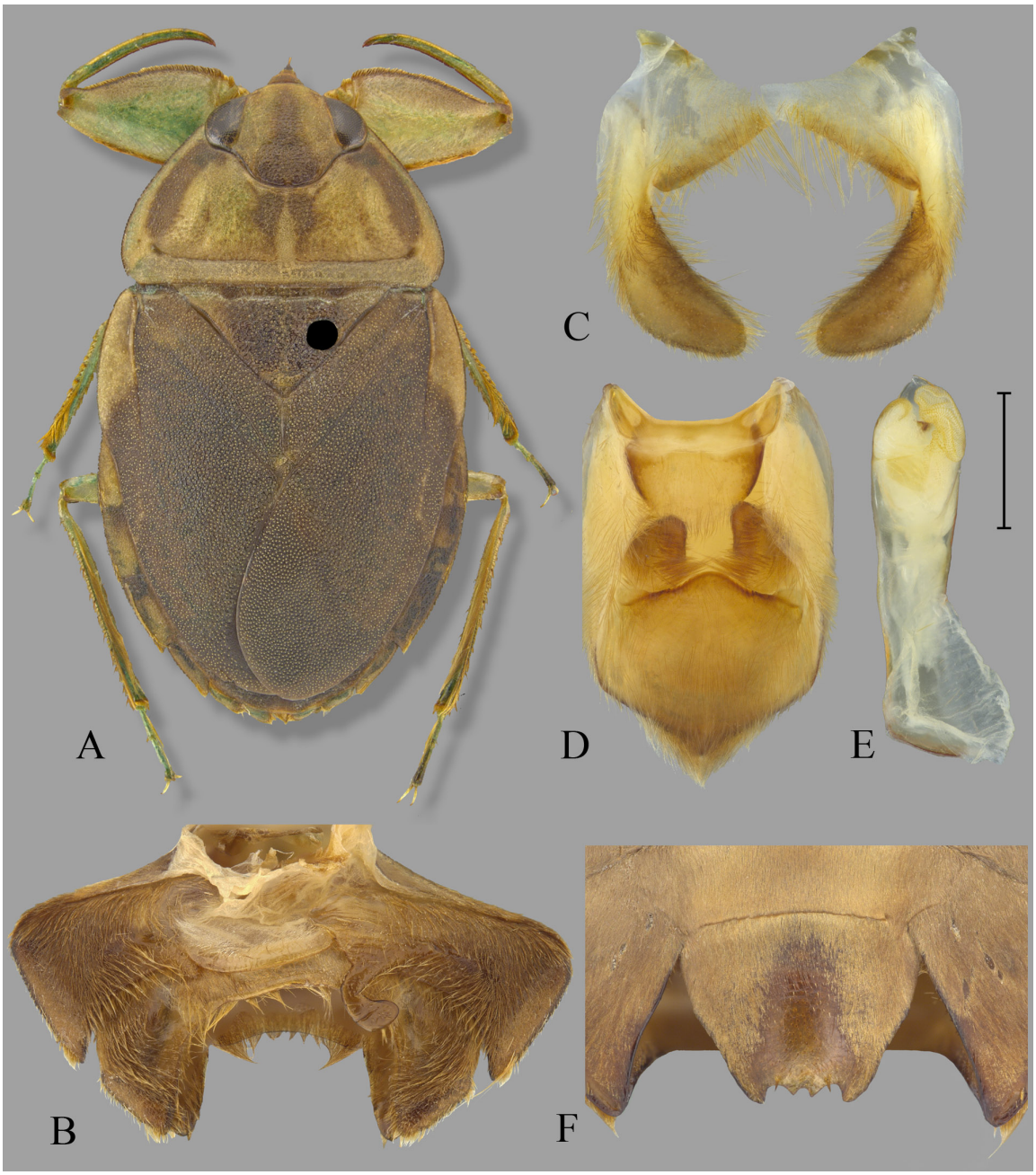

Figure 10. Structures of *Ambrysus totonacus* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal segments removed). Size bar = 0.5 mm and applies only to Figs. D and E.

Habitat Description. Río Tizapam is a small stream that originates on the eastern slopes of the Sierra Madre Oriental (Veracruz). The river is part of the Río La Antigua Basin that drains to the Gulf of Mexico. At the type locality the river is small with boulders and cobbles (Fig. 11). Most of the collecting was conducted in areas with current and among the roots of riparian vegetation.

Figure 11. Type locality of *Ambrysus totonacus* **n. sp.** at Río Tizapam (Veracruz, México).

Distribution. In central Veracruz this species is distributed in rivers of the Río La Antigua Basin, an area that is a transition zone between the Transmexican Volcanic Belt and the Sierra Madre Oriental biogeographic provinces. The northern distribution of the species in the states of Hidalgo and Puebla is on the eastern slopes of the highlands forming the Sierra Madre Oriental biogeographic province (Fig. 4). We found *A. totonacus* and *A. circumcinctus* syntopically in the states of Hidalgo (L-1522) and Veracruz (L-1290, L-1296, L-1549). Also, we found *A. totonacus* and *A. xico* **n. sp.** at the same locality in the state of Veracruz (L-1557).

Etymology. The specific epithet refers to the Totonac culture of the Totonacapan region, which originally included parts of the east-central Mexican states of Hidalgo, Puebla, and

Veracruz, the states where this species occurs.

Repository. The holotype and some paratypes will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the California Academy of Sciences (San Francisco), Colección Entomológica del Instituto de Ecología A.C. (Xalapa), Enns Entomology Museum (University of Missouri), and the United States National Museum of Natural History (Washington D.C.).

Type Material Examined (brachypterous unless otherwise noted). HOLOTYPE ♂. **MÉXICO: VERACRUZ:** Mpio. Xico, [Río Tizapam], 1.86 km SW of Xico, 19° 24' 26.7" N, 97° 00' 53.5" W, 1300 m, 16 June 2013, L-1559 / Sites, Shepard, Novelo, Reynoso-Velasco & Reynoso-Hernández; PARATYPES: same data as holotype (1♂, 2♀). **HIDALGO:** Mpio. Tlanchinol, 3.4 km W of Chalchocotipa, road to Santa Maria Catzotipan, 06 June 2013, L-1522 / west of Hwy 105, km 3+400, 528 m, 21° 02' 36.4" N, 98º 36' 00.8" W, Shepard, Sites, Reynoso-Velasco & Reynoso-Hernández (1♂, 1♀). **PUEBLA:** Cuetzalan, El Cuichat, 870 m, 12-Jul-2007, R. Novelo col. (3♂, 5♀). **VERACRUZ:** Mpio. Coatepec, Agua Alegre, Río Huehueyapan, 4 April 2011, L-1290, colls. R. Sites & V. Amaya / elev. 1198 m, 18° [19º] 26.884' N, 96° 58.867' W (3♂, 6♀); Coatepec, Arroyo Bola de Oro, 7-Nov-2009, R. Novelo col. (7♂, 4♀); Coatepec, Río Huehueyapan, 04-Apr-2011, R. Novelo col. (2♂, 4♀); Coatepec, Consolapa, Río Pixquiac (in riffles), 15-May-2004, R. Novelo col. (2♂, 5♀); Mpio. Atzalán, Pte. Tomata, Río Alseseca, 19° 55' 15.7" N, 97° 13' 28.2" W, 514 m, 13-Jun-2013, L-1549 / rock, gravel, riffles, and marginal veg., Sites, Shepard, Novelo, Reynoso-Hernández & Reynoso-Velasco, colls. (3♀); Mpio. Atzalán, Pte. Tomata, Río Alseseca, 6 April 2011, L-1296 / 500 m, 19° 55.335' N, 97° 13.385' W, Sites, Shepard, Amaya & Novelo colls.

(1♀ macropterous); Mpio. Xico, Arroyo Avestruces, vegetated margin of rocky stream in cattle pasture, 16-Jun-2013, L-1557 / 1401m, 19° 23' 53.8" N, 97° 02' 29.9" W, Sites, Shepard, Novelo, Reynoso-Hernández & Reynoso-Velasco, colls., (3♂, 1♀); Mpio. Xico, Arroyo Avestruces, 1395 m, 29-May-2014, L-1799 / 19° 23' 53.8" N, 97° 02' 29.9" W, Reynoso-Velasco & Reynoso-Hernández (1♀).

Ambrysus xico Reynoso, Sites, & Novelo NEW SPECIES
(Figs. 4, 12–13)

Description. Brachypterous male. HOLOTYPE, length 7.92; maximum width 4.76. Paratypes (n = 2), length 7.92; maximum width 4.32–4.48 (mean = 4.40). General shape elongate, parallel-sided; widest across embolia (Fig. 12A). Dorsal coloration of head, pronotum, and hemelytra dark brown; legs yellowish brown. Dorsal surface coarsely punctate and tuberculate. Ventral coloration of head and thorax medium brown, abdomen with dense golden brown pubescence.

Head. Head length 1.56; maximum width 1.96. Mostly dark brown with yellowish brown stripe on midline posteriorly and on either side of midline between eyes, coarsely punctate and tuberculate. Eyes convergent anteriorly, synthlipsis 1.08; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 10% of head length; posterior margin between eyes strongly convex, extending posteriorly 41% of head length. Labrum width 1.9× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.44 beyond labrum not including extruded stylets. Antennal proportions 3:7:10:7, length 0.54, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate and tuberculate, ground color yellowish brown; transverse sulcus marking anterior border of transverse band in posterior 1/4; transverse band pale yellow with color extending anteriorly on midline as elongate, pointed marking; ovoid dark brown mark on either side of midline at anterior margin; dark, broad, submarginal band extending from eye to transverse band, reaching lateral margin; lateral margins dark brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.8× length; length at midline 1.36; maximum width at posterolateral corners 3.92. Prothorax ventrally pruinose throughout; apices of propleura meeting at midline, closely appressed to prosternellum; propleuron brown throughout, medial 2/3 of posterior margin with elongate golden setae. Probasisternum with sharp median carina, with row of short setae lateral to carina. Prosternellum covered by apices of propleura. Scutellum coarsely punctate and tuberculate, triangular, entirely brown with light brown on corners, width 2.0× length, width 2.48, length 1.22. Hemelytra densely punctate and tuberculate, dark brown, surpassing apex of tergum V, length 5.44 (chord measurement). Clavus with thin, yellow transverse stripe at base, length 4.8× width, length 2.88, width 0.60; claval commissure yellowish brown, length 0.98. Embolium length 2.36, greatest width 0.62; lateral margin convex, light brown in anterior 2/3, becoming darker posteriorly. Oblique suture connecting claval and embolar sutures near bases. Hind wings extending to anterior 1/4 of tergum V. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments brown to yellowish brown. Profemur brown; posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third, spines generally single proximally becoming small combs of two to five spines distally; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral, ventromedial, dorsolateral, and dorsomedial rows of stout reddish-brown spines; ventromedial rows intermixed with combs of two to five spines. Metatibia with ventrolateral, dorsolateral, and dorsomedial rows of stout reddish-brown spines. Meso- and metatibia with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin, lateral margin without spines at apex to accommodate flexed tarsus. Meso- and metatibiae and metatarsi with long, pale swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.12, tibia 1.94, tarsus 0.40; middle leg, femur 2.2, tibia 1.96, tarsomeres 1–3, 0.18, 0.34, 0.44; hind leg, femur 2.56, tibia 2.84, tarsomeres 1–3, 0.20, 0.50, 0.56.

Abdomen. Dorsally with connexiva III–VIII exposed, each laterotergite dark brown in posterior half and light brown in anterior half giving checkered appearance (Fig. 12A); lateral margin finely serrate, marginal row of short yellow setae, group of

trichobothria near posterolateral corners. Posterolateral corners of II (visible ventrally) – IV narrowly rounded to right angled and not spinose, V obtuse and not spinose, VI–VII bluntly acute. Accessory genitalic process of tergum VI short, curved to right at approximately 45 degrees, acuminate distally (Fig. 12B). Medial lobes of tergum VIII (pseudoparameres) long, semirounded, asymmetrical, with left pseudoparamere slightly narrower (Fig. 12C). Ventrally entirely golden brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VII. Phallosoma elongate, linear, constricted basally, sclerotized dorsally; ventral surface lightly-sclerotized and papillose subapically (Fig. 12E). Parameres symmetrical, almost as long as wide, mesal margin straight, narrowly rounded anteriorly, long setae on posterior half. Proctiger short, length 0.6× width. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush of elongate setae on posterior margin (Fig. 12D).

Brachypterous female. Paratypes (n = 3), length 8.48–9.28 (mean = 8.80); maximum width 4.88–5.20 (mean = 4.99). Similar to male in general structure and coloration except as follows: Hemelytra surpassing posterior margin of tergum VI. Mediosternite VII (subgenital plate) width 1.4× length; length at midline 0.88; maximum width 1.30; with medial deep concavity twice as wide as long; posterolateral corners rounded (Fig. 12F).

Macropterous male. Unknown.

Macropterous female. Unknown.

Variation. The small number of specimens (3♂, 3♀) did not allow us to assess variation of the diagnostic features. The holotype was deformed in that the right mesopretarsal

claws were exceedingly small; all other legs and segments were normally developed.

This deformation was not present on the paratypes.

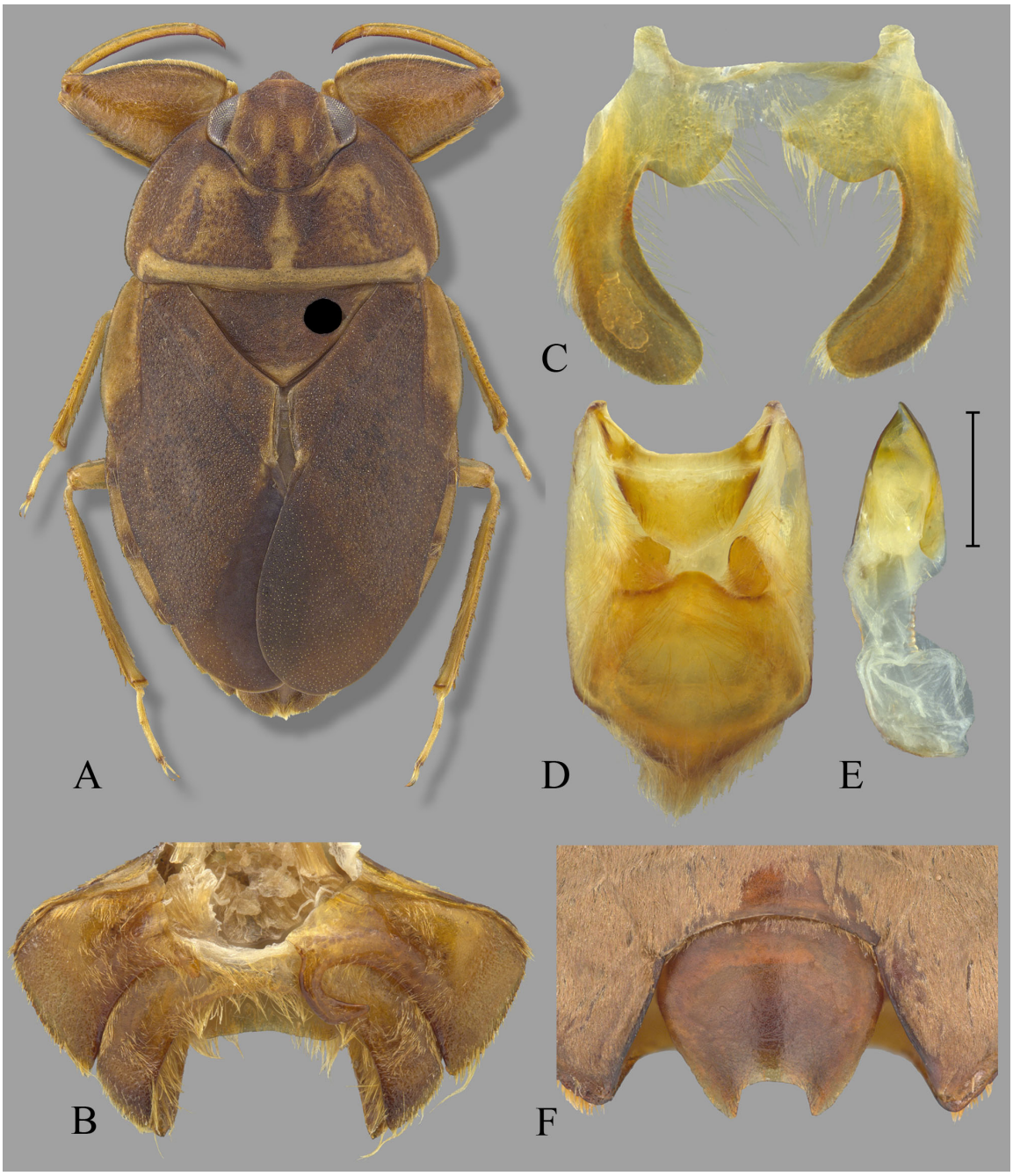

Figure 12. Structures of *Ambrysus xico* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal segments removed). Size bar = 0.5 mm and applies only to Figs. D and E.

Diagnosis. *Ambrysus xico* presents minute, individual tubercles on the head, prothorax, scutellum, and hemelytra not connected by ridges. The other species revised in this study present these tubercles interconnected by sclerotized ridges, resulting in a polygonal pattern. This species has darker coloration when compared with the other Mexican species of *Syncollus*. The dark brown submarginal band on the prothorax is wider and reaches the lateral margins anteriorly. The posterolateral corner of tergum V is not acutely angled as in the other the species, but is rounded and obtuse. The pseudoparameres are asymmetrical with the left pseudoparamere slightly longer and narrower. These pseudoparameres are similar to those of *A. circumcinctus*, although not as constrained medially. The female subgenital plate has a concavity that is exactly twice as wide as long and is similar to that of *A. baeus* although the posterolateral corners of the latter species are narrower.

Habitat Description. The stream at the type locality (Fig. 13) is part of the Río La Antigua basin in the central area of Veracruz state. The stream originates on the eastern slopes of the Cofre de Perote volcano at the eastern limit of the Transmexican Volcanic Belt. This mountain stream is approximately 5 meters wide and has areas with strong current and riffles. Most of our collecting was conducted in those areas, and although species in this subgenus prefer habitats with strong current, *A. xico* was not commonly collected; thus, this species might have other habitat preferences.

Distribution. This species was collected in Veracruz from three mountain streams above 1400 meters elevation in the Río La Antigua Basin in the central part of the state, the transition zone between the Transmexican Volcanic Belt and the Sierra Madre Oriental biogeographic provinces. In the state of Querétaro *A. xico* was collected in a small

stream at 2000 meters elevation. Our extensive collecting suggests that *A. xico* could be endemic to streams at high elevation in the Transmexican Volcanic Belt biogeographic province (Fig. 4). We found *A. xico* and *A. totonacus* **n. sp.** syntopically at L-1557 in the state of Veracruz.

Figure 13. Type locality of *Ambrysus xico* **n. sp.** at Arroyo Piedra Blanca (Veracruz, México).

Etymology. The specific epithet is a noun in apposition and refers to the municipality of Xico, in the central part of Veracruz, where most of the specimens were collected.

Repository. The holotype and one female paratype will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes are deposited in the Enns Entomology Museum (University of Missouri) and the Essig Museum of Entomology Collection (Berkeley).

Type Material Examined. HOLOTYPE ♂. **MÉXICO: VERACRUZ:** Mpio. San Andrés Tlalnehuayocan, 1.16 km NW of Tres Marias, Arroyo Piedra Blanca, 19º 30' 55.6" N, 97º 00' 27.4" W, 15 June 2013, L-1556 / 1602 m, [Arroyo Piedra Blanca] rocky mountain stream, Reynoso-Velasco, Sites, Shepard, Novelo & Reynoso-Hernández, colls. PARATYPES: **QUERÉTARO:** Mpio. Amealco, Puerta de Alegrías, Arroyo las Zúñigas,

8-VII-2000, C. B. Barr / S of Galindo, 20º 20' 28" N, 100º 07' 10" W, elev. 2000 m (1♀ EMEC). **VERACRUZ:** Mpio. Xico, Arroyo Avestruces, vegetated margin of rocky stream in cattle pasture, 16 June 2013, L-1557 / 1401 m, 19º 23' 53.8" N, 97º 02' 29.9" W, Sites, Shepard, Novelo, Reynoso-Hernández & Reynoso-Velasco, colls. (1♂); same locality information but rootmats, 29 May 2014, L-1799, DRV & PRH (1♂); Mpio. Xico, Xico Viejo, 19º 27' 14.10" N, 97º 03' 31.5" W, 1780 m, 30-Ago-1997, R. Arce col. (2♀).

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References Cited

Davis, J. R. 1986. New distributional records of Naucoridae (Hemiptera) from the United States and Mexico, with morphological and taxonomic notes. The Southwestern Naturalist 31: 535–539.

Dinger, E. C., A. E. Cohen, D. A. Hendrickson & J. C. Marks. 2005. Aquatic invertebrates of Cuatro Ciénegas, Coahuila, México: Natives and exotics. The Southwestern Naturalist 50: 237–281.

Espinosa Organista, D., S. Ocegueda Cruz, C. Aguilar Zúñiga, O. Flores Villela & J. Llorente-Bousquets. 2008. El conocimiento biogeográfico de las especies y su regionalización natural, pp. 33–65. *In*: Capital natural de México, vol. I: Conocimiento actual de la biodiversidad. CONABIO, México.

Halffter, G., J. Llorente-Bousquets & J. J. Morrone. 2008. La perspectiva biogeográfica histórica, pp. 67–86. *In*: Capital natural de México, vol. I: Conocimiento actual de la biodiversidad. CONABIO, Mexico.

Herrera, F. 2013. Estado del conocimiento y catálogo de la familia Naucoridae (Insecta: Heteroptera) en Centroámerica. Dugesiana 20: 221–232.

Hungerford, H. B. 1919. The biology and ecology of aquatic and semiaquatic Hemiptera. The University of Kansas Science Bulletin 21: 1–341.

Kirkaldy, G. W. 1906. List of the genera of the pagiopodous Hemiptera-Heteroptera, with their type species, from 1758 to 1904 (and also of the aquatic and semi-aquatic Trochalopoda). Transactions of the American Entomological Society 32: 117–156, 156a, 156b.

La Rivers, I. 1951. A revision of the genus *Ambrysus* in the United States (Hemiptera: Naucoridae). University of California Publications in Entomology 8: 277–338.

La Rivers, I. 1952. A new subgenus of *Ambrysus* from South America (Hemiptera: Naucoridae). Entomological News 63: 33–39.

La Rivers, I. 1953. The *Ambrysus* of Mexico (Hemiptera, Naucoridae). The University of Kansas Science Bulletin 35: 1279–1349.

La Rivers, I. 1965. The subgenera of the genus *Ambrysus*. Biological Society of Nevada Occasional Papers 4: 1–7.

La Rivers, I. 1967. Descriptions of new bugs. Biological Society of Nevada Occasional Papers 14: 1–8.

La Rivers, I. 1971. Studies of Naucoridae (Hemiptera). Biological Society of Nevada Memoirs 2:1–120.

La Rivers, I. 1974. Catalogue of taxa described in the family Naucoridae (Hemiptera), Supplement No.1: Corrections, emendations and additions, with descriptions of new species. Biological Society of Nevada Occasional Papers 38: 1–17.

La Rivers, I. 1976. Supplement No. 2 to the catalogue of taxa described in the family Naucoridae (Hemiptera) with descriptions of new species. Biological Society of Nevada Occasional Papers 41: 1–17.

La Rivers, I. & N. Nieser. 1972. The *Ambrysus* of Surinam, with the description of a new species, *A. bifidus* (Hemiptera, Naucoridae). Biological Society of Nevada Occasional Papers 29: 1–8.

Lee, C.E. 1991. Morphological and phylogenetic studies on the true water bugs (Hemiptera : Heteroptera). Nature & Life 21: 1–183.

Mayr, E. 1982. Of what use are subspecies? The Auk 99: 593–595.

Mbogho, A. Y. & R. W. Sites. 2013. Naucoridae Leach, 1815 (Hemiptera: Heteroptera) of Tanzania. African Invertebrates 54: 513–542.

Mittermeier, R. A. & C. Mittermeier. 1992. La importancia de la diversidad biológica de México, pp. 63–73. *In*: Sarukhán, J. & R. Dirzo (eds.). México frente a los retos de la biodiversidad, CONABIO, Mexico.

Montandon, A. L. 1897. Hemiptera Cryptocerata. Fam. Naucoridae. Sous-fam. Cryptocricinae. Verhandlungen der kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien 47: 6–23.

Montandon, A. L. 1910. Trois espèces nouvelles de la famille Naucoridae. Bulletin de la Société des Sciences de Bucarest-Roumanie 19: 498–444.

Morrone, J. J. 2005. Hacia una síntesis biogeográfica de México. Revista Mexicana de Biodoversidad 76: 207–252.

Nieser, N., A. Pelli & A. L. de Melo. 1999. Two new Ambrysinae (Heteroptera: Naucoridae) from Minas Gerais, Brazil. Acta Societatis Zoologicae Bohemicae 63: 157–163.

Polhemus, D.A. & J. T. Polhemus. 1988. Family Naucoridae, Leach, 1815: The creeping water bugs, pp. 521-527. *In*: Henry, T. J. & R. C. Froeschner, (eds.), Catalog of Heteroptera, or True Bugs, of Canada and the Continental United States. Brill, Leiden.

Polhemus, J. T. 2008. Aquatic and semiaquatic Hemiptera, pp. 385–423. *In*: Merrit, R. W., K. W. Cummins & M. B. Berg (eds.). An introduction to the aquatic insects of North America. Kendal/Hunt, Dubuque, Iowa, USA.

Polhemus, J. T. & D. A. Polhemus. 1981. Three new species of *Ambrysus* from Mexico (Hemiptera: Naucoridae). The Pan-Pacific Entomologist 57: 397–401.

Polhemus, J. T. & D. A. Polhemus. 1983. Notes on Neotropical Naucoridae II. A new species of *Ambrysus* and review of the genus *Potamocoris* (Hemiptera). The Pan-Pacific Entomologist 58: 326–329.

Polhemus, J. T. & D. A. Polhemus. 2008. Global diversity of true bugs (Heteroptera; Insecta) in fresh water. Hydrobiologia 595: 379–391.

Polhemus, J. T. & R. W. Sites. 1995. The identity of *Pelocoris biimpressus* Montandon and synonymy of *Pelocoris* species in the southwestern United States (Heteroptera Naucoridae). Proceedings of the Entomological Society of Washington 97: 654–658.

Sarukhán, J., P. Koleff, J. Carabias, J. Soberón, R. Dirzo, J. Llorente-Bousquets, G. Halffter, R. González, I. March, A. Mohar, S. Anta & J. de la Maza. 2009. Capital natural de México. Síntesis: conocimiento actual, evaluación y perspectivas de sustentabilidad. CONABIO, Mexico.

Sites, R. W. 2015. New taxa of Cryphocricinae (Heteroptera: Naucoridae) from the Guiana Shield: *Hygropetrocoris* Sites, n. gen. and two new species of *Ambrysus* Stål. Zootaxa 4033: 427–438.

Sites, R. W. & D. Reynoso-Velasco. 2015. Review of the *Ambrysus stali* La Rivers species complex (Heteroptera: Nepomorpha: Naucoridae) with the description of a new species from Mesoamerica. Zootaxa 4018: 279–291.

Sites, R. W., D. Reynoso-Velasco & R. Novelo-Gutiérrez. 2013. Revision of the Mesoamerican genus *Cataractocoris* Usinger (Hemiptera: Heteroptera: Nepomorpha: Naucoridae). Zootaxa 3682: 475–484.

Sites, R. W. & W. D. Shepard. 2015. Neotropical Genera of Naucoridae (Hemiptera: Heteroptera: Nepomorpha): New species of *Ambrysus* and *Procryphocricos* from Belize and Peru. Annals of the Entomological Society of America, 108: 613–620.

Stål, C. 1862. Hemiptera Mexicana enumeravit speciesque novas descripsit (continuatio). Stettiner Entomologische Zeitung 23: 437–462.

Štys, P. & A. Jansson. 1988. Check-list of recent family-group and genus-group names of Nepomorpha (Heteroptera) of the world. Acta Entomologica Fennica 50: 1–44.

Usinger, R. L. 1941. Key to the subfamilies of Naucoridae with a generic synopsis of the new subfamily Ambrysinae (Hemiptera). Annals of the Entomological Society of America 34: 5–16.

Usinger, R. L. 1946. Notes and descriptions of *Ambrysus* Stål with an account of the life history of *Ambrysus mormon* Montd. (Hemiptera, Naucoridae). The University of Kansas Science Bulletin 31: 185–210.

Wilson, E. O. & W. L. Brown Jr. 1953. The subspecies concept and its taxonomic application. Systematic Zoology 2: 97–111.

CHAPTER IV

Revision of the *Ambrysus hybridus* Montandon species complex (Heteroptera: Nepomorpha: Naucoridae) with the description of a new species from Mexico

Abstract

The North American *Ambrysus hybridus* Montandon species complex is revised and includes *A. convexus* Usinger, *A. fuscus* Usinger **stat. rev.**, *A. hybridus* Montandon, *A. lattini* La Rivers, *A. plautus* Polhemus & Polhemus, *A. spiculus* Polhemus & Polhemus, *A. thermarum* La Rivers, and *A. ultimus* La Rivers. *Ambrysus lariversi* **n. sp.** is the ninth species in this complex and is described from Mexico. *A. tridentatus* La Rivers and *A. woodburyi* Usinger are proposed as junior synonyms of *A. hybridus* Montandon. Most of the species in this complex occur only in Mexico, although *A. thermarum* is known only from the United States and *A. hybridus* occurs from the southwestern United States to southern Mexico and has the widest distribution of any species in this complex. Features uniting these species are related to male genitalia and structures associated with the male and female genitalia.

Introduction

The genus *Ambrysus* Stål (Naucoridae: Cryphocricinae: Ambrysini) currently comprises 83 described species and its distribution extends from the northern United States (La Rivers 1951a) south to Argentina (La Rivers 1971). *Ambrysus* currently is represented by five subgenera: *Ambrysus*, *Acyttarus*, *Meloiella*, *Picrops*, and *Syncollus* (La Rivers 1952,

1965; Nieser et al. 1999). Of these, the subgenus *Ambrysus* is the most species-rich with 70 described species.

La Rivers (e.g., 1951a, b; 1953a) made reference to distinct species complexes within the subgenus *Ambrysus*, but in many cases did not provide supporting criteria for membership in the complexes. The genus *Ambrysus* was divided into the *Coalescens* and *Disjunctus* divisions by La Rivers (1951a). The former included species with the propleura closely appressed to the adjacent prosternellum and the latter included species with the propleura detached from the prosternellum. The *Coalescens* division included two species complexes (*oblongulus* and *planus*), whereas the *Disjunctus* division included three species complexes for South American species (*fossatus, fucatus, stali*) and eight complexes (*californicus*, *funebris*, *melanopterus*, *pudicus*, *pulchellus*, *puncticollis*, *signoreti*, *vanduzeei*) for North American species.

La Rivers (1952) described the monotypic subgenus *Picrops* for the South American species *A. usingeri* and placed the remaining species from the *Coalescens* and *Disjunctus* divisions in the subgenus *Ambrysus*. In a later paper, La Rivers (1965) elevated the *Coalescens* division to subgeneric rank as *Syncollus* and included seven species (*A. circumcinctus, A. geayi, A. maldonadus, A. montandoni, A. planus, A. pygmaeus,* and *A. teutonius*), but he did not specified the status of the two species complexes (*oblongulus, planus*) previously considered (La Rivers 1951a) in the *Coalescens* division. In the same study, the 52 species originally placed in the *Disjunctus* division were assigned to the subgenus *Ambrysus* and the monotypic subgenus *Acyttarus* was created for *A. funebris* (La Rivers 1965).

The last subgenus assigned in *Ambrysus* was *Melloiella* (Nieser et al. 1999), which was downgraded from generic status and contained two South American species (*A. lamprus*, *A. truncaticollis*). No species complex was assigned to this subgenus.

In his work on the *Ambrysus* of Mexico, La Rivers (1953a) considered *A. pygmaeus* to be the most distinctive species of the *oblongulus* complex. Later, the *oblongulus* complex was used to include *A. bifidus*, *A. oblongulus*, *A. scolius*, and *A. stali* (La Rivers 1970, La Rivers & Nieser 1972), but no longer included *A. pygmaeus* as was originally proposed (La Rivers 1953a). A recent study (Sites & Reynoso-Velasco 2015) found that the species *A. oblongulus* is not closely related to the other three South American species in this complex as proposed by La Rivers (1970) and La Rivers & Nieser (1972); thus, Sites & Reynoso-Velasco (2015) excluded this species from the group and placed the remaining three species together with *A. tricuspis* and *A. maya* in the denominated *A. ståli* complex.

The *A. hybridus* species complex was first considered to include the four Mexican species *A. hybridus*, *A. lattini*, *A. tridentatus*, and *A. ultimus* as well as *A. woodburyi* from the United States (La Rivers 1976). Later, *A. spiculus* was described (Polhemus & Polhemus 1981) and considered to be related to *A. tridentatus*.

Materials and Methods

This work represents the second contribution in a series of papers from a larger project to clarify the taxonomy of species in genus *Ambrysus* from Mexico (see Chapter I). Unless otherwise noted, all specimens were collected by Daniel Reynoso-Velasco (DRV) and Pedro Reynoso-Hernández (PRH).

Photographs of the localities are available in a Locality Image Database via a link from the internet site of the Enns Entomology Museum, University of Missouri. The holotype was measured for body length and width and major structures, and all measurements are in mm. Body length and width also are given as a mean and range for paratypes. Length of the body is measured from the anterior margin of the head to the posterior margin of the abdomen, and width at the widest point, usually across the embolia. Abdominal segment numbers are expressed as Roman numerals. The male accessory genitalic process of tergum VI in species of *Ambrysus* typically angles to the right at differing degrees. The angle is measured using the basal portion of the process as the axis from which the degree of departure of the distal portion can be measured (Fig. 3B). Images of all species were obtained by use of a Leica MZ16 stereo microscope coupled with the Leica Application Suite V4.4 Extended Depth of Focus module, followed by image preparation with Photoshop CS5 (Adobe Systems Inc., San Jose, California). The margin of the subgenital plate is an important diagnostic character in these species, but it often is difficult to discern because of heavy setation and lack of contrast with terminal segments. Thus, we removed the setae and terminal segments to enable a better view of this feature in the figures. Information given in brackets [ ] here did not appear on the labels or was not provided in publications, but was inferred from available data, or represents corrections to misspellings on the labels, or was provided post hoc by the collector (*A. lariversi* **n. sp.** additional data were provided by Rodolfo Novelo-Gutiérrez). A slash (/) separates data on different labels. Specimens are deposited in the museums corresponding with the following abbreviations.

Museums and Collection Abbreviations

BMNH	The Natural History Museum (London, England)
BYUC	Brigham Young University (Provo, United States)
CAS	California Academy of Sciences (San Francisco, United States)
CNIN	Colección Nacional de Insectos (Mexico City, Mexico)
CSCA	California State Collection of Arthropods (Sacramento, United States)
EMEC	Essig Museum of Entomology Collection (Berkeley, United States)
IEXA	Colección Entomológica del Instituto de Ecología A.C. (Xalapa, Mexico)
LACM	Natural History Museum of Los Angeles County (Los Angeles, United States)
NHMW	Naturhistorisches Museum (Vienna, Austria)
UAQE	Colección Entomológica de la Universidad Autónoma de Querétaro (Juriquilla, Mexico)
UMC	University of Missouri (Columbia, United States)
UMMZ	University of Michigan Museum of Zoology (Ann Arbor, United States)
USNM	United States National Museum of Natural History (Washington D.C., United States)
ZSM	Zoologische Staatssammlung (Munich, Germany)

Systematics

Discussion: The first species of the complex to be described was the Mexican *A. hybrida* (Montandon 1897). Champion (1901) emended the original incorrect termination in the name to *A. hybridus*. La Rivers (1976) first proposed the *A. hybridus* complex when he described *A. lattini* and *A. ultimus* from Mexico and included the previously described

species *A. hybridus*, *A. tridentatus*, and *A. woodburyi*. La Rivers (1976) referred to this species group as either the *hybridus-woodburyi-tridentata-ultimus* species complex or the *woodburyi-tridentata-hybrida-lattini* chain. The relationship among the species was based on the overall similar shape of the male accessory genitalic process of tergum VI and the shape of the posterior margin of the female mediosternite VII, the subgenital plate. Polhemus & Polhemus (1981) described *A. spiculus* from the northern Mexican state of Durango and based on the morphology of the accessory genitalic process and the subgenital plate, they considered this species to be related to *A. tridentatus*, which was described from Puebla (La Rivers 1962). This species group should be referred to as the *A. hybridus* Montandon complex because it was the first species in the complex to be described (Montandon 1897).

The *A. hybridus* complex includes the Mexican species *A. convexus*, *A. fuscus* **stat. rev.**, *A. lariversi* **n. sp.**, *A. lattini*, *A. plautus*, *A. spiculus*, and *A. ultimus* as well as *A. thermarum* from the United States and the widely distributed *A. hybridus*. The species *A. tridentatus* and *A. woodburyi* are proposed as junior synonyms of *A. hybridus*. The species in this complex apparently occur predominantly in streams at high elevations in montane areas of the Mexican Plateau, Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, and the Transmexican Volcanic Belt biogeographic provinces in Mexico, and the southern part of the North American Cordillera in the United States.

Diagnosis: The most reliable unifying features among species in the *A. hybridus* complex include males with the right and left endosomal sclerites acutely tapered (e.g., Fig. 1E), the overall similar shape of the accessory genitalic process of tergum VI (e.g.,

Fig. 1B), and the similar shape of the medial lobes (pseudoparameres) of abdominal tergum VIII (e.g., Fig. 1C). Females of this complex exhibit some degree of variation of a generalized shape of the subgenital plate (e.g., Fig. 1F), although these variations provide the most reliable interspecific diagnostic attributes. A more generalized feature of the complex includes dark brown to reddish brown coloration on head, thorax, and hemelytra (e.g., Fig. 1A).

Key to the species of the *Ambrysus hybridus* species complex

In this species complex, the female subgenital plate (SGP) is the most reliable diagnostic feature for species recognition. The accessory genitalic process (AGP) and pseudoparameres are instructive for males, although these features exhibit sufficient similarity among species in the complex that reliance on them alone can lead to misidentifications. Thus, collectors should endeavor to obtain multiple specimens at a site to maximize the likelihood that females will be represented. The key presented here relies heavily on females; males are included although clear interspecific distinctions sometimes are not possible.

1. Female with posterior margin of mediosternite VII (SGP) without posterolateral corners posteriorly produced, with a broadly rounded central lobe (Fig. 1F). Male accessory genitalic process of tergum VI (AGP) evenly curved to right (Fig. 1B); medial lobes of tergum VIII (pseudoparameres) elongate and taper to a narrow posteromedially produced apical lobe (Fig. 1C)……*Ambrysus convexus* Usinger

1'. Female with posterior margin of SGP with posterolateral corners posteriorly produced and a central lobe (Figs. 3F, 5F, 6F, 8F, 9F, 11F), or posterolateral corners bounding a central concavity (Figs. 7F, 10F). Male AGP curved to right close to the base at 50–90 degree angle, but if evenly curved throughout, then pseudoparameres without posteromedially produced apical lobe (Fig. 6C); pseudoparameres without narrow posteromedially produced apical lobe, although broad lobe possible (Fig. 5C) 2

2. Female with posterior margin of SGP bearing a central concavity without prominent median lobes or notched lobe (Figs. 7F, 10F). Male with AGP curved to right close to the base at approximately 50–60 degree angle (Figs. 7B, 10B); pseudoparameres with broad apical lobe rounded and posterolaterally directed (Figs. 7C, 10C). 3

2'. Female with posterior margin of SGP with pointed posterolateral corners and one median lobe (Figs. 5F, 8F, 9F), two median lobes (Fig. 6F), or notched central lobe (Figs. 3F, 11F). Male with AGP curved to right close to the base at approximately 55–90 degree angle (Figs. 3B, 5B, 6B, 8B, 9B, 11B); pseudoparameres with apical lobe rounded (Figs. 3C, 6C, 11C) or slightly pointed (Figs. 5C, 8C, 9C) 4

3. Female SGP with rounded sublateral lobes; posterior margin with acuminate posterolateral corners bounding a subrectangular concavity; anterior margin of concavity flat or with slight median protuberance (Fig. 7F). Male AGP curved to right close to the base at approximately 60 degree angle (Fig. 7B)... ……..... *Ambrysus lattini* La Rivers

3'. Female SGP without rounded sublateral lobes; posterior margin with rounded posterolateral corners bounding an evenly curved concavity (Fig. 10F). Male AGP curved to right close to the base at approximately 50 degree angle (Fig. 10B)….. ……...*Ambrysus thermarum* La Rivers

4. Female with posterior margin of SGP clearly tetralobate, with paired pointed posterolateral corners and central lobes (Fig. 6F). Male AGP curved to right close to the base at approximately 60 degree angle, then evenly curving to apex (Fig. 6B); pseudoparameres with rounded and posterolaterally directed apical lobe, with medial convexity slightly produced, and mesal margin convex posterior to medial convexity (Fig. 6C).....*Ambrysus lariversi* **n. sp.**

4'. Female with posterior margin of SGP trilobate (Figs. 3F, 5F, 8F, 9F, 11F), but if appearing tetralobate, then single central notched lobe appearing as two lobes (Fig. 3F). Male AGP curved to right close to the base at approximately 55–90 degree angle, at mid-length angled abruptly to right to continue almost perpendicular to the body axis (Figs. 3B, 5B, 8B, 9B) or not curved abruptly to right but straight at mid-length (Fig. 11B).....5

5. Female with posterior margin of SGP with elongate posterolateral corners and central lobe notched (Figs. 3F, 11F). Male AGP curved to right close to the base at approximately 80 or 90 degree angle, at mid-length angled to right to continue almost perpendicular to the body axis (Fig. 3B) or not angled, but straight (Fig. 11B).....6

5'. Female with posterior margin of SGP with short posterolateral corners and central lobe without a notch (Figs. 5F, 8F, 9F); central lobe usually pointed. Male AGP curved to right close to the base at approximately 55–80 degree angle, at mid-length angled abruptly to right to continue almost perpendicular to the body axis (Figs. 5B, 8B, 9B). 7

6. Female with posterior margin of SGP with prominences of notched central lobe approximately as far from each other as each is from posterolateral corner (Fig. 3F). Male AGP curved to right close to the base at approximately 90 degree angle, at mid-length angled abruptly to right to continue almost perpendicular to the body axis (Fig. 3B)..... *Ambrysus fuscus* Usinger **stat. rev.**

6'. Female with posterior margin of SGP with prominences of notched central lobe much closer to each other as each is from posterolateral corner (Fig. 11F). Male AGP curved to right close to the base at approximately 80 degree angle, then continuing almost straight to apex (Fig. 11B…….*Ambrysus ultimus* La Rivers

7. Female with lateral margins of SGP straight, posterior margin with pointed central lobe produced posteriorly ≥ 2× length than posterolateral corners (Fig. 9F). Connexiva with posterolateral corners generally blunt (Fig. 9A). Male AGP curved to right close to the base at approximately 55 degree angle (Fig. 9B); pseudoparameres broadly lanceolate, tapering to a narrowly rounded apex (Fig. 9C)……..…..*Ambrysus spiculus* Polhemus & Polhemus

7'. Female with lateral margins of SGP convex, posterior margin with pointed central lobe and posterolateral corners subequal in length (Figs. 5F, 8F), but if central lobe produced posteriorly beyond posterolateral corners, then central lobe rounded or truncate. Connexiva with posterolateral corners blunt or spinose (Figs. 5A, 8A). Male AGP curved to right close to the base at approximately 65 or 80 degree angle (Figs. 5B, 8B); pseudoparameres with distinct posteromedially produced apex (Figs. 5C, 8C).....8

8. Embolium narrow, barely surpassing lateral margin of abdomen (Fig. 5A). Connexiva with posterolateral corners generally blunt, but if spinose then moderately produced (Fig. 5A). Female with posterior margin of SGP with posterolateral corners and central lobe subequal in length (Fig. 5F), but if central lobe posteriorly produced further than posterolateral corners, then central lobe rounded or truncate. Male AGP curved to right close to the base at approximately 80 degree angle (Fig. 5B)… ……..……....*Ambrysus hybridus* Montandon

8'. Embolium wide, conspicuously surpassing lateral margin of abdomen (Fig. 8A). Connexiva with posterolateral corners spinose and strongly produced (Fig. 8A). Female with posterior margin of SGP with posterolateral corners and central lobe subequal in length (Fig. 8F). Male AGP curved to right close to the base at approximately 65 degree angle (Fig. 8B)…..*Ambrysus plautus* Polhemus & Polhemus

Annotated List of Species

Ambrysus convexus **Usinger**
(Figs. 1, 2)

A. convexus Usinger 1946: Univ. of Kans. Sci. Bull. 31: 196–198 (original description).

A. convexus: La Rivers 1953a, Univ. of Kans. Sci. Bull. 35: 1315–1316 (supplemental description).

Diagnosis. *Ambrysus convexus* can be distinguished from other species in this complex by the posterior margin of the female SGP with rounded, inconspicuous posterolateral corners and a broadly rounded central lobe (Fig. 1F). The male AGP is evenly curved to right (Fig. 1B). The pseudoparameres are elongate and taper to a narrow, posteromedially produced apical lobe. The parameres are rounded (Fig. 1D).

Discussion. This species was described from specimens collected in at least two localities (Real de Arriba, La Cumbre) in the Estado de Mexico (Usinger 1946). Usinger (1946) inaccurately considered this species to be related to *A. dilatus* [species later synonymized under *A. mexicanus* (La Rivers 1974)] based on gross morphological features. Usinger (1946) reported this species was found syntopically with *A. fuscus*. We found this species syntopically with *A. fuscus* in San Andrés de Los Gama (L-1457), near the town of Real de Arriba in the Estado de Mexico.

Variation. The most common condition of the AGP is evenly curved to the right; however, some specimens, including the holotype, presented the AGP angled to the right close to the base at approximately 60 degrees before evenly curving to the apex. A few specimens had the AGP angled to the right at approximately 60 degrees close to the base and angled to the right at mid-length to continue nearly perpendicular to the body axis.

On some females, the central lobe of the posterior margin of the SGP can be slightly pointed.

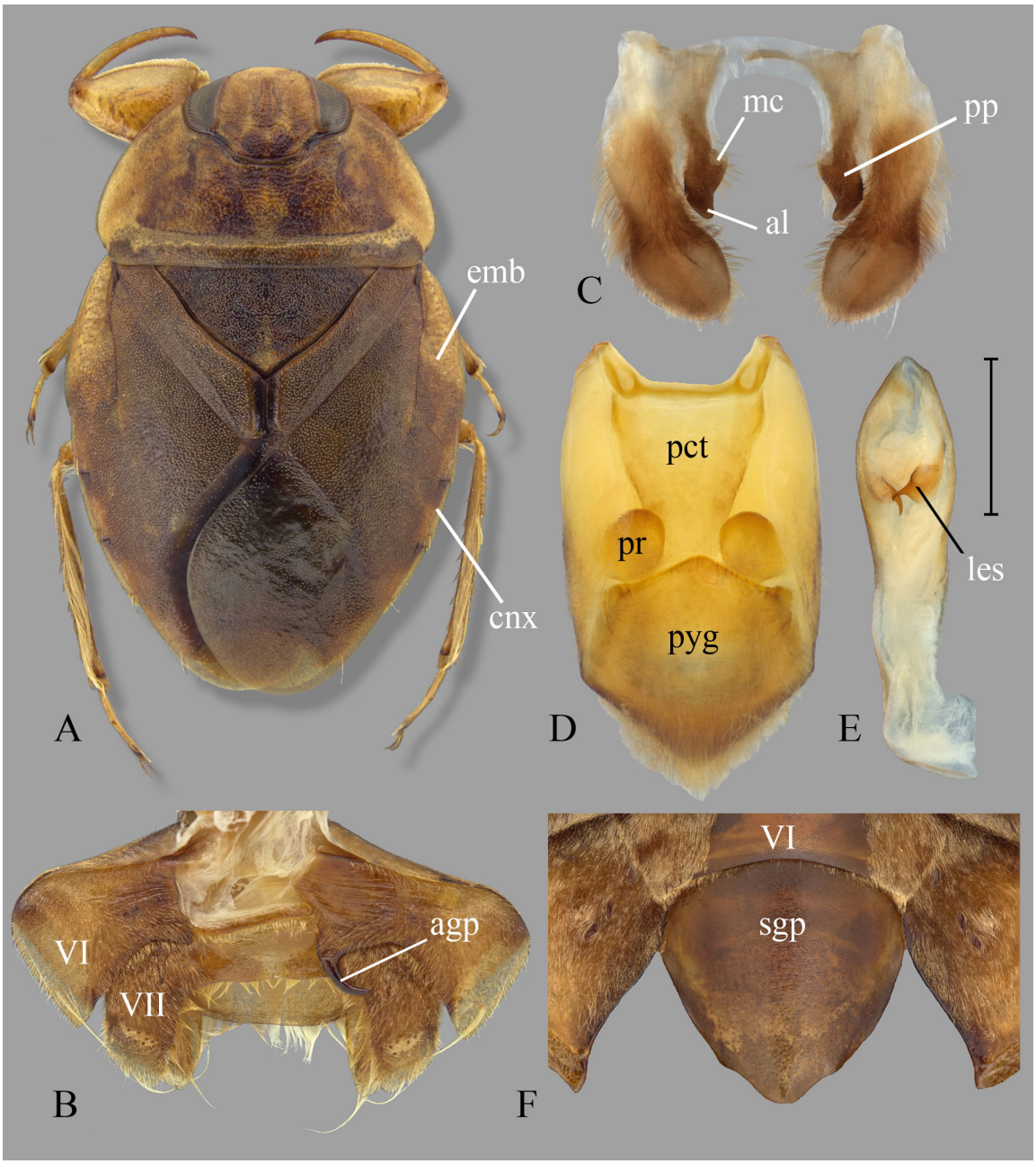

Figure 1. Structures of *Ambrysus convexus*. (A) dorsal habitus of female, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed). agp = accessory genitalic process, al = apical lobe, cnx = connexivum, emb = embolium, les = left endosomal sclerite, mc = medial convexity, pct = proctiger, pp = pseudoparamere, pr = paramere, pyg = pygophore, sgp = subgenital plate.

Type Locality. México: Estado de México: Mpio. Temascaltepec, Real de Arriba.

Repository. Holotype is housed at the CAS.

Distribution. The species has been reported from the type locality in Real de Arriba (Estado de México) and the state of Jalisco. We re-collected it at the type locality and also collected it in the states of Michoacán and Morelos. The collecting localities are in the Transmexican Volcanic Belt biogeographic province, except for that in Morelos, which is in the Balsas Basin biogeographic province (Fig. 2).

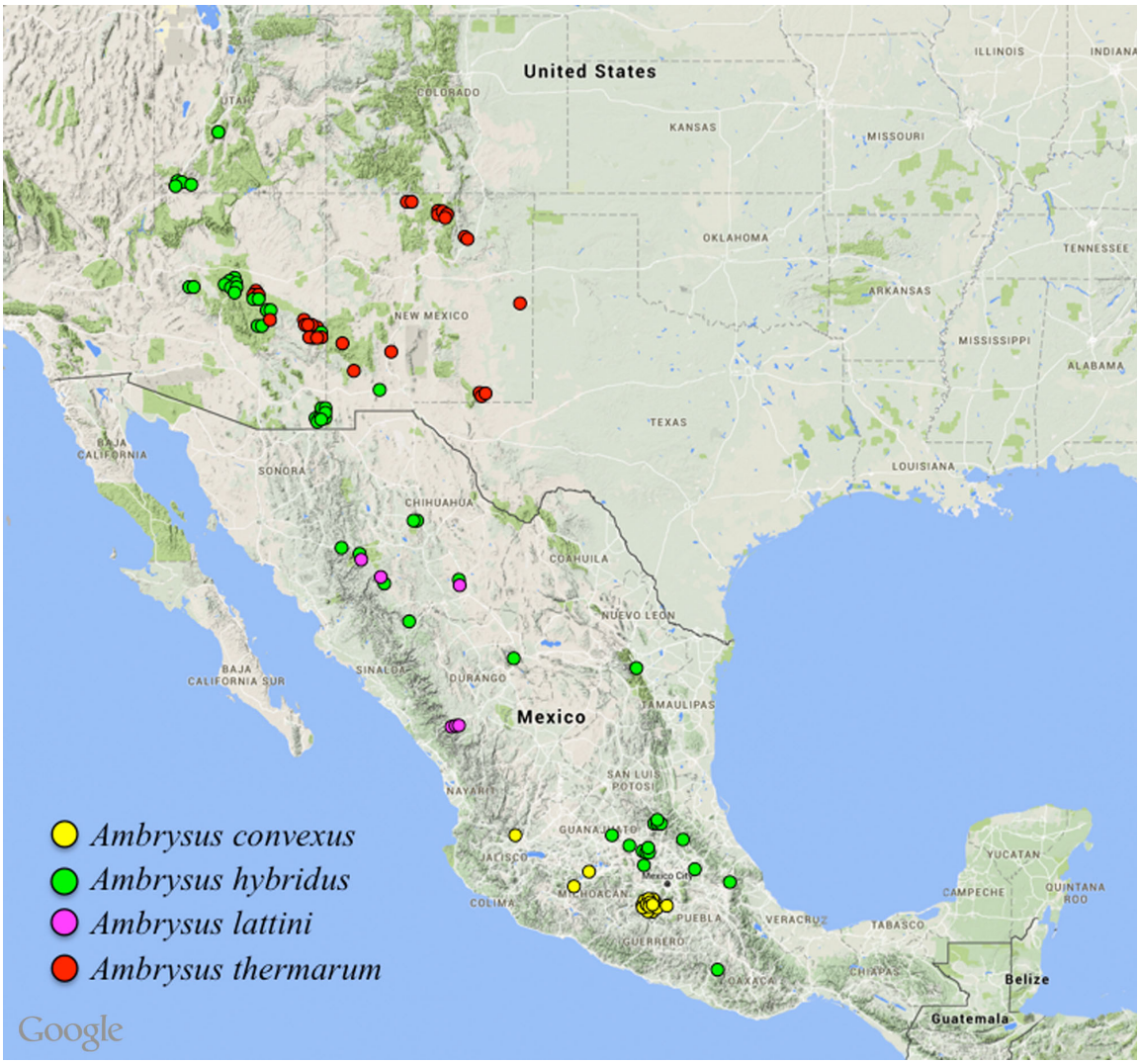

Figure 2. Distribution of *Ambrysus convexus*, *A. hybridus*, *A. lattini*, and *A. thermarum* in North America.

Published Records. México: Estado de México, Jalisco (Usinger 1946; De Carlo 1950; La Rivers 1953a, 1971; Davis 1986).

Type Material Examined. HOLOTYPE ♂: **[MÉXICO: MÉXICO:** Mpio.**]** Temescaltepec [Temascaltepec], Mex. V-25-33 / H. E. Hinton, R. L. Usinger Collectors / HOLOTYPE *Ambrysus convexus* Usinger / California Academy of Sciences Type No. 7161. PARATYPES: Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / ALLOTYPE *Ambrysus convexus* Usinger / Collection of the California Academy of Sciences, San Francisco, California (1♀ CAS); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus convexus* Usinger (1♀ EMEC); same but / 52-54 [without terminal abdominal segments] (3♂ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus convexus* Usinger / Homotype (1♀ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus convexus* Usinger / *Ambrysus convexus* Usinger determined by Ira La Rivers '50 (1♀ EMEC); same but / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (1♂ CAS); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus convexus* Usinger / *Ambrysus convexus* Usinger 1946 (Ira La Rivers) (2♀ EMEC); same but / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (1♀ CAS).

Material Examined. MÉXICO: MÉXICO: Mpio. Temascaltepec, camino a Chilchotla, 23 April 2004, R. Novelo coll. (2♂, 2♀ UMC); Mpio. Temascaltepec, camino

a Chichotla [Chilchotla], 2000 m, 23 April 2004, R. Novelo coll. (1♂, 1♀ UMC; 1♀ IEXA); [Mpio. Temascaltepec] Real de Arriba, Río Puente Colorado, 5 April 2015, L-1908, Sites, Reynoso-Velasco / 1895 m, 19º 2.163' N, 99º 59.650' W, shaded rocky stream (1♂ UMC); Mpio. Temascaltepec, Real de Arriba, [1950 m], 21 April 2004, R. Novelo coll. (3♂, 5♀ UMC; 2♂, 2♀ IEXA); [Mpio. Temascaltepec] Real de Arriba, 21 IV 2004, 6280', Rio Arriba ?? / William D. Shepard leg. (2♀ EMEC); Mpio. Temascaltepec, Real de Arriba, 29 January 2008, R. Novelo coll. (1♂, 2♀ UMC; 1♂, 1♀ IEXA); same but 01 May 2008 (2♂, 3♀ UMC); Mpio. Temascaltepec, San Andrés de Los Gama, Los Jales bridge, 19 Dec. 2012, L-1457 / rd. to Mina del Rincón, 1912 m, 19º 02' 09.6" N, 99º 59' 39.9" W, DRV & PRH colls. (5♂, 3♀ UMC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-21-1933/ R. L. Usinger Collector (1♂ EMEC); same but V-28-29-'33 (9♂, 9♀ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors (3♂, 1♀ EMEC); same but VI-8-1933 (1♂, 4♀ EMEC); same but / creek over the hill [La Cumbre ?], VI-8-33 (1♂ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., VI-21-1933 / R. L. Usinger Collector (21♂, 18♀ EMEC); Temescaltepec [Temascaltepec], Mex., V-28-1933 / H. E. Hinton, R. L. Usinger Collectors (1♀ EMEC); same locality information but VI-1-2-1933 / R. L. Usinger Collector (2♀ EMEC); same but VI-2-1933 (1♀ EMEC); Temescaltepec [Temascaltepec], Mex., VII. [no day] 1934 / H. E. Hinton (4♀ EMEC). **MICHOACÁN: [**Mpio. Ziracuaretiro], Uruapan, Tzirimícuaro II [Zirimícuaro], 1475 m, 6 June 1998, R. Novelo coll. (2♂, 3♀ UMC; 1♀ IEXA); 8000', El Salto, E Morelia, CL751, VI-15-1975, J. T. Polhemus / *Ambrysus convexus* Usinger det. J. T. Polhemus (1♀ USNM); same but / J. T. Polhemus Collection

(1♂ USNM). **MORELOS:** Cuernavaca, Mex., 1934 / H. E. Hinton / *Ambrysus convexus* Usinger 1946 (Ira La Rivers) / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (1♀ CAS).

Ambrysus fuscus **Usinger, stat. rev.**
(Figs. 3–4)

Ambrysus fuscus Usinger 1946: Univ. of Kans. Sci. Bull. 31: 198–199 (original description).

A. fuscus: La Rivers 1953a, Univ. of Kans. Sci. Bull. 35: 1333–1334 (supplemental description).

A. fuscus: La Rivers 1958, Proc. Ent. Soc. Wash. 60: 74 (synonym of *A. hybridus* Montandon).

Diagnosis. This species can be distinguished from the others in the complex by the posterior margin of the female SGP with the posterolateral corners pointed and with a widely notched central lobe, such that the prominences of the notched central lobe are approximately as far from each other as each is from the posterolateral corner (Fig. 3F). Males can be distinguished by the shape of the AGP, which curves to the right close to the base at an approximately 60 degree angle, then at mid-length it angles abruptly to the right to continue almost perpendicular to the body axis (Fig. 3B). The pseudoparameres are relatively short and present a short, truncate, and posterolaterally produced apical lobe. The parameres are longer than wide with a convex mesal margin (Fig. 3D).

Discussion. This species was described (Usinger 1946) from specimens collected in Real

de Arriba in the Estado de Mexico. Usinger considered this species to be related to *A. convexus* and *A. hybridus*; however, he incorrectly related this species to *A. dilatus*.

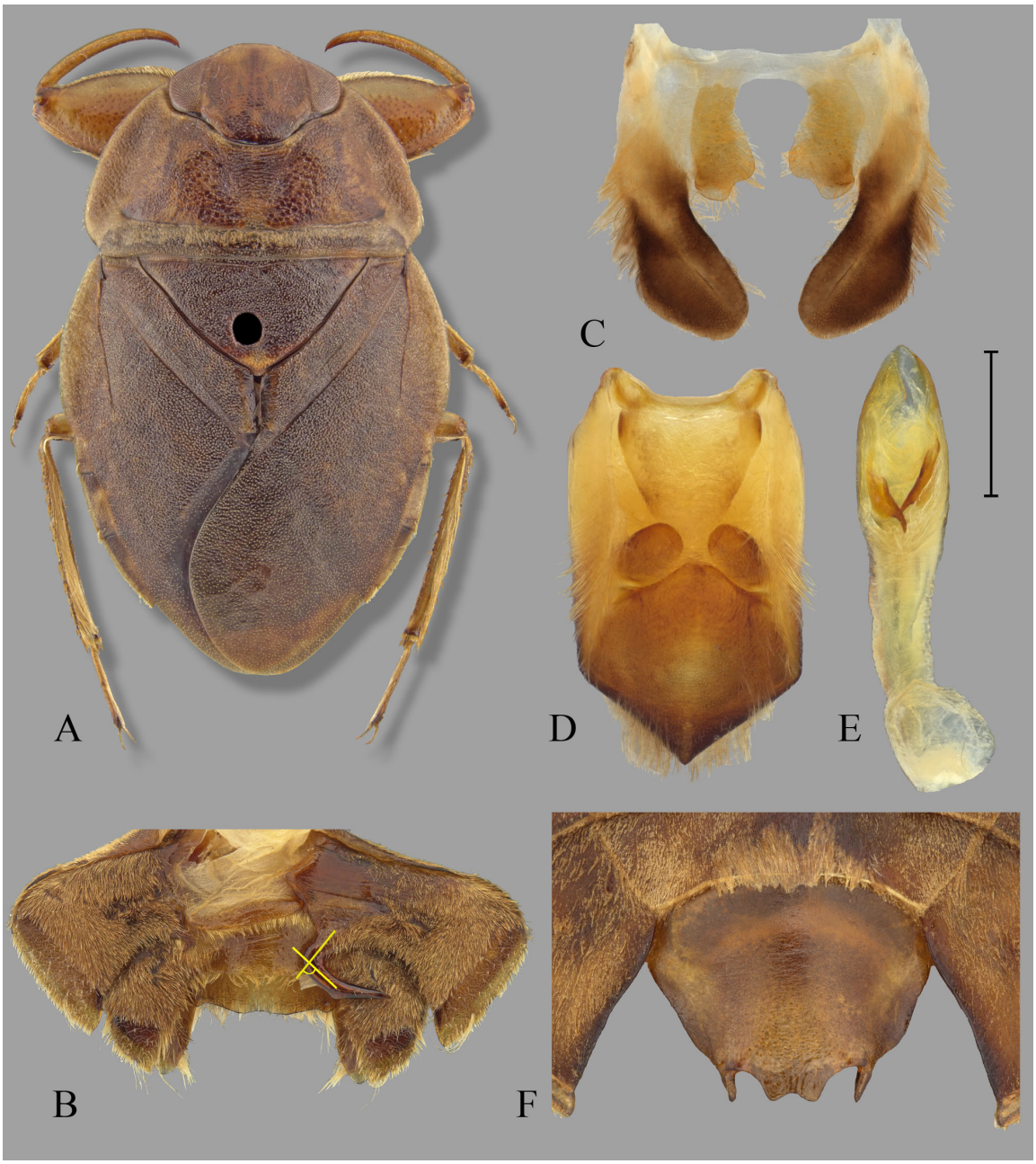

Figure 3. Structures of *Ambrysus fuscus*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, angle of curvature of the agp is determined as indicated by yellow lines, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Based on comparison with a specimen of *A. hybridus* deposited in the NHMW, La Rivers (1958) considered *A. fuscus* to be a junior synonym of *A. hybridus*. After examining the holotypes of both species, it was evident that the shape of the pseudoparameres, which is one of the most important diagnostic features in this genus, is different between *A. fuscus* and *A. hybridus*. Thus, I consider *A. fuscus* to be a valid species as originally proposed by Usinger (1946). This species was reported to occur syntopically with *A. convexus* and was found more commonly in the flume that supplied water to the Rincon mine (Usinger 1946). During our collecting trip, we found this species occupying the same habitat with *A. convexus* in San Andrés de Los Gama (L-1457), near the town of Real de Arriba. This species exhibits a general dark brown coloration (Fig. 3A), which probably is why Usinger (1946) used the specific epithet *fuscus* (from the Latin *fusc,* meaning dark) for this species. When this species is collected together with *A. convexus,* it is difficult to distinguish between them because they have a similar dark brown color, although *A. fuscus* specimens are slightly larger than those of *A. convexus*.

Variation. In some specimens, the central lobe on the posterior margin of the SGP was produced further posteriorly than the posterolateral corners.

Type locality. México: Estado de México: Mpio. Temascaltepec, Real de Arriba.

Repository. Holotype is housed at the CAS.

Distribution. Previously, the species had been reported only from the type locality. This species also has been collected in the state of Morelos. The localities reported here are in the Transmexican Volcanic Belt (Estado de México) and Balsas Basin (Morelos) biogeographic provinces (Fig. 4).

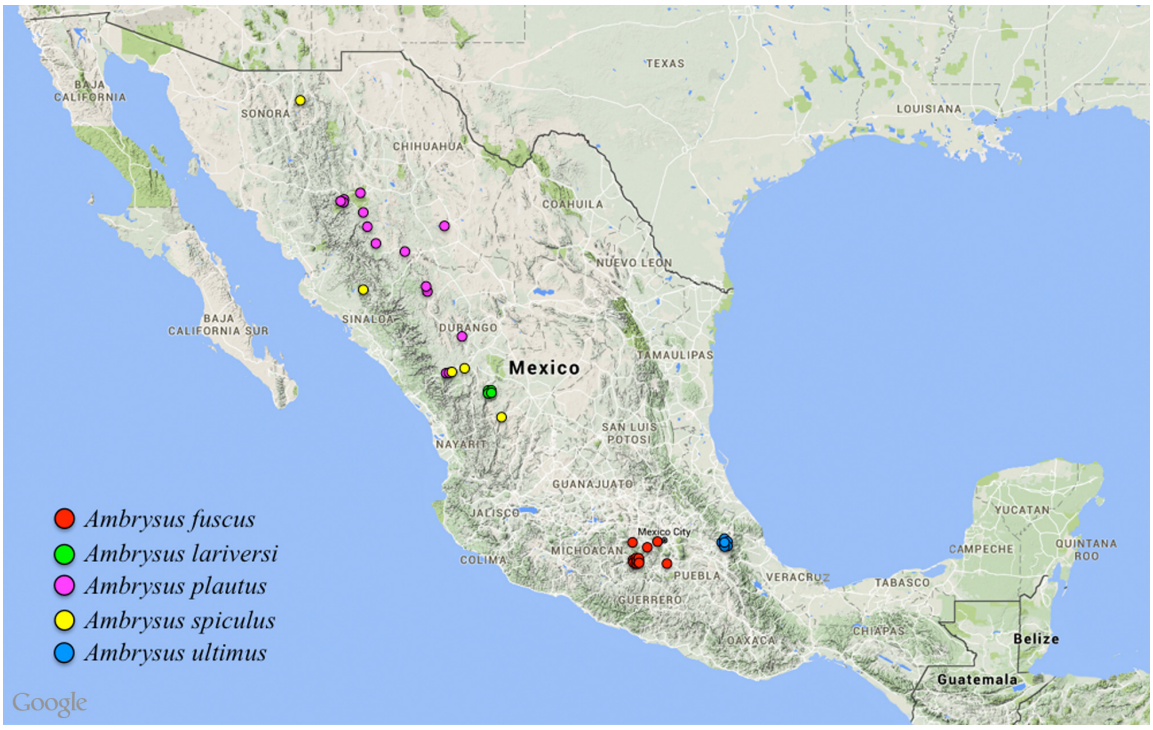

Figure 4. Distribution of *Ambrysus fuscus*, *A. lariversi* **n. sp.**, *A. plautus*, *A. spiculus*, and *A. ultimus* in Mexico.

Published Records. México: Estado de México (Usinger 1946, De Carlo 1950, La Rivers 1953a).

Type Material Examined. HOLOTYPE ♂: **[MÉXICO: MÉXICO:** Mpio.**]** Temescaltepec [Temascaltepec], Mex., VII-10-33 / H. E. Hinton, R. L. Usinger Collectors / HOLOTYPE *Ambrysus fuscus* Usinger / California Academy of Sciences Type No. 7162. PARATYPES: Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., VII-3-33 / H. E. Hinton, R. L. Usinger Collectors / ALLOTYPE *Ambrysus fuscus* Usinger / Collection of the California Academy of Sciences, San Francisco, California (1♀ CAS); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., VII-3-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus fuscus* Usinger (1♂, 2♀ EMEC); same but / 55 [without terminal abdominal segments] (1♂ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., VII-3-33 / H. E. Hinton, R. L.

Usinger Collectors / PARATYPE *Ambrysus fuscus* Usinger / *Ambrysus fuscus* Usinger 1946 (Ira La Rivers) (2♀ EMEC; 1♂ CAS); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., VII-3-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus fuscus* Usinger / *Ambrysus fuscus* Usinger determined by Ira La Rivers '50 (1♂ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., VII-3-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus fuscus* Usinger / HOMOTYPE / *Ambrysus fuscus* Usinger determined by Ira La Rivers '50 / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (1♂ CAS).

Material Examined. MÉXICO: MÉXICO: [Mpio Lerma], Salazar, 26.X.69, P. Reyes (1♀ CNIN); Mpio. Temascaltepec, Real de Arriba, 29 January 2008, R. Novelo Coll. (1♀ UMC); Mpio. Temascaltepec, San Andrés de Los Gama, Los Jales bridge, 19 Dec. 2012, L-1457 / rd. to Mina del Rincón, 19º 02' 09.6" N, 99º 59' 39.9" W, DRV & PRH Colls. (1♂, 1♀ UMC); [Mpio Temascaltepec], Temescaltepec [Temascaltepec], Mex., VII. [no day] 1934 / H. E. Hinton (1♂, 3♀ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., V-28-29-33 / R. L. Usinger Collector (2♂ EMEC); same locality information but VI-4-1933 / H. E. Hinton, R. L. Usinger Collectors (1♂ EMEC); same locality information but VI-9-33 / R. L. Usinger Collector (4♂, 8♀ EMEC); same but / H. E. Hinton, R. L. Usinger Collectors (1♂ EMEC); Real de Arriba, [Mpio.] Temescaltepec [Temascaltepec], Mex., VI-9-33 / Top of hill, Alt. 8000 ft. / H. E. Hinton, R. L. Usinger Collectors / *Ambrysus fuscus* Usinger 1946 (Ira La Rivers) (1♂, 2♀ CAS); 12 miles W. of Villa Victoria, Mexico State, Alt. 2560 met. / Mexico, Mar. 23-1939, Hobart Smith / 383 / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (1♀ CAS); 19 miles E. Toluca, D. F. [México], Mex. XII-8-48 / H. B. Leech Collector /

stop 45 (3♂ CAS); same but / *Ambrysus hybrida* ? (1♀ CAS). **MORELOS:** Xochitepec, 23-VI-73, Halffter [&] Reyes (1♂ CNIN).

***Ambrysus hybridus* Montandon**
(Figs. 2, 5)

Ambrysus hybrida Montandon 1897: Verh. K.-K. Zool.-Bot. Ges. Wien 47: 22 (original description).

A. hybridus: Champion 1901, Biol. Cent.-Amer., Insecta 2: 357 (correction of the original incorrect termination of the specific epithet).

A. tridentata La Rivers 1962: Wasmann J. Biol. 20: 129–133 (original description) (**new synonym**).

A. woodburyi Usinger 1946: Univ. of Kans. Sci. Bull. 31: 194–195 (original description) (**new synonym**).

Diagnosis. This species can be distinguished from the others in the complex by the posterior margin of the SGP with the posterolateral corners and the pointed central lobe subequal in length (Fig. 5F). Males can be distinguished by the shape of the AGP, which curves to the right close to the base at an approximately 80 degree angle, and then at mid-length it angles abruptly to the right to continue almost perpendicular to the body axis (Fig. 5B). The pseudoparameres are elongate and taper to a short, rounded, and posteromedially produced apical lobe (Fig. 5C). The parameres are longer than wide with a slightly convex mesal margin (Fig. 5D).

Discussion. This species was described based on at least two male specimens from Mexico, which were both listed in the original description (Montandon 1897). One of the

specimens was reported to be deposited in the NHMW but is currently housed in the BMNH, and the other specimen was in Montandon's personal collection and is presently housed in the NHMW. Examination of both male specimens revealed that they are not conspecific. The specimen in the BMNH actually is *A. mexicanus*, which is also a Montandon species and was described in the same work in which he described *A. hybridus* (Montandon 1897). It is evident that the description of *A. hybridus* (Montandon 1897) was based only on the specimen currently in the NHMW. Supporting evidence is that in the *A. hybridus* original description, Montandon compared this species with *A. mexicanus*. If he had compared only the specimen of *A. hybridus* presently in the BMNH with specimens from *A. mexicanus*, he would not have found important differences to consider them different species (e.g., length, overall shape). Considering that both specimens were used in the original description of *A. hybridus*, they should be considered syntypes despite the fact that the specimen in the BMNH has Montandon's label with the handwritten word "type." Further, Champion (1901) considered the specimen currently in the NHMW to be the type specimen of *A. hybridus.* To create taxonomic stability, I here designate the male specimen in the NHMW as the lectotype of *A. hybridus*. The specimen in the BMNH originally considered to be *A. hybridus* is not designated as paralectotype, but simply represents a misidentification of *A. mexicanus*.

La Rivers (1962) indicated that *A. tridentatus* could be distinguished from the closely related *A. woodburyi* because in the former the central lobe of the posterior margin of the SGP was longer than the posterolateral corners, whereas in *A. woodburyi* the central lobe and the posterolateral corners were equal in length. La Rivers based many of his species descriptions on few specimens and was not able to assess variation in

the diagnostic features (e.g., shape of the posterior margin of the SGP). *Ambrysus tridentatus* was described based on a small series of 12 specimens and the shape of the posterior margin of the SGP was used as the most important feature to consider this a distinct species.

A generalized shape of the posterior margin of the SGP consists of three pointed lobes (posterolateral corners and central lobe) in females of *A. hybridus, A. tridentatus*, and *A. woodburyi*. Throughout the broad range of the species, there exists slight variation in the length of the posterolateral corners; however, substantial variation exists in the shape and length of the central lobe, especially in specimens from central Mexico. Differences in the shape and length of the central lobe on the posterior margin of the SGP represent intraspecific variation, which is more evident in specimens from Hidalgo (L-1518) and the specimens in the type series of *A. tridentatus*. Comparison of the type specimens of the three species with specimens from museum collections and the extensive material we collected, it is evident that the shape of the male AGP and pseudoparameres, which are two of the most important features to distinguish among species of *Ambrysus*, was consistent among specimens of *A. hybridus*, *A. tridentatus*, and, *A. woodburyi*. Therefore, I propose *A. tridentata* and *A. woodburyi* to be junior synonyms of *A. hybridus*.

Variation. Specimens collected in Hidalgo (L-1518) exhibited a lighter coloration along the clavus and contiguous area of the corium. The spinose posterolateral corners of laterotergites II (visible ventrally) –IV in males and II–V in females generally are not produced, although some specimens presented these corners slightly produced.

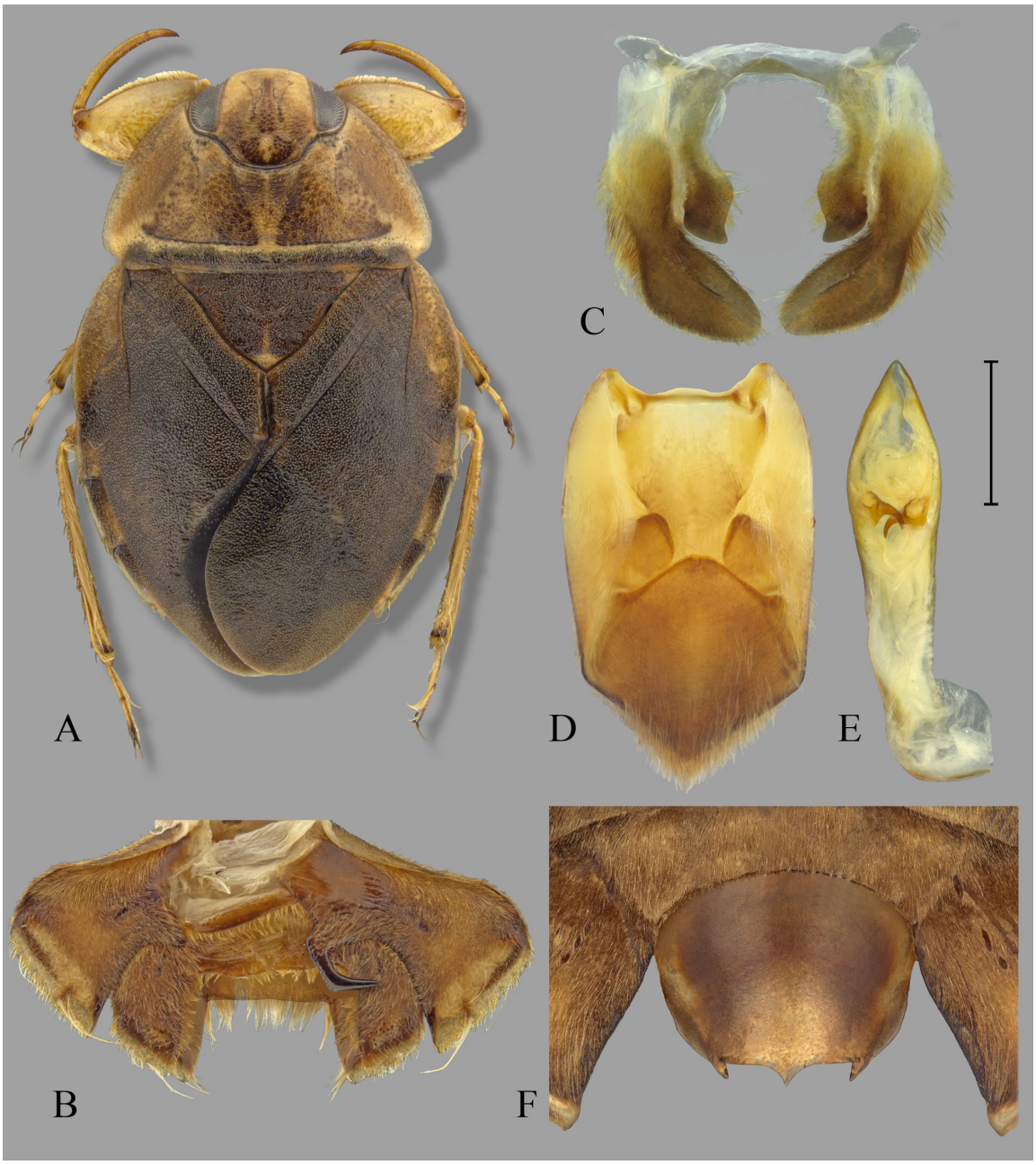

Figure 5. Structures of *Ambrysus hybridus*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Some specimens from the southwestern United States had pseudoparameres with the apical lobe slightly pointed. The central lobe on the posterior margin of the SGP can be pointed and the same length as the posterolateral corners, or rounded and produced

posteriorly further than the posterolateral corners (Puebla), or narrow, truncate, and produced posteriorly further than the posterolateral corners (Hidalgo).

Type Locality. México.

Repository. Lectotype is housed at the NHMW.

Distribution. This species is distributed from the southwestern United States (Arizona, Nevada, New Mexico, Texas, Utah) to southern Mexico. In Mexico, the species presents a distribution pattern that includes streams at high elevations in the Mexican Plateau (Chihuahua, Durango), Sierra Madre del Sur (Oaxaca), Sierra Madre Occidental (Chihuahua, Durango, Sonora), Sierra Madre Oriental (Hidalgo, Nuevo León, Puebla, Querétaro), and Transmexican Volcanic Belt (Estado de México, Guanajuato) biogeographic provinces (Fig. 2). This species occurred syntopically with *A. thermarum* in the East Fork Black River in Arizona.

Published Records. In the original description, Montandon (1897) reported *A. hybridus* from Mexico without designating a specific collecting locality. Thus, most subsequent citations for the species only reported Mexico as the available distributional data for the species (Torre-Bueno 1906; Kirkaldy & Torre-Bueno 1909; Montandon 1909; De Carlo 1950; La Rivers 1958, 1965, 1971); however, Champion (1901) reported the specific locality of Xalapa (Veracruz) and Van Duzee (1923) reported *A. hybridus* from Mulegé (Baja California Sur), although La Rivers (1971) considered the Van Duzee record to be erroneous. As *A. woodburyi,* the species was reported from the states of Arizona, Nevada, New Mexico, Texas, and Utah in the southwestern United States (Usinger 1946; De Carlo 1950; La Rivers 1951a, 1971; Davis 1986). Davis (1986) questioned the validity of the records reported for *A. woodburyi* from the states of New Mexico (Jemez

Springs) and Texas (Davis Mountains), but he was not able to examine the specimens from those localities because they were apparently lost. During this study, I examined a female specimen from New Mexico and confirm the presence of the species in this state. As *A. tridentatus,* the species was reported only from the type locality in the state of Puebla in central Mexico.

Type Material Examined. LECTOTYPE ♂ by present designation: **[MÉXICO:]** *Amb. hybrida* Mont. det. Montandon / Sp. figured / *hybrida* det. Champ. / ♂ / *ambrysus hybrida* Montand. 1896 / Mexico Coll. Signoret / *guttatipenis* ? det. Signoret / *guttatipennis* (?) Stål. HOLOTYPE ♀: **[PUEBLA:]** Chignaulingo, Puebla, Mexico, VIII-16-1959 / A. S. Menke, L. A. Stange Collectors / *Ambrysus tridentatus* La Rivers HOLOTYPE (LACM). PARATYPES: Chignaulingo, Puebla, Mexico, VIII-16-1959 / A. S. Menke, L. A. Stange Collectors / *Ambrysus tridentatus* La Rivers ALLOTYPE (1♂ LACM); same locality information but / *Ambrysus tridentatus* PARATYPE (3♂, 2♀ LACM); same but / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (5♂ CAS). HOLOTYPE ♂: **[UNITED STATES: UTAH:]** Zion Nat'l Park, Utah / A. M. Woodbury Collector / HOLOTYPE *Ambrysus woodburyi* Usinger / California Academy of Sciences Type No. 7169 (CAS). PARATYPES: Zion Nat'l Park, Utah / A. M. Woodbury Collector / ALLOTYPE *Ambrysus woodburyi* Usinger / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (1♀ CAS); Zion Nat'l Park, Utah / A. M. Woodburyi Collector / PARATYPE *Ambrysus woodburyi* Usinger / *Ambrysus woodburyi* Usinger 1946 (Ira La Rivers) / *Ambrysus woodburyi* Usinger determined by Ira La Rivers '50 (1♀ EMEC)..

Material Examined. MÉXICO: CHIHUAHUA: La Laguna, 9 Aug 52, J. D. Lattin / *Ambrysus woodburyi* Usinger 1946 (Ira La Rivers) / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (2♂, 1♀ CAS); Mpio. Chihuahua, ca. 16.5 km on road 160 to Namiquimipa, Arroyo el Potrero, L-1709 / 31 December 2013, 1777 m, 29º 05' 34.8" N, 106º 28' 42.8" W, DRV & PRH Colls. (25♂, 32♀ UMC); Mpio. Ocampo, ca. 7 km S of El Durazno, 28 Dec. 2013, L-1696 / elev. 2207 m, 28º 08' 44.7" N, 108º 08' 00" W, DRV & PRH Colls. (1♀ UMC); Río Chuviscar, off Rd. to Namiquipa [Namiquimipa] Hwy 160, 29º 05' 30.4" N, 106º 28' 51.4" W, D. E. Bowles (1♂, 1♀ UMC); Río Concheño, CL2326, 22 April 1988, J. T. & D. A. Polhemus (2♂, 2♀ UMC); 23 mi S Creel, July 18, 1960 / S. L. Wood & J. B. Karren / *A. woodburyi* det. C. A. Olson 82 (4♂, 1♀ BYUC); Río Verde, 8 August 1952, John D. Lattin Cal. Acad. Sci. Coll. / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (12♂, 5♀ CAS). **DURANGO:** El Rayo, 14 July 1952, J. D. Lattini Cal. Acad. Sci. Coll. / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (8♂, 9♀ CAS); same but / *Ambrysus woodburyi* Usinger det. J. R. Davis 91 (6♂, 8♀ CAS). **GUANAJUATO:** Sta. Rosa, Cañada de la Virgen, 6 May 1997, R. Novelo coll. (2♂, 2♀ UMC). **HIDALGO:** Laguna de Chimalapa [Chimalpa], 2 November 1985, G. Rodríguez, coll. (1♂ UMC); Mpio. Molango, Río Malila at Malila, 20º 43' 43.8" N, 98º 43' 14.2" W, 1386 m, 5 June 2013, L-1518 / Sites, DRV, PRH & Shepard, heavily shaded rocky strm. w[ith] leaf packs (20♂, 10♀ UMC). **MÉXICO:** Mpio. Aculco de Espinoza, Cascada la Concepción, Río Ñando, 12 May 2014, L-1749 / elev. 2311 m, 20º 09' 05.1" N, 99º 54' 40.4" W, DRV & PRH Colls. (40♂, 19♀ UMC). **NUEVO LEÓN:** spring and stream at Potrero Redondo, 1250 m, CL2341, 30 April 1988, 18º C., D. A. & J. T.

Polhemus (2♂, 2♀ UMC). **OAXACA:** [Mpio. Tlaxiaco], km 64.5 carr. Putla-Tlaxiaco, 6 km SW of Tlaxiaco, 31 May 2012, L-1402 / 2010 m, 17º 13' 22" N, 97º 43' 14.8" W, DRV & PRH Colls. (4♂, 1♀ UMC). **QUERÉTARO:** Mpio. Amealco, Cañón Zúñigas, 2100 m, 20º 20' 28" N, 100º 07' 10" W, 26-V-00, R. Jones (5♂, 1♀ UAQE) same but 8-VIII-00 (1♀ UAQE); Mpio. Amealco, Puerta de Alegrías, Arroyo las Zúñigas, 8-VII-2000, C. B. Barr / S of Galindo, 20º 20' 28" N, 100º 07' 10" W, elev. 2000 m (9♂, 1♀ EMEC); Mpio. Amealco, 1 km N El Granjeno / 20º 19.31' N, 100º 8.9' W, 23-IV-2005, R. Jones, 1470 m, Bos. Riparia (1♂ UAQE); same locality information but 20º 19.26' N, 100º 9.18' W, 1-IV-06, R. Jones, 2000 m, Riparian (1♂ UAQE); Mpio Pinal de Amoles, Cañón de la Angostura, Río Escanela, 13 May 2014, L-1753 / elev. 1241 m, 21º 11' 47.6" N, 99º 36' 19.1" W, DRV & PRH Colls. (40♂, 20♀ UMC); Mpio. Pinal de Amoles, Chuveje, Arroyo Chuveje (El Tigre), 14 May 2014, L-1755 / elev. 1271 m, 21º 10' 16.7" N, 99º 33' 25.9" W, DRV & PRH Colls. (1♂, 4♀ UMC); Mpio. Pinal de Amoles, Chuveje, Cascada de Chuveje, Arroyo Chuveje, 14 May 2014, L-1754 / elev. 1313 m, 21º 10' 10.4" N, 99º 33' 28.7" W, DRV & PRH Colls. (5♂, 5♀ UMC); Mpio. Querétaro, NW Col. Villas de Santiago, 20º 38' 22.42" N, 100º 24' 31.11" W, 03-VI-09, C. Ledesma (1♀ UAQE); Pinal de Amoles, Río Escalena [Escanela], 30-IV-06, G. Hdez. (1♂, 1♀ UAQE); Sierra Gorda Biosphere Reserve, Arroyo Jalpan, ca. 1 km S Huasquilico [Huazquilico], 11-VII-2000 / 21º 09' 04" N, 99º 34' 42" W, elev. 1725 m, coll. C. B. Barr (3♂ EMEC). **SONORA:** Mpio. Yécora, El Kipur, 28 Dec. 2013, L-1693, DRV & PRV Colls. / elev. 1553 m, 28º 24' 14.4" N, 108º 35' 47.1" W (1♀ UMC). **UNITED STATES: ARIZONA:** Apache Co., E. Fork Black Riv. above Diamond Rock Cpgd., 7,920 ft. elev., 6 June 1993, pool / *A. woodburyi* Usinger det. R. W. Sites 1993 (3♀ UMC); Apache Co., E. Fork

Black River at FR 249, 18–19 May 1996, coll: M. Miller (1♂ UMC); Cochise Co., Cave Ck., nr Portal, 3 Sep. 1989, Coll: J. A. Back, gravel substratum (1♀ UMC); Cochise Co., Cave Ck., 4 mi. W Portal, 17 July 1987, coll: R. W. Sites, sluggish stream bottom / *A. woodburyi* Usinger det. R. W. Sites 1988 (1♀ UMC); Cochise Co., Cave Creek, 1.2 mi. W Southwest Research Station, V-5-1988, F. Andrews & T. Eichlin / collected in stream (8♂, 7♀ CSCA); Cochise Co., Herb Martyr Dam, IX-9-1976, Fred G. Andrews (1♀ CSCA); Cochise Co., Rucker Can. pools in streambed, 25 April 2000, K. B. Miller colr. / 31º 45' 00" N, 109º 21' 13" W, 1691 m, 00-04 (1♂, 1♀ UMC); Cochise Co., Rucker Can. pools, intermittent stream, 25 April 2000, K. B. Miller colr. / 31º 45' 35" N, 109º 19' 17" W, #00-05 (1♀ UMC); Cochise Co., Rucker Canyon, flood tributary to Whitewater Creek, 22-VI-1959 / colls. R. R., G. H. & F. L. Miller, UMMZ fish M59-79 (1♀ UMC); Cochise Co., 3 mi. W. Portal, Cave Ck, 12 Aug 1988, coll: R. Morris (1♂, 2♀ UMC); same but / *A. woodburyi* Usinger det. R. W. Sites 1989 (1♂ UMC); Coconino Co., East Clear Creek, Kinders Crossing, elev. 6450 ft, riffle, 22 June 1992, coll: R. W. Sites (1♂, 1♀ UMC); Coconino Co., East Clear Creek above Mack's Crossing, 22 June 1992, elev. 6,265 ft., riffle [coll: R. W. Sites] (3♂, 1♀ UMC); Coconino Co., Oak Cr. @ Pine Flat Camp Ground (Hwy 89), 35º 00' 43.1" N, 111º 44' 13.1" W, 27-V-1999, D. E. Baumgardner, Elev: ca. 5,800 ft. / *A. woodburyi* ♀ det. R. W. S. 2000 (1♀ UMC); Coconino Co., West Fork Oak Ck., above 4th trail crossing, 5,310 ft. elev., pool, 30 Sept. 1992 / *A. woodburyi* Usinger det. R. W. Sites 1993 (2♂, 1♀ UMC); Coconino Co., West Fork Oak Ck., above 5,310 ft. elev., 13 May 1992, pool / *A. woodburyi* Usinger det. R. W. Sites 1993 (1♂, 1♀ UMC); Conger Ck., 4-12-93, CGR1 P (1♂ UMC); Conger mit., 4-21-93 (1♂ UMC); Cottonwood Ck., 4-22-93, COT1R (3♀ UMC); same but COT1P

(1♀ UMC); E. Clear Ck. (KC), 6-9-93, ECL1 R (1♀ UMC); E. Fk. Black R., 6-17-93, EFB1P (1♂, 1♀ UMC); Gila Co., Canyon Ck. above Valentine Canyon, 6,270 ft. elev., 16 June 1992, riffle / *A. woodburyi* Usinger det. R. W. Sites 1993 (3♂, 5♀ UMC); Gila Co., Canyon Creek, upper pool above Valentine Canyon, 6,270 ft. elev., 16 June 1992 / *A. woodburyi* Usinger det. R. W. Sites 1993 (1♂, 4♀ UMC); Gila Co., Salome Creek, 11 May 1992, elev. 4,820 ft., riffle (5♂, 3♀ UMC); Gordon Ck., 5-24-93, GOR1 P (1♂ UMC); Salome Ck., 5-5-93, SAL1 R (1♂ UMC); Spring Ck., 5-26-93, SPG1 (2♀ UMC); W. Fk. Oak Ck., 5-11-93, WFO1 (1♂, 2♀ UMC); same but WFO1R (1♂, 3♀ UMC); Webber Ck., 6-8-93, WEB1R (1♀ UMC); West Fork Oak Ck., 9-30-92, field sort series 3 count = A91 (1♂, 1♀ UMC). **NEW MEXICO:** Sierra Winder Ranch, J. Davis, XI-19-95 / 18355 AM (1♀ UMC). **UTAH:** Wash. Co., Leeds Canyon, 28-30 Jun 1984, Hanson, Keller (1♀ UMC); Washington Co. Leeds Cany., 22 Jul 1981, Hanson, Clemons & Keller (1♂ UMC); Zion Nat'l Park, Wash. Co., G.V.S. Swp., 16 Aug 1976, stream veg., A. Lindahl (1♂ UMC); same but 11 Aug 1976, #28 (1♂ UMC).

Ambrysus lariversi **Reynoso & Sites NEW SPECIES**

(Figs. 4, 6)

Description. Macropterous female. HOLOTYPE, length 7.44; maximum width 4.80. Paratypes (n = 8), length 7.20–7.84 (mean = 7.48); maximum width 4.32–4.88 (mean = 4.54). General shape elongate, parallel-sided; widest across embolia (Fig. 6A). Overall dorsal coloration medium brown to dark brown, legs lighter. Dorsal surface coarsely punctate. Ventral coloration yellowish brown except brown pro-, meso-, and metapleura.

Head. Head length 1.52; maximum width 2.08. Mostly yellowish brown with

medium brown posteriorly, coarsely punctate. Eyes convergent anteriorly, synthlipsis 0.96; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 8.5% of head length; posterior margin between eyes strongly convex, extending posteriorly 33% of head length. Labrum width 2.25× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.40 beyond labrum not including extruded stylets. Antennal proportions 2:7:12:7, length 0.60, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color medium brown, yellowish brown laterally; transverse sulcus marking anterior border of transverse band in posterior 1/4; transverse band pale yellow; lateral margins dark brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.7× length; length at midline 1.32; maximum width at posterolateral corners 3.68. Prothorax ventrally pruinose throughout; apices of propleura not meeting at midline, not appressed to prosternellum; propleuron yellowish brown, brown medially, medial 2/3 of posterior margin with elongate golden setae. Probasisternum with sharp median carina and row of setae lateral to carina. Prosternellum not covered by apices of propleura. Scutellum coarsely punctate, triangular, dark brown, light brown coloration on posterior apex, width 1.9× length, width 2.52, length 1.28. Hemelytra densely punctate, pale brown, membrane brown, length 5.20 (chord measurement); corium brown medially. Clavus pale brown, length 4.9× width, length 2.76, width 0.56; claval commissure brown, length 0.68.

Embolium length 2.24, greatest width 0.70, lateral margin convex, pale brown in anterior 2/3, brown posteriorly. Oblique suture connecting claval and embolar sutures near bases. Hind wings extending to posterior margin of tergum VI. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments yellowish brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third, spines generally single proximally becoming small combs of two to five spines distally; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to five spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin, lateral margin without spines at apex to accommodate flexed tarsus. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 1.68, tibia 1.30, tarsus 0.46; middle leg,

femur 1.76, tibia 1.52, tarsomeres 1–3, 0.18, 0.36, 0.40; hind leg, femur 2.24, tibia 2.48, tarsomeres 1–3, 0.20, 0.62, 0.54.

Abdomen. Dorsally with connexiva of III–V exposed, laterotergites brown (Fig. 6A); lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners. Posterolateral corners of II (visible ventrally) – V narrowly rounded to right angled and not spinose, VI–VII bluntly acute. Ventrally yellowish brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VI. Mediosternite VII (subgenital plate) width 1.1× length; length at midline 0.90; maximum width 1.04; posterior margin with short, pointed lobe on either side of midline, generally extending posteriorly same distance as posterolateral corners; posterolateral corners pointed (Fig. 6F).

Macropterous male. Paratype (n = 1), length 6.8; maximum width 4.24. The poor condition of the single male in the type series did not allow examination of color pattern. Setation, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for the holotype. Otherwise hind wings extending to posterior margin of tergum VI. Accessory genitalic process of tergum VI curved to right close to the base at approximately 60 degree angle, continuing evenly curved to acuminate apex (Fig. 6B). Medial lobes of tergum VIII (pseudoparameres) symmetrical; convex mesally; apical lobe broadly rounded, posterolaterally directed (Fig. 6C). Parameres symmetrical, longer than wide, mesal margin slightly convex, setae emanating from basal half of dorsal surface. Proctiger length 1.2× width at base. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 6D).

Phallosoma elongate, linear, constricted basally; ventrally with right and left plate-like endosomal sclerites with conspicuous spiked apices (Fig. 6E).

Variation. The color pattern described for the holotype is not consistent among the paratypes. Most specimens (some specimens have lost the color pattern because of lengthy alcohol preservation) present a solid brown color on the hemelytra with yellowish brown color on the clavus and anterior 2/3 of the embolium. Also, connexiva IV–V presented dark brown coloration in the anterior half and brown posteriorly, giving a checkered appearance. The central lobes on the posterior margin of the SGP can be slightly rounded and the posterolateral corners can be produced posteriorly slightly further than the central lobes.

Diagnosis. This species can be distinguished from the others in the complex by the posterior margin of the SGP with the posterolateral corners pointed and two short central pointed lobes that are subequal in length to the posterolateral corners (Fig. 6F). The presence of two central lobes on the posterior margin of the SGP is a characteristic not present in any other species in this complex. The males can be distinguished by the shape of the AGP, which curves to right close to the base at an approximately 60 degree angle, then continues evenly curved to the apex (Fig. 6B). The pseudoparameres are short and present a short, rounded, and posterolaterally directed apical lobe (Fig. 6C). The parameres are longer than wide with the mesal margin slightly convex (Fig. 6D).

Habitat Description. La Michilía Biosphere Reserve is in the municipalities of Súchil and El Mezquital in the state of Durango. It has an elevation range of 2000 to 2985 meters and vegetation is composed mostly of pine-oak forest. The Río El Alemán basin receives waters from the central and southern part of the Reserve and after merging with

the Río Verde it drains to the Pacific Ocean (Gadsden & Reyes-Castillo 1991). The localities where the specimens of *A. lariversi* were collected are part of this basin. The stream El Temazcal is permanent and at the type locality it is shallow, 7 to 10 meters wide, with cobble and gravel (Novelo-Gutiérrez, per. comm.).

Distribution. This species has been collected only from three localities in La Michilía Biosphere Reserve in the northwestern Mexican state of Durango. The localities are in the highlands of the Sierra Madre Occidental biogeographic province (Fig. 4). *Ambrysus lariversi* was found syntopically with *A. pygmaeus* at El Temazcal stream.

Etymology. The specific epithet "*lariversi"* honors the American entomologist Dr. Ira J. La Rivers (1915–1977), who was particularly interested in the study of Naucoridae and published a large number of studies that presently still remain as the primary source of information on this aquatic group.

Repository. The holotype and some paratypes will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the California Academy of Sciences (San Francisco), Enns Entomology Museum (University of Missouri), and the United States National Museum of Natural History (Washington D.C.).

Type Material Examined. HOLOTYPE ♀. **MÉXICO: DURANGO:** Mpio. Súchil, Reserva de la Biósfera La Michilía, Arroyo El Temazcal, [camino a El Alemán], [23º 19' 24.22" N, 104º 09' 58.13" W], 10-Dec-1987, R. Novelo col. PARATYPES: same data as holotype (1♂, 2♀); [Mpio. Súchil], Res. Biósfera de Michilía, Arroyo El Tamascal [Temazcal], 1-VII-1985, 2260 msnm, C. Castillo [&] P. Reyes (3♀); [Mpio. Súchil] Res. Biósfera de Michilía Est. Piedra Herrada, 1-VII-1985, 2350 msnm, C. Castillo [&] P.

Reyes (2♀); Mpio. Súchil, Reserva de la Biósfera La Michilía, Arroyo San Juan Michis, 10-Abr-1988, R. Novelo col. (1♀).

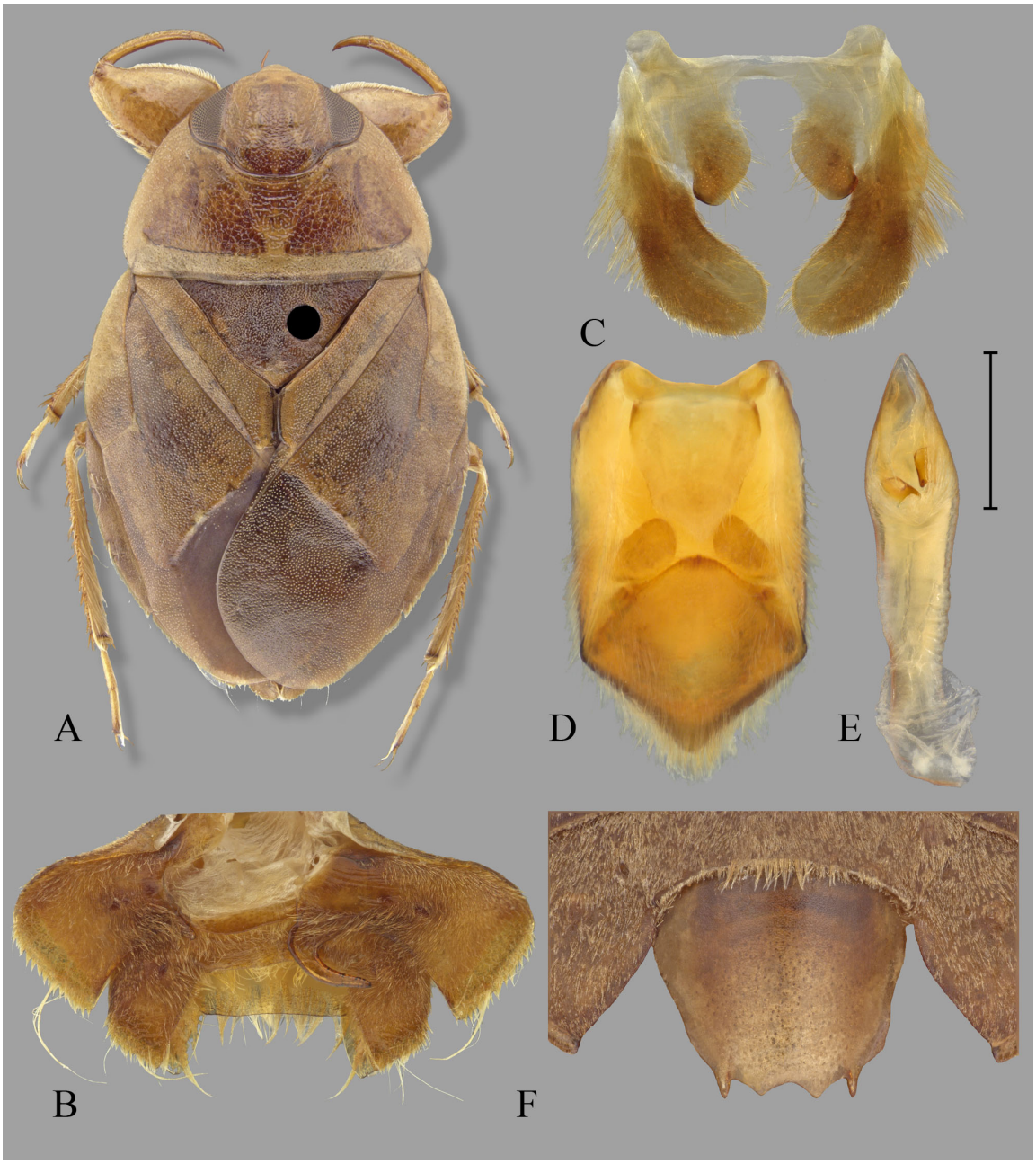

Figure 6. Structures of *Ambrysus lariversi* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Ambrysus lattini **La Rivers**
(Figs.)

Ambrysus lattini La Rivers 1976: Biol. Soc. Nev. Occas. Pap. 41: 1–3 (original description).

Diagnosis. This species can be distinguished from the others in the complex by the lateral margins of the female SGP nearly straight to the sublateral lobes and the posterior margin with acuminate posterolateral corners bounding a subrectangular concavity. The anterior margin of the concavity is flat or with a slight protuberance (Fig. 7F). The males can be distinguished by the shape of the AGP that curves to right close to the base at an approximately 60 degree angle, then angles abruptly to the right at mid-length to continue almost perpendicular to the body axis (Fig. 7B). The pseudoparameres are relatively short and present a short, broadly rounded, and posterolaterally directed apical lobe similar to that of *A. fuscus* and *A. ultimus* (Fig. 7C), or pseudoparameres tapered to a short, rounded and posteromesally directed apical lobe; with a strong medial convexity (Fig. 7C). The parameres are longer than wide with a straight mesal margin (Fig. 7D).

Discussion. *Ambrysus lattini* was described based on six specimens collected in the northwestern Mexican states of Chihuahua and Durango (La Rivers 1976). The species appears to not be common since we collected only two specimens. We visited the type locality (L-1596), which is a montane rocky stream where we did not find any naucorids. When La Rivers (1976) described this species together with *A. ultimus*, he made reference for the first time to the *A. hybridus* species complex and suggested that *A. lattini* was related to *A. hybridus*, *A. tridentatus*, *A. ultimus*, and *A. woodburyi*.

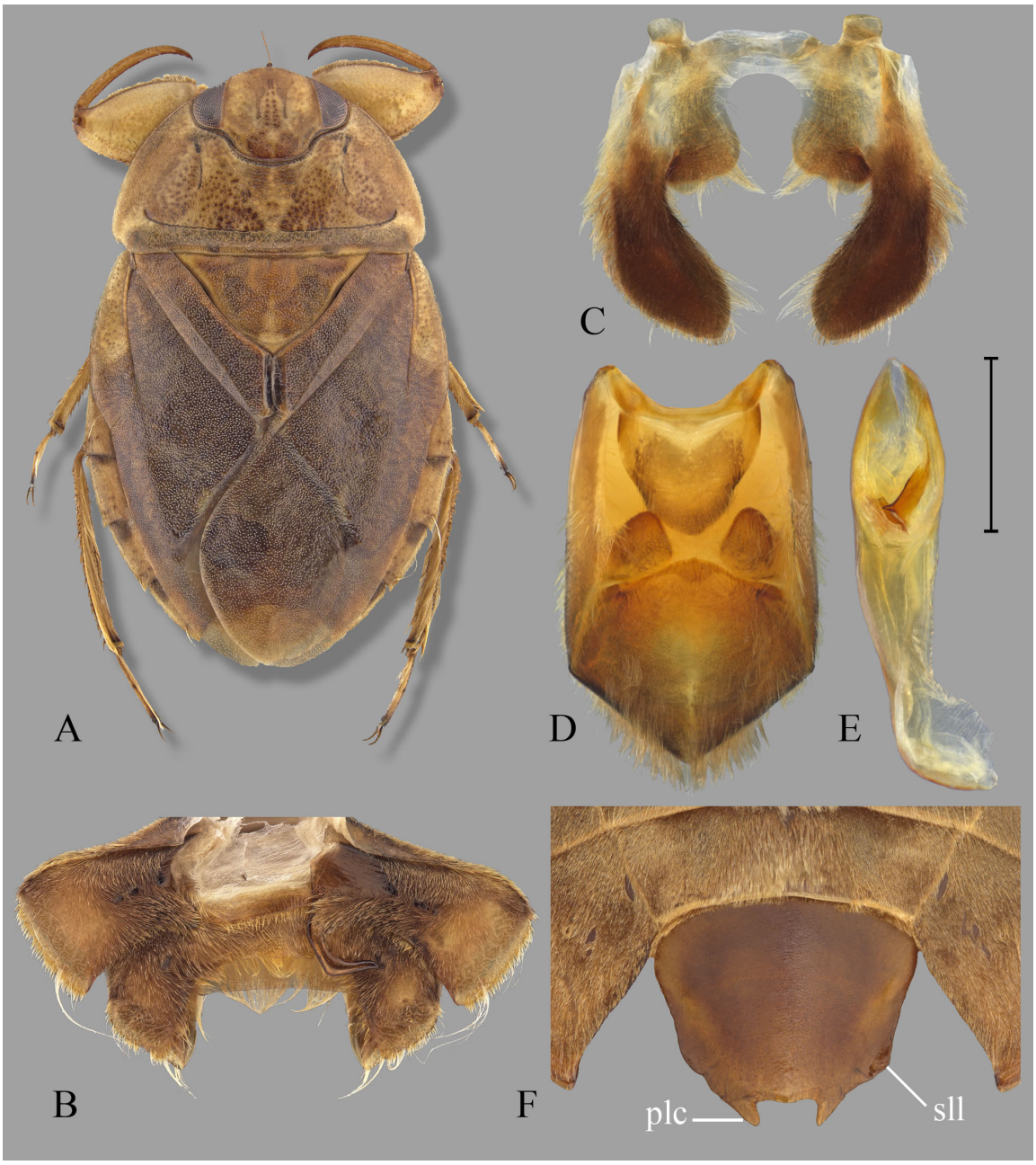

Figure 7. Structures of *Ambrysus lattini*. (A) dorsal habitus of female, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed). plc = posterolateral corner, sll = sublateral lobe.

The relationship among these species was based on the shape of the posterior margin of the SGP. A general characterization of the features present in these five species is the posterior margin of the SGP with the posterolateral corners and the central lobe pointed.

In *A. lattini* the posterior margin of the SGP is narrower than in the other species, with acuminate posterolateral corners bounding a subrectangular concavity which can have a flat anterior margin or slight median convexity.

Variation. One paratype (CAS) presented only the right pseudoparamere tapered to a short, rounded, and posteromedially directed apical lobe. The median convexity in the central concavity of the posterior margin of the SGP can be slightly pointed.

Type Locality. México: Durango: Mpio. Pueblo Nuevo, 2 miles West of Las Adjuntas.

Repository. Holotype is housed at the CAS.

Distribution. Previously, this species has been reported from the states of Chihuahua and Durango. We collected the species in two additional localities in the state of Chihuahua. The localities from which *A. lattini* is now known are in the Sierra Madre Occidental and the Mexican Plateau biogeographic provinces (Fig. 2). This species was found syntopically with *A. plautus* in two localities in the state of Chihuahua (L-1696, L-1698).

Published Records. México: Chihuahua, Durango (La Rivers 1976)

Type Material Examined. HOLOTYPE ♀: **MÉXICO: DURANGO: [**Mpio. Pueblo Nuevo], 2 mi. W Las Adjuntas, 30 June 1952, John D. Lattin, Cal. Acad. Sci. Coll. / HOLOTYPE ♀, *Ambrysus lattini* La River (sic) Det. 1978 by Vincent F. Lee / Type / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 / California Academy of Sciences Type No. 13402. PARATYPES: [Mpio. Pueblo Nuevo], 2 mi W Las Adjuntas, 30 June 1952, J. D. Lattin, Cal. Acad. Sci. Coll. / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 / PARATYPE *Ambrysus lattini* La Rivers Det. V. F. Lee 1978 (7♂, 1♀ CAS; 1♀ CNIN).

CHIHUAHUA: 15 mi S La Laguna at Arroyo La Rana, 9 August 1952, John D. Lattin, Cal. Acad. Sci. Coll. / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 / PARATYPE *Ambrysus lattini* La Rivers Det. V. F. Lee 1978 (3♀ CAS).

Material Examined. MÉXICO: CHIHUAHUA: Mpio. Bocoyna, Valle de Cusárare, L-1698, 29 December 2013, DRV & PRH Colls. / elev. 2186 m 27° 36' 15.2" N, 107° 33' 15.5" W (1♂ UMC); Mpio. Ocampo, ca. 7 km S of El Durazno, 28-Dec-2013, 2207 m, L-1696 / 28° 08' 44.7" N, 108° 08' 00" W, DRV & PRH colls. (1♀ UMC). **DURANGO:** [Mpio. Pueblo Nuevo], Las Adjuntas, 1 July 1952, J. D. Lattin, Cal. Acad. Sci. Coll. / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (2♂ CAS); 71 M W of Durango, CL1015, 20 Aprl 1964, J. T. & M. S. Polhemus / *A. lattini* La R. / J. T. Polhemus Collection (1♂, 1♀ USNM).

Ambrysus plautus **Polhemus & Polhemus**
(Figs. 4, 8)

Ambrysus plautus Polhemus & Polhemus 1983: Pan-Pac. Ent. 58: 326–328 (original description).

Diagnosis. This species can be distinguished from the others in the complex by the wide embolia and the strongly produced corners of connexiva III–IV in males (Fig. 8A) and III–V in females. The posterior margin of the SGP presents pointed posterolateral corners and central lobe, which are subequal in length (Fig. 8F). The AGP curves to the right close to the base at an approximately 65 degree angle, then at mid-length it angles abruptly to the right to continue almost perpendicular to the body axis (Fig. 8B). The

pseudoparameres are long and taper to a short, rounded, posteromedially produced apical lobe (Fig. 8C). The parameres are longer than wide with a convex mesal margin (Fig. 8D).

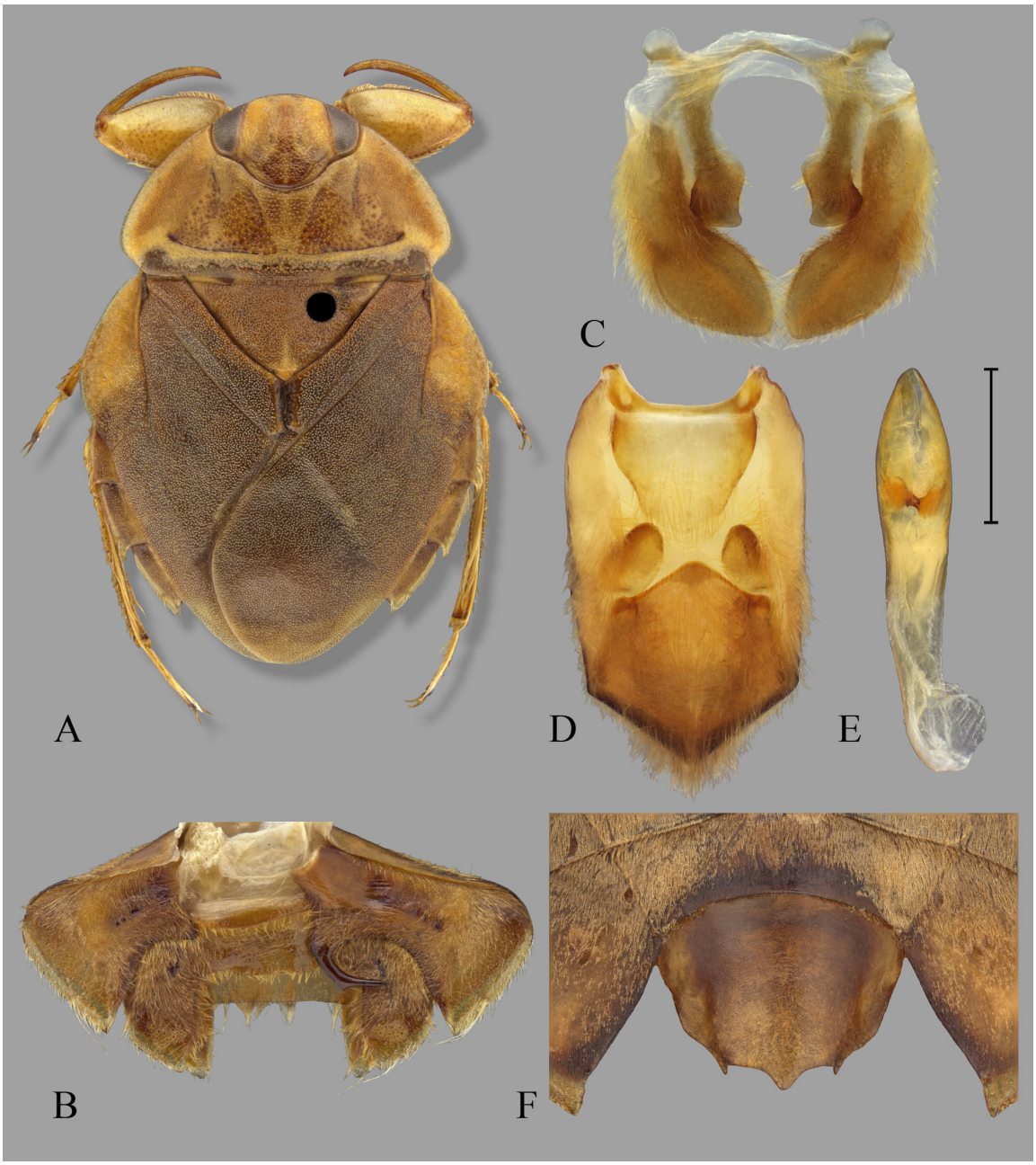

Figure 8. Structures of *Ambrysus plautus*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Discussion. This species was described from the states of Chihuahua and Durango based on a large series of specimens (Polhemus & Polhemus 1983) and it appears to be closely related to the widely distributed *A. hybridus*. Both species present an almost identical shape of the male pseudoparameres and the AGP. Also, the female posterior margin of the SGP presents three pointed lobes in both species. Polhemus & Polhemus (1983) remarked about the resemblance between *A. plautus* and *A. drakei* (La Rivers) because both species had similarly wide embolia and spinose posterolateral corners of the connexiva, but a different condition of the female SGP. This similarity between the species is superficial, whereas a close examination of the ventral side of the phallosoma reveals that the two species belong to different species complexes. The specific epithet *plautus* comes from Latin and refers to the broad body shape of this naucorid (Polhemus & Polhemus 1983). In the original description, Polhemus & Polhemus (1983) reported 24 male and 24 female paratypes collected at the type locality (20 miles east of La Ciudad) on April 22, 1981 (IV-22-1981). The locality information on the label of the four paratypes that I examined, which were collected on April 22, 1981 (IV-22-1981), does not correspond to the type locality cited in Polhemus & Polhemus (1983); instead, the locality data on the label reads 23.7 miles east of La Ciudad.

Variation. The paratype specimens examined during this study were larger than the specimens we collected in the field. Polhemus & Polhemus (1983) reported mean lengths of 8.44 mm for males (n = 7) and 9.36 mm for females (n = 5), and mean widths of 6.23 mm and 6.9 mm, respectively. The mean lengths of our specimens were 7.79 mm for males (n = 15) and 8.59 mm for females (n = 15), and mean widths were 5.30 mm and 5.88 mm, respectively. Although the specimens we collected were slightly smaller than

those reported in the original description, the diagnostic features agreed with the original description, including the characteristic wide embolia and produced corners of the connexiva.

Type Locality. México: Durango: 20 mi. east of La Ciudad.

Repository. Holotype is housed at the USNM.

Distribution. *Ambrysus plautus* is distributed in areas of the Mexican Plateau and the Sierra Madre Occidental biogeographic provinces in the states of Chihuahua and Durango (Fig. 4). This species was found syntopically with the less common *A. lattini* in Valle de Cusárare, Chihuahua (L-1698).

Published Records. México: Chihuahua, Durango (Polhemus& Polhemus 1983).

Type Material Examined. HOLOTYPE ♂: **MEX[ICO]: D[URAN]GO:** 8700', 20 mi. E. La Ciudad, CL726, VI-6-1975, J. T. Polhemus / HOLOTYPE *Ambrysus plautus* J. T. Polhemus [&] D. A. Polhemus. PARATYPES: 23.7 mi. E. La Ciudad, CL638, IV-22-81, J. T. & D. A. Polhemus / PARATYPE *Ambrysus plautus* J. T. & D. A. Polhemus (1♂, 1♀ CAS; 1♂, 1♀ UMC).

Material Examined. MÉXICO: CHIHUAHUA: Arroyo Pajarito, Hwy 16, 26 mi W Tomachic [Tomochi], 23-VIII-1986, Baumann & Sargent (1♂ BYUC); Mpio. Balleza, El Padre, 6 km W of Balleza, Río de Agujas, L-1701, 29 December 2013 / 26º 57' 01.8" N, 106º 24' 00.8" W, elev. 1572 m, DRV & PRH Colls. (1♀ UMC); Mpio. Bocoyna, Bocoyna, L-1697, 29 December, DRV & PRH Colls. / elev. 2232 m, 27º 50' 21.1" N, 107º 35' 34" W (22♂, 38♀ UMC; 10♂, 10♀ CNIN); Mpio. Bocoyna, Valle de Cusárare, L-1698, 29 December, 2013, DRV & PRH Colls. / elev. 2186 m, 27º 36' 15.2" N, 107º 33' 15.5" W (6♂, 5♀ UMC); Mpio. Guachochi, Mesa de Bocoyna, Arroyo de Bocoyna,

L-1700, 29 December 2013 / 27º 05' 27.1" N, 107º 14' 43.8" W, elev. 2347 m, DRV & PRH Colls. (3♂, 7♀ UMC); Mpio. Ocampo, ca. 7 km S of El Durazno, 28 Dec. 2013, L-1696 / elev. 2207 m, 28º 08' 44.7" N, 108º 08' 00" W, DRV & PRH Colls. (1♂, 4♀ UMC); Río de Triquitos, 45.5 km W of La Junta on new hwy. to Basaseachic [Basaseachi], June 17 1978, R. R. [&] F. H. Miller, 28º 26' N, 107º 48' W, M78-36 (1♀ UMMZ); rocky stream above Basaseachi Falls, 1950 m, CL2327, 23 April 1988, J. T. & D. A. Polhemus (1♂, 1♀ UMC); 15 mi. S La Laguna, Arroyo Agua Caliente, 10 August 1952, John D. Lattin, Cal. Acad. Sci. Coll. / Ira La Rivers collection Bequeathed to the California Academy of Sciences - 1978 (1♂ CAS). **DURANGO:** Mpio. Canatlán [Nuevo Ideal], Guatimapé, Puente Guatimapé, L-1718, 03 January 2014 / elev. 1966 m, 24º 48' 41.7" N, 104º 55' 15.8" W, DRV & PRH Colls. (5♂, 7♀ UMC); Mpio. Guanaceví, El Cuervito, Puente Morelos, L-1715, 02 January 2014 / elev. 1963 m, 25º 45' 14.3" N, 105º 47' 30.6" W, DRV & PRH Colls. (4♂, 2♀ UMC); Mpio. Guanaceví, El Potrero Viejo, Río Sextín, L-1713, 02 January 2014 / elev. 1931 m, 25º 56' 28.7" N, 105º 49' 43" W, DRV & PRH Colls. (2♂ UMC).

Ambrysus spiculus **Polhemus & Polhemus**
(Figs. 4, 9)

Ambrysus spiculus Polhemus & Polhemus 1981: Pan-Pac. Ent. 57: 400–401 (original description).

Diagnosis. This species can be distinguished most easily from the others in the complex by the condition of the female SGP; the lateral margins are straight and the acute central lobe of the posterior margin is produced posteriorly ≥ 2× the length of the posterolateral

corners (Fig. 9F). Males can be distinguished by the pseudoparameres broadly lanceolate, tapering to a narrowly rounded apex (Fig. 9C). The AGP curves to right close to the base at an approximately 55 degree angle, at mid-length it angles abruptly to the right to continue perpendicular to the body axis (Fig. 9B). The parameres are rounded (Fig. 9D).

Discussion. This species was described by Polhemus & Polhemus (1981) from specimens collected in the northwestern states of Durango, Sonora, and Zacatecas. Polhemus & Polhemus (1981) noticed similarity in the shape of the AGP and SGP of *A. spiculus* and *A. tridentatus* and distinguished between the two species mainly based on features of the SGP. Because the shapes of the AGP and pseudoparameres exhibited by males of *A. spiculus* are similar to those of *A. hybridus,* with which *A. tridentatus* has been synonymized herein, features of the female SGP are used here to diagnose the species. If variation exists in the shape of the lateral margins of the SGP (straight or convex) and the length of the central lobe (compared with the posterolateral lobes) in specimens of the type series, this species could be considered a junior synonym of *A. hybridus* Montandon. I did not have access to more female paratypes of *A. spiculus* (housed at the USNM) in order to assess such variation and examination of those specimens is needed to evaluate the taxonomic status of the species. As such, *A. spiculus* is conditionally considered a valid species.

Variation. The male paratype examined during this study had a wider AGP (Fig. 9B) that that of the holotype. In the original description, Polhemus & Polhemus (1981) reported that the posterior margin of the SGP only had a single median projection (central

lobe) and no posterolateral corners posteriorly produced. The specimens examined in this study had conspicuously produced posterolateral corners.

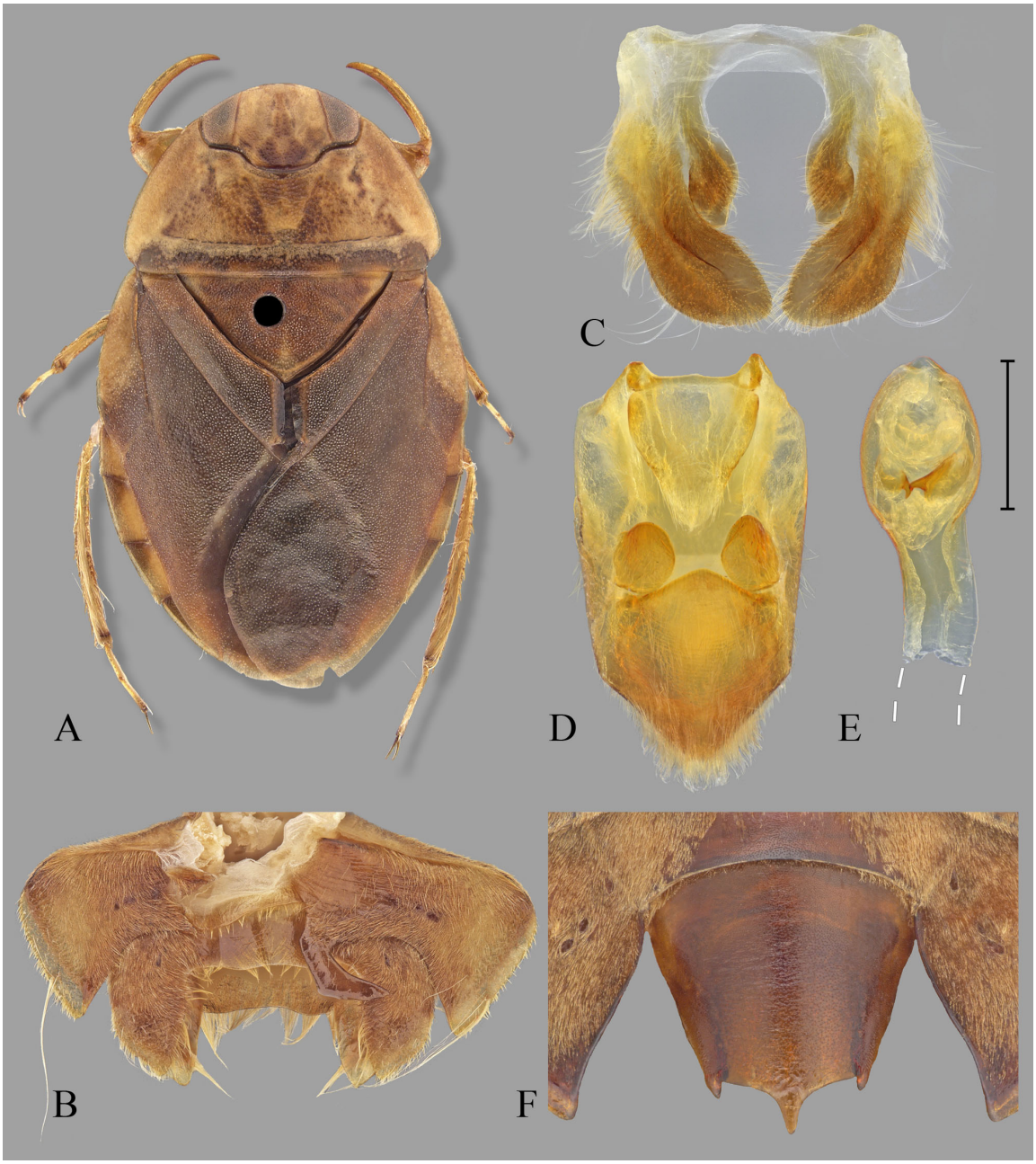

Figure 9. Structures of *Ambrysus spiculus*. (A) dorsal habitus of female, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Type Locality. México: Durango: [Mpio. Durango ?], La Palmita.

Repository. Holotype is housed at the USNM.

Distribution. This species is distributed along the Sierra Madre Occidental biogeographic province in the states of Durango, Sinaloa, Sonora, and Zacatecas (Fig. 2).

Published Records. México: Durango, Sonora, Zacatecas (Polhemus & Polhemus 1981)

Type Material Examined. HOLOTYPE ♂: **MEX[ICO]: DURANGO:** [Mpio. Durango ?], La Palmita, CL1018, 20 April 1964, J. T. & M. S. Polhemus / HOLOTYPE *Ambrysus spiculus* J. T. Polhemus [&] D. A. Polhemus. PARATYPES: [Mpio Durango ?], La Palmita, CL1018, 20 Apr. 1964, J. T. & M. S. Polhemus / PARATYPE *Ambrysus spiculus* J. T. Polhemus [&] D. A. Polhemus (1♂, 1♀ CAS). **ZACATECAS:** 61 mi W of Fresnillo, Alt. 8100 feet / pool stream bed, 25.VI.1954, R. H. Brewer / PARATYPE *Ambrysus spiculus* J. T. & D. A. Polhemus / Collection of the California Academy of Sciences, San Francisco, Calif. (1♂, 1♀ CAS).

Material Examined. MÉXICO: DURANGO: San Antonio, 5000 ft, El Salto,Vi-10-1937 / Embury Coll. / *Ambrysus convexus* Usinger 1946 (Ira La Rivers) (1♂ EMEC); 2.5 mi. W. San Luis, 8000', March 24, 1953, #66d, I. J. Cantrall (1♀ UMMZ). **SINALOA:** Los Hornos, Sierra Surutato, 1980 m, 7-III-1971, DE Breedlove col. (1♀ CAS).

Ambrysus thermarum **La Rivers**

(Figs. 2, 10)

Ambrysus thermarum La Rivers 1953b: Proc. U.S. Nat. Mus. 103: 1–3 (original description).

Diagnosis. This species can be distinguished from the others in the complex by the posterior margin of the SGP with rounded posterolateral corners bounding an evenly

curved concavity (Fig. 10F). The AGP curves to the right close to the base at an approximately 50 degree angle, and at mid-length curves abruptly to the right to continue almost perpendicular to the body axis (Fig. 10B). The pseudoparameres are relatively short with the apical lobe broadly rounded and directed posterolaterally (Fig. 10C). The parameres are longer than wide with a slightly convex mesal margin (Fig. 10D).

Discussion. This species was described from specimens collected in an area with thermal springs in New Mexico. La Rivers (1953b) erroneously considered this species to be related to *A. mormon* based on the general shape of the posterior margin of the SGP. Also, La Rivers (1953b) mentioned that the AGP in *A. thermarum* was very similar to that of *A. woodburyi*, but he argued that the variable *mormon*-type AGP could have easily given rise to this similarity. This species is not closely related to *A. mormon*. Close examination of the features on the ventral side of the phallosoma reveals that *A. thermarum* belongs to the *A. hybridus* species complex. In the original description, La Rivers (1953b) compared the small size of this species (7–8 mm) with that of *A. funebris* and he considered *A. thermarum* the smallest species in the genus. Later, Davis (1986) reported new records of *A. thermarum* from Arizona and New Mexico and mentioned that those specimens were larger (8.5–10 mm) than the specimens reported by La Rivers (1953b). Davis (1986) suggested the warm water at the type locality was the probable cause of the reduced size of the specimens of *A. thermarum*. Polhemus (1973) posited that all the *A. thermarum* he had collected were from cold mountain streams and that it was probable that the specimens of the type series had been collected in such cold habitat, and not from hot springs. This idea is unlikely and counter to the concept of small

individuals of *Ambrysus* resulting from ontogenetic development in warmer environmental temperatures than those developing in colder water (Sites et al. 1996).

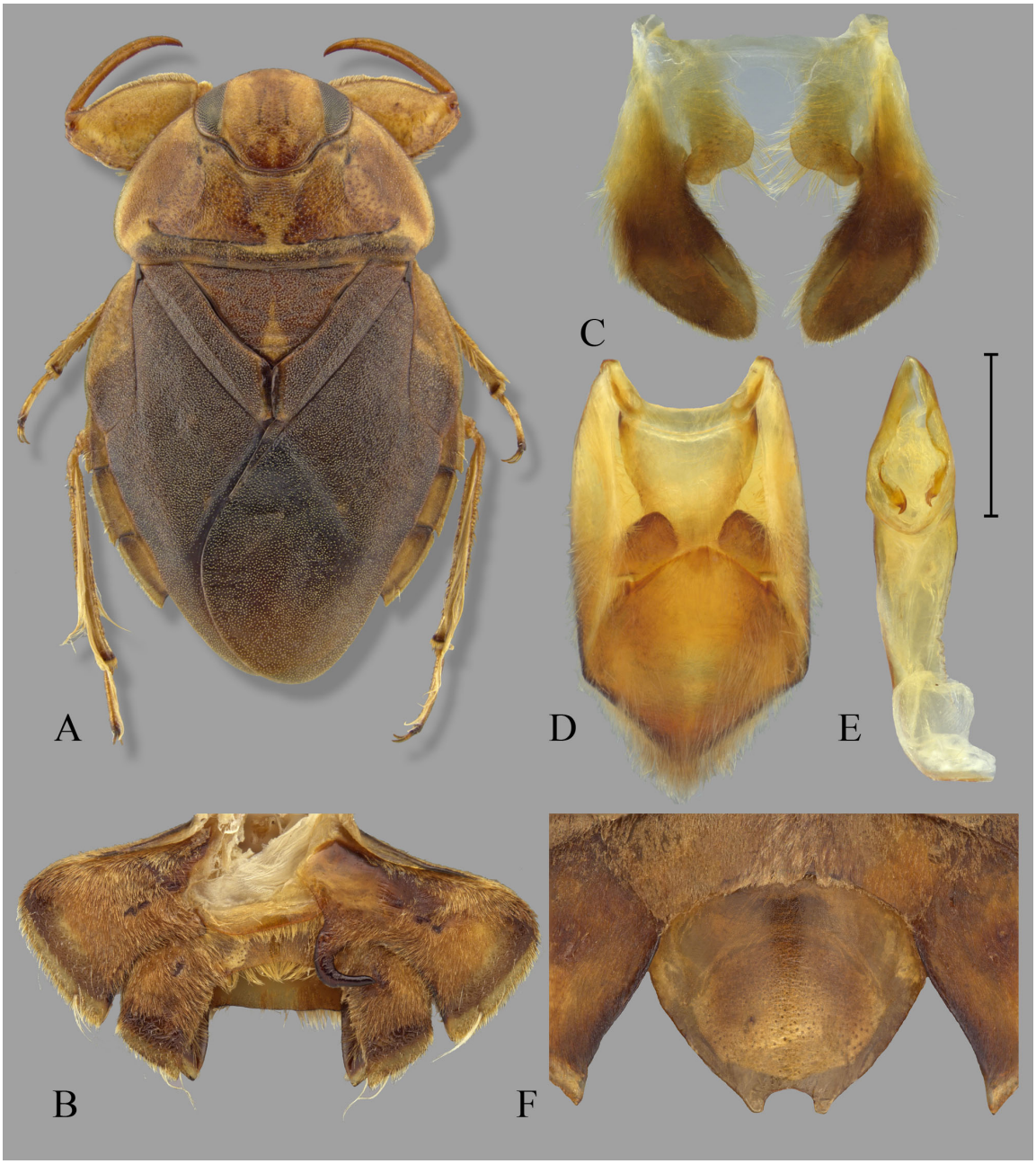

Figure 10. Structures of *Ambrysus thermarum*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Variation. It is common to find specimens of *A. thermarum* with the AGP curved to the right close to the base at a 60 degree angle. In some specimens, the AGP is not abruptly curved to the right at mid-length; instead, it is evenly curved resulting in a hook-shape. Female specimens varied in the width of the concavity on the posterior margin of the SGP, but the general concave shape remained the same.

Type Locality. United States: New Mexico: Sierra County, Hot Springs [Truth or Consequences].

Repository. Holotype is housed at the USNM.

Distribution. This species is distributed in the southwestern states of Arizona and New Mexico in the United States (Fig. 2). This species was found occurring syntopically with *A. hybridus* in the East Fork Black River (Arizona).

Published Records. United States: Arizona, New Mexico (La Rivers 1953b, Polhemus 1973, Davis 1986).

Type Material Examined. [UNITED STATES: NEW MEXICO:] Hotspa [Truth or Consequences], N. M., Sep11 / PRUhler Collection / *Ambrysus thermarum* La Rivers HOLOTYPE / *Ambrysus thermarum* La Rivers determined by Ira La Rivers '50 / Type No. 60987 USNM.

Material Examined. UNITED STATES: ARIZONA: Apache Co., Coleman Ck. 6.2 mi. S. intersection Hwy 191-180, 18-19 May 1996, coll: M. Miller (1♂, 1♀ UMC); Apache Co., E. Fork Black River at FR 249, 18-19 May 1996, coll: M. Miller (3♂ UMC); Apache Co., E. Fork Little Colorado River @ FR 113, 18-19 May 1996, coll: M. Miller (2♂, 2♀ UMC); Apache Co., Little Colorado Riv., 8 July 1992, riffle (2♂, 2♀ UMC); Apache Co., S. Fork Little Colorado R., 8 July 1992, 7,620 ft. elev., riffle (1♂,

2♀ UMC); Apache Co., W. Fork Black Riv. at FR 68, 18-19 May 1996, coll: M. Miller (1♂, 4♀ UMC); Apache Co., W. Fork Black River, 7,800 ft. elev., 8 June 1992, riffle (3♂, 1♀ UMC); Barbershop [Canyon ?] (upper), MH, 6-11-93 (1♀ UMC); Coconino Co., Barbershop Canyon, 24 June 1992, riffle (1♂, 2♀ UMC); East Fork Black R., EFB1, 6-17-93 (1♂, 1♀ UMC); same but EFB1P (1♂ UMC); Greenlee Co., Campbell Blue River, 1 mi. above Blue R. confluence, 6,670 ft. elev., 18 May 1992, riffle (1♂ UMC); Little Col. Rv. ab[o]ve. S. F[or]k, LCR1 R, 6-14-93 (2♂, 4♀ UMC); Navajo Co., E. Fork White R. at Rock Creek, elev. ca. 1800 m, coll: Cheryl Carnes, 04-15-95 (1♀ UMC); Reservation Ck., RES1 R, 6-17-93 (1♂ UMC); Rudd Ck., MH, 6-1-93 (1♀ UMC); S[outh] F[or]k L[i]t[tle] Col[orado], 6-16-93, SLC1 (2♀ UMC); S. Fk. Little Colorado, MH, 6-16-93 (1♀ UMC); W. Fk. Black R[iver], WFB1P, 6-15-93 (2♂, 1♀ UMC); same but WFB1R (1♂UMC). **NEW MEXICO:** Arriba Co., Chama River @ Herron Dam, 10 June 1989, coll: Doug W. Paxton (1♂, 1♀ UMC); Arriba Co., Chama River under bridge, 11 June 1989, coll: Doug W. Paxton (2♂, 4♀ UMC); Catron, Co., Willow Creek, Willow Creek Campgrd., Gila National Forest, 17 May 1987, coll: R. Leschen (2♂, 1♀ UMC); Eddy Co., Sitting Bull Falls, 10 March, 1989, coll: Morris & Vadder (3♂, 8♀ UMC); same locality information but 14 October 1989, coll: J. A. Back (6♂, 10♀ UMC); same but coll: R. Murphy (1♂, 1♀ UMC); Eddy Co., Sitting Bull Falls, 14-X-1989, coll: M. Sudduth / river (1♂, 2♀ UMC); Mora Co., Coyote Creek @ Coyote Creek St. Pk., 7-8-1994, coll: B. Croyle (3♂, 2♀ UMC); Mora Co., Coyote Ck. State Pk., Coyote Ck., [no day] June 1994, coll: B. Croyle (5♂, 6♀ UMC); Taos Co., Rio Hondo, 2 mi W. of Arroyo Hondo, 24 May 1989, coll: R. W. Sites (13♂, 9♀ UMC); Taos Co., 1 mi. W Arroyo

Hondo, 16 August 1988, coll: R. W. Sites, under rocks in creek (11♂, 10♀ UMC); Taos Co., 2 mi. W Arroyo Hondo, Rio Grande R. 24 May 1989, coll: R. W. Sites (1♀ UMC).

Ambrysus ultimus **La Rivers**
(Figs. 4, 11)

Ambrysus ultimus La Rivers 1976: Biol. Soc. Nev. Occas. Pap. 41: 4–6 (original description).

Diagnosis. This species can be distinguished from the others in the complex by the posterior margin of the female SGP with long, pointed posterolateral corners and a wide, notched central lobe (Fig. 11F). The prominences of the notched central lobe are much closer to each other than each is to the posterolateral corner. Males can be distinguished by the shape of the AGP that curves to right close to the base at an approximately 80 degree angle, then continues almost straight to the apex. A small protuberance occurs at mid-length on the posteromesal margin, giving the impression that the AGP slightly curves to the right at mid-length; however, if considering the anterolateral margin, the AGP clearly continues straight to the apex after it curves to the right close to the base (Fig. 11B). The pseudoparameres are relatively short and present a truncate, posterolaterally directed apical lobe (Fig. 11C). The parameres are longer than wide with a straight mesal margin (Fig. 11D).

Discussion. *Ambrysus ultimus* was described from specimens collected in Alchichica Crater Lake in the state of Puebla in central Mexico (La Rivers 1976). In the original description, La Rivers (1976) indicated that the female holotype and the allotype were deposited in the Dr. H. H. Weber personal collection (Kiel, Germany). Two paratypes

with the same information as the holotype were deposited in the Collection of the Biological Society of Nevada (Verdi, United States) and eventually were to be deposited in the CAS (La Rivers 1976). The holotype and allotype of *A. ultimus* currently are housed at the ZSM. The two paratypes that were to be deposited in the CAS were not found during a recent visit to that collection; thus, the location of the paratypes is unknown. Nonetheless, we collected a large series of topotypes.

Ambrysus ultimus exhibits a similar shape of the pseudoparameres and the posterior margin of the SGP to those of *A. fuscus*; however, the posterolateral corners and central lobe of the SGP of *A. ultimus* are substantially longer.

The Alchichica Crater Lake is a phraetic explosion maar that originated during the Pleistocene. It is located at an elevation of 2320 meters on the western part of the Transmexican Volcanic Belt in a semi-arid climate. This alkaline lake has a pH of 8.8–8.9, maximum depth of 63 meters, and water temperature ranging from 14º–22º Celsius (Armienta et al. 2008). At least seven endemic species (e.g., atherinid fish *Poblana alchichica* de Buen, diaptomid copepod *Leptodiaptomus garciai* (Osorio-Tafall), canthocamptid copepod *Cletocamptus gomezi* Suárez-Morales, Barrera-Moreno & Ciros-Pérez.) have been described from Lake Alchichica, including the water boatman *Krizousacorixa tolteca* Jansson (Corixidae) (Suárez-Morales et al. 2013).

Organisms living in Lake Alchichica are clearly adapted to the high salinity of this aquatic environment, which could limit their ability to colonize surrounding water bodies with lower salinity (Suárez-Morales et al. 2013). Because of this and that we did not find this species outside Lake Alchichica during our extensive sampling, *A. ultimus* apparently is endemic to this crater lake.

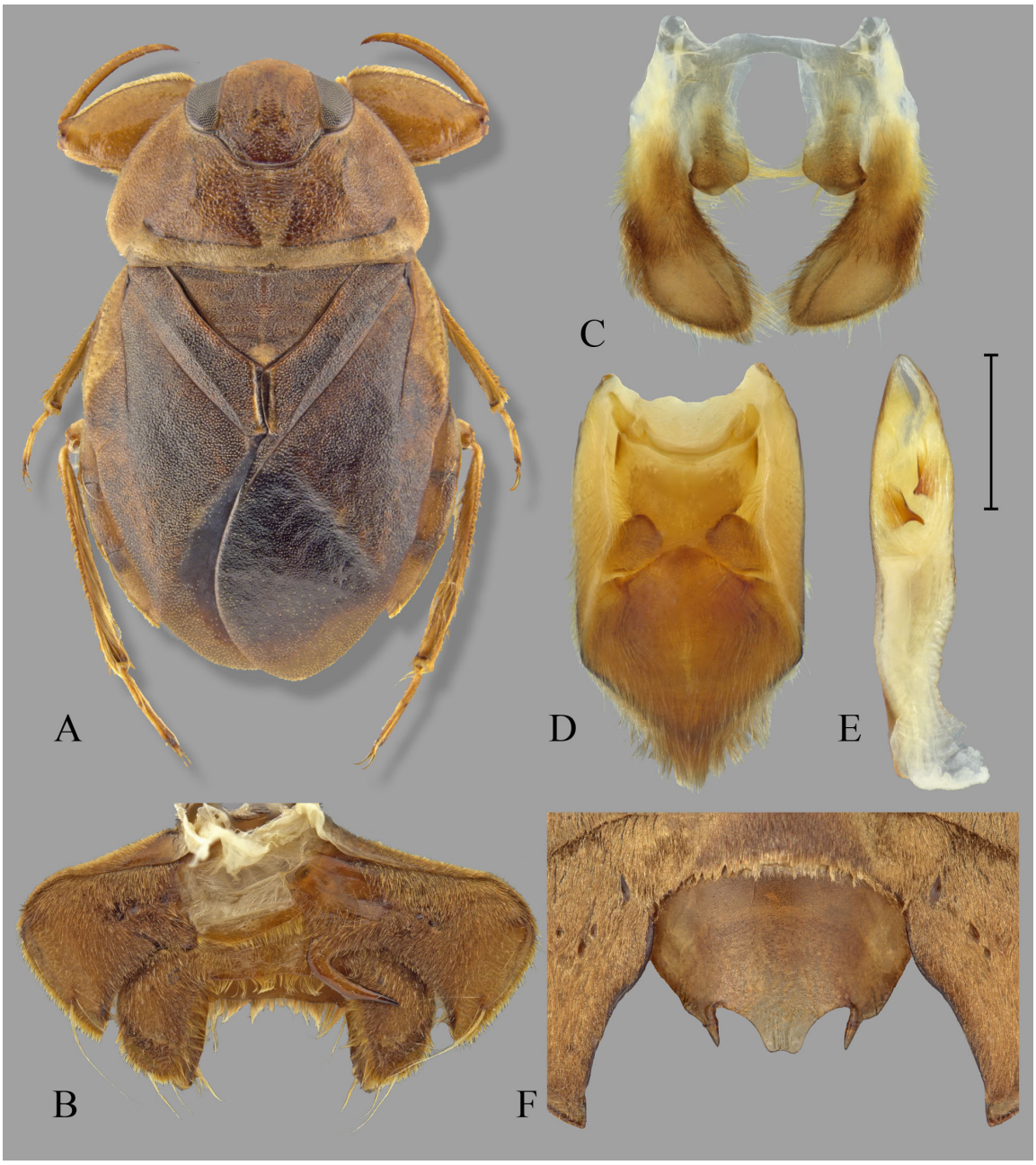

Figure 11. Structures of *Ambrysus ultimus*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) genital capsule of male (phallosoma removed), (E) ventral side of phallosoma, (F) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Variation. Some specimens exhibited the AGP slightly curved to right at mid-length. The central lobe on the posterior margin of the SGP can be produced further posteriorly than the posterolateral corners.

Type Locality. México: Puebla: Mpio. Tepeyahualco de Hidalgo, Laguna de Alchichica.

Repository. Holotype is housed at the ZSM.

Distribution. This species is known to occur only in Lake Alchichica in the state of Puebla. This crater lake is situated on the western part of the Transmexican Volcanic Belt biogeographic province (Fig. 4).

Published Records. México: Puebla (La Rivers 1976).

Type Material Examined. No type material of *A. ultimus* was examined during this study.

Material Examined. MÉXICO: PUEBLA: [Mpio. Tepeyahualco de Hidalgo], Alchichica, Puebla, 16-VIII-74, Harry Brailovsky Col. (9♂, 13♀ CNIN); same but / *Ambrysus ultimus* La Rivers det. R. W. Sites 2011 (1♂ CNIN); [Mpio. Tepeyahualco de Hidalgo], Alchichica, Puebla, 16-VIII-74, Harry Brailovsky Col. /*Ambrysus hybridus* Montandon 1897 (Ira La Rivers) (1♂ CNIN); same but / *Ambrysus ultimus* La Rivers det. R. W. Sites 2011 (1♀ CNIN); Alchichica, Puebla, 16-VIII-74, Harry Brailovsky Col. / *Ambrysus ultimus* La Rivers det. R. W. Sites 2010 (1♂ CNIN); [Mpio. Tepeyahualco de Hidalgo], Alchichica, Puebla, Brailovsky, 1975 Feb 20 / *Ambrysus hybridus* Montandon 1897 (Ira La Rivers) (1♂, 1♀ CNIN); same but 20-II-75 (1♂, 1♀ CNIN); [Mpio. Tepeyahualco de Hidalgo], Alchichica, Puebla, 7-IX-77 (1♀ CNIN); [Mpio. Tepeyahualco de Hidalgo], Alchichica, Puebla, Mexico, 7-IX-77, Harry Brailovsky Col. (2♂, 2♀ CNIN); same but 17-IX-77 (7♂ CNIN); same but / *Ambrysus hybridus* Montandon det. J. Polhemus (1♂, 3♀ CNIN); [Mpio. Tepeyahualco de Hidalgo], Alchichica, 5-X-85, Col. J. Bueno (2♂, 3♀ CNIN); same but / *Ambrysus ultimus* La Rivers det. R. W. Sites 2011 (1♀ CNIN); [Mpio. Tepeyahualco de Hidalgo], Alchichica,

05-Abril-2011, *Ambrysus ultimus* R. Novelo col. y det. (9♂, 5♀ IEXA); [Mpio. Tepeyahualco de Hidalgo], Lago Alchichica, XII-19-1948 / H. B. Leech Collector (1♂ CAS); [Mpio. Tepeyahualco de Hidalgo], Laguna de Alchichica, 5 April 2011, L-1293, colls: Sites, Shepard, Amaya & Novelo / 2329 m, 19º 24.532' N, 97º 23.833' W, shallow water, under rocks (6♂, 6♀ UMC); Mpio. Tepeyahualco de Hidalgo, Laguna de Alchichica, 2331 m, 02 June 2012, L-1409 / 19º 24' 25.8" N, 97º 23' 54" W, DRV & PRH Colls. (66♂, 41♀ UMC); [Mpio. Tepeyahualco de Hidalgo], Laguna de Alchichica, under tufa deposits at lake margin, 17 June 2013, L-1560 / Sites, DRV, PRH & Shepard, 19º 24' 25.2" N, 97º 23' 55.1" W, 2324 m (59♂, 49♀ UMC); [Mpio. Tepeyahualco de Hidalgo], Lake Alchichica near Alchichica Alt. ≈ 7500 [ft.], Aug. 28, 1951(4♂, 10♀ UMMZ); [Mpio. Tepeyahualco de Hidalgo], Loc. J. Bueno, Alchichica, Puebla, 20-II-75 / H. Brailovsky A. det. *Ambrysus hybridus* (1♂, 1♀ CNIN); Salayeta, Laguna de Alchichica, N19º25' W97º24' WDS.A. 1863 / William Shepard leg. (6♂, 4♀ EMEC).

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References Cited

Armienta, M. A., G. Vilacra, S. de la Cruz-Reyna, S. Ramos, N. Ceniceros, O. Cruz, A. Aguayo & F. Arcega-Cabrera. 2008. Water chemistry of lakes related to active and inactive Mexican volcanoes. Journal of Volcanology and Geothermal Research 178: 249–258.

Champion, G. C. 1901. Fam. Naucoridae, pp. 354–361. *In*: Godman F. D. & O. Salvino (eds.). Biologia Centrali-Americana Vol. II Rynchota. Hemiptera-Heteroptera. R. H. Porter, London, [1897–1901].

Davis, J. R. 1986. New distributional records of Naucoridae (Hemiptera) from the United States and Mexico, with morphological and taxonomic notes. The Southwestern Naturalist 31: 535–539.

De Carlo, J. A. 1950. Géneros y especies de la subfamilia Ambrysinae Usinger (Hemiptera-Naucoridae). Anales de la Sociedad Científica Argentina 150: 3–27.

Gadsden, H. & P. Reyes-Castillo. 1991. Caracteres del ambiente físico y biológico de la Reserva de la Biósfera "La Michilía", Durango, México. Folia Entomológica Mexicana 81: 1–19.

Kirkaldy, G. W. & J. R. de la Torre-Bueno. 1909. A catalogue of American aquatic and semiaquatic Hemiptera. Proceedings of the Entomological Society of Washington 10: 173–215.

La Rivers, I. 1951a. A revision of the genus *Ambrysus* in the United States (Hemiptera: Naucoridae). University of California Publications in Entomology 8: 277–338.

La Rivers, I. 1951b. Two new Ambrysi from South America (Hemiptera, Naucoridae). Proceedings of the Entomological Society of Washington 53: 288–293.

La Rivers, I. 1952. A new subgenus of *Ambrysus* from South America (Hemiptera: Naucoridae). Entomological News 63: 33–39.

La Rivers, I. 1953a. The *Ambrysus* of Mexico (Hemiptera, Naucoridae). The University of Kansas Science Bulletin 35: 1279–1349.

La Rivers, I. 1953b. Two new naucorid bugs of the genus *Ambrysus*. Proceedings of the United States National Museum 103: 1–7.

La Rivers, I. 1958. New *Ambrysus* records for Mexico (Hemiptera, Naucoridae). Proceedings of the Entomological Society of Washington 60: 71–74.

La Rivers, I. 1962. A New species of *Ambrysus* from Mexico (Hemiptera: Naucoridae). The Wasmann Journal of Biology 20: 129–133.

La Rivers, I. 1965. The subgenera of the genus *Ambrysus*. Biological Society of Nevada Occasional Papers 4: 1–7.

La Rivers, I. 1970. A new *Ambrysus* from Venezuela (Hemiptera, Naucoridae). The Great Basin Naturalist 30: 1–4.

La Rivers, I. 1971. Studies of Naucoridae (Hemiptera). Biological Society of Nevada Memoirs 2: 1–120.

La Rivers, I. 1974. Catalogue of taxa described in the family Naucoridae (Hemiptera), Supplement No.1: Corrections, emendations and additions, with descriptions of new species. Biological Society of Nevada Ocassional Papers 38: 1–17.

La Rivers, I. 1976. Supplement No. 2 to the catalogue of taxa described in the family Naucoridae (Hemiptera) with descriptions of new species. Biological Society of Nevada Occasional Papers 41: 1–17.

La Rivers, I. & N. Nieser. 1972. The *Ambrysus* of Surinam, with the description of a new species, *A. bifidus* (Hemiptera, Naucoridae). Biological Society of Nevada Occasional Papers 29: 1–8.

Montandon, A. L. 1897. Hemiptera Cryptocerata. Fam. Naucoridae. Sous-fam. Cryptocricinae. Verhandlungen der kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien 47: 6–23.

Montandon, A. L. 1909. Tableau synoptyque des *Ambrysus* et descriptions d'espèces nouvelles. Bulletin de la Société des Sciences de Bucarest-Roumanie 17: 316–330.

Nieser, N., A. Pelli & A. L. De Melo. 1999. Two new Ambrysinae (Heteroptera: Naucoridae) from Minas Gerais, Brazil. Acta Societatis Zoologicae Bohemicae 63: 157–163.

Polhemus, J. T. 1973. Notes on aquatic and semiaquatic Hemiptera from the southwestern United States (Insecta: Hemiptera). Great Basin Naturalist 33: 113–119.

Polhemus, J. T. & D. A. Polhemus. 1981. Three new species of *Ambrysus* from Mexico (Hemiptera: Naucoridae). The Pan-Pacific Entomologist 57: 397–401.

Polhemus, J. T. & D. A. Polhemus. 1983. Notes on Neotropical Naucoridae II. A new species of *Ambrysus* and review of the genus *Potamocoris* (Hemiptera). The Pan–Pacific Entomologist 58: 326–329.

Sites, R. W. & D. Reynoso-Velasco. 2015. Review of the *Ambrysus stali* La Rivers species complex (Heteroptera: Nepomorpha: Naucoridae) with the description of a new species from Mesoamerica. Zootaxa 4018: 279–291.

Sites, R. W., M. R. Willig & R. S. Zack. 1996. Morphology, ontogeny, and adaptation of *Ambrysus mormon* (Hemiptera: Naucoridae): Quantitative comparisons among population in different thermal environments. Annals of the Entomological Society of America 89: 12–19.

Suárez-Morales, E., O. Barrera-Moreno & J. Ciros-Pérez. 2013. A new species of *Cletocampus* Schmankewitsch, 1875 (Crustacea, Copepoda, Harpacticoida) from high altitude saline lake in Central Mexico. Journal of Limnology 72: 313–325.

Torre-Bueno, J. R. de la. 1906. The Cryptocerate Hemiptera of America in the writings of professor Arnold L. Montandon. Proceedings of the Entomological Society of Washington 8: 45–58.

Usinger, R. L. 1946. Notes and descriptions of *Ambrysus* Stal with an account of the life history of *Ambrysus mormon* Montd. (Hemiptera, Naucoridae). The University of Kansas Science Bulletin 31: 185–210.

Van Duzee, E. P. 1923. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The Hemiptera (true bugs, etc.). Proceedings of the California Academy of Sciences, 4th Series, 12: 123–200.

CHAPTER V

Revision of the *Ambrysus guttatipennis* Stål species complex (Heteroptera: Nepomorpha: Naucoridae) with the descriptions of six new species from Mexico

Abstract

The North American *Ambrysus guttatipennis* Stål species complex is revised and includes *A. arizonus* La Rivers, *A. drakei* La Rivers, *A. guttatipennis* Stål, *A. mexicanus* Montandon, and *A. mormon* Montandon. Six new species that belong to this complex are described from Mexico: *A. ayoyolin* **n. sp.**, A. *bowlesi* **n. sp.**, *A. contrerasi* **n. sp.**, *A. itsipatsari* **n. sp.**, *A. noveloi* **n. sp.**, and *A. veracruzanus* **n. sp.** The subspecies *A. mormon australis* La Rivers, *A. m. heidemanni* Montandon, and *A. m. minor* La Rivers are proposed as junior synonyms of *A. m. mormon* Montandon. A supplemental redescription of *A. guttatipennis* Stål based on the holotype is provided. Most of the species in this complex occur only in Mexico, although *A. arizonus* and *A. mormon* are distributed in Mexico and the United States. *Ambrysus mormon* has the widest distribution of any species in this complex. Features uniting these species are related to male genitalia and structures associated with the male and female genitalia.

Introduction

The genus *Ambrysus* Stål (Naucoridae: Cryphocricinae: Ambrysini) currently comprises 83 described species and its distribution extends from the northern United States (La Rivers 1951a) south to Argentina (La Rivers 1971). *Ambrysus* is divided into five subgenera: *Ambrysus*, *Acyttarus*, *Melloiella*, *Picrops*, and *Syncollus* (La Rivers 1952,

1965; Nieser et al. 1999); *Ambrysus* is the most species-rich subgenus with 70 described species.

La Rivers (e.g., 1951a, b; 1953) made reference to distinct species complexes within the subgenus *Ambrysus*, but in most cases did not provide supporting evidence. As originally proposed by La Rivers (1951a), the genus was divided into the *Coalescens* and *Disjunctus* divisions. The former division included two species complexes (*oblongulus, planus*), whereas the *Disjunctus* division included three species complexes for the South American species (*fossatus, fucatus, ståli*) and eight complexes (*californicus*, *funebris*, *melanopterus*, *pudicus*, *pulchellus*, *puncticollis*, *signoreti*, *vanduzeei*) for the North American species.

In a later paper, La Rivers (1965) elevated the *Coalescens* division to subgeneric rank as *Syncollus* and included seven species (*A. circumcinctus, A. geayi, A. maldonadus, A. montandoni, A. planus, A. pygmaeus, A. teutonius*), but he did not specify the status of the two species complexes (*planus*, *oblongulus*) previously considered (La Rivers 1951a) in the *Coalescens* division.

In his work on the *Ambrysus* of Mexico, La Rivers (1953) considered *A. pygmaeus* the most distinctive species of the *oblongulus* complex. Also, *A. teutonius* was placed in this complex (La Rivers 1951b). Later, the *oblongulus* complex was used to include the species *A. bifidus*, *A. oblongulus*, *A. scolius*, and *A. stali* (La Rivers 1970, La Rivers & Nieser 1972). The complex no longer included *A. pygmaeus* as was originally proposed (La Rivers 1953) or *A. teutonius*. A recent study (Sites & Reynoso-Velasco 2015) found that *A. oblongulus* is not closely related to the other three South American species in this complex as proposed by La Rivers (1970) and La Rivers & Nieser (1972);

thus, Sites & Reynoso-Velasco (2015) excluded this species from the group and placed the remaining three species together with *A. tricuspis* and *A. maya* in the denominated *A. ståli* complex. Sites & Reynoso-Velasco (2015) found that characteristics of the medial lobes of male tergum VIII (pseudoparameres) and the ventral side of the phallosoma include important features for recognition of species complexes (see also Chapters III & IV of this study).

La Rivers (1957a) first mentioned the *A. mexicanus* Montandon species complex when he described *A. drakei* from the northwestern state of Durango (Mexico). In this work, La Rivers (1957a) compared the *A. mexicanus* and *A. signoreti* Stål species complexes and assigned *A. drakei* to the latter complex.

Materials and Methods

This work represents the third contribution in a series of papers from a larger project to clarify the taxonomy of species in genus *Ambrysus* from Mexico (see chapters III & IV).

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. The holotypes were measured for body length and width and major structures, and all measurements are in mm. Body length and width also are given as a mean and range for paratypes. Length of the body is measured from the anterior margin of the head to the posterior margin of the abdomen, and width at the widest point, usually across the embolia. The species sizes reported in the Diagnosis sections are based on measurements from 20 specimens, except for *A. ayoyolin* **n. sp.** and *A. itsipatsari* **n. sp**., which are described based on 7 and 15 specimens, respectively.

Abdominal segment numbers are expressed as Roman numerals. The length of the posterolateral corners of the connexiva is an important feature; when cited in the Diagnosis sections, it refers to connexiva III–V in females and III–IV in males. The male accessory genitalic process of tergum VI in species of *Ambrysus* typically angles to the right at differing degrees. The angle is measured using the basal portion of the process as the axis from which the degree of departure of the distal portion can be measured (Fig. 1B). Images of all species were obtained by use of a Leica MZ16 stereo microscope coupled with the Leica Application Suite V4.4 Extended Depth of Focus module, followed by image preparation with Photoshop CS5 (Adobe Systems Inc., San Jose, California). The margin of the subgenital plate is an important diagnostic character in these species, but it often is difficult to discern because of heavy setation and lack of contrast with terminal segments. Thus, we removed the setae and terminal segments to enable a better view of this feature in the figures. Information given in brackets [ ] here did not appear on the labels or was not provided in publications, but was inferred from available data or represents corrections to misspellings on the labels, except for the information of *A. itsipatsari* **n. sp.** and *A. noveloi* **n. sp.,** which was provided by Rodolfo Novelo-Gutiérrez. A slash (/) separates data on different labels. Unless otherwise noted, all specimens were collected by Daniel Reynoso-Velasco (DRV) and Pedro Reynoso-Hernández (PRH). Specimens are deposited in the museums corresponding with the following abbreviations.

Museums and Collection Abbreviations

BMNH The Natural History Museum (London, England)

BYUC Brigham Young University (Provo, United States)

CAS California Academy of Sciences (San Francisco, United States)

CNIN Colección Nacional de Insectos (Mexico City, Mexico)

CSCA California State Collection of Arthropods (Sacramento, United States)

EMEC Essig Museum of Entomology Collection (Berkeley, United States)

FMNH Field Museum of Natural History (Chicago, United States)

IEXA Colección Entomológica del Instituto de Ecología A.C. (Xalapa, Mexico)

MNHN Muséum National d'Historie Naturelle (Paris, France)

SEMC Snow Entomological Collection, University of Kansas (Lawrence, United States)

SMNH Swedish Museum of Natural History (Stockholm, Sweden)

UAQE Colección Entomológica de la Universidad Autónoma de Querétaro (Juriquilla, Mexico)

UIEC University of Idaho Entomological Collection (Moscow, United States)

UMC University of Missouri (Columbia, United States)

UMMZ University of Michigan Museum of Zoology (Ann Arbor, United States)

USNM United States National Museum of Natural History (Washington D.C., United States)

WSUC Washington State University Collection (Pullman, United States)

Systematics

Discussion: When La Rivers (1957a) compared the *A. mexicanus* and *A. signoreti* species complexes, he described unifying characteristics of species in the *A. mexicanus*

complex to be: a) narrow body shape with narrow embolia, b) uniform coloration, and c) posterolateral corners of connexiva not produced. In contrast, the closely related species in the *A. signoreti* species complex presented: a) broad body shape with wide embolia, b) prominent maculation, and c) posterolateral corners of connexiva produced. Although La Rivers (1957a) provided diagnostic features to enable species to be assigned to these two complexes, he did not list the species included in each group, except for the type species of both groups (*A. mexicanus*, *A. signoreti*) and *A. drakei* which he assigned to the *A. signoreti* complex.

The posteriorly produced corners of the connexiva (connexival spination) were considered an important diagnostic feature of species in the *A. signoreti* complex (La Rivers 1957a). Based on the shape of the pseudoparameres and features of the ventral lobes of the phallosoma, *A. drakei* is more closely related to *A. mexicanus* than to *A. signoreti*. The posteriorly produced corners of the connexiva (spinose condition) is a feature also present in other species of *Ambrysus* that are not members of this species complex. Thus, the condition of the posterolateral corners of the connexiva is not an informative feature at the species complex level as was originally proposed by La Rivers (1957a). After he examined the type specimen of *A. signoreti* housed at the SMNH and found that the corners of the connexiva were not produced (La Rivers 1957b), La Rivers (1957a) stubbornly continued to consider the posteriorly produced corners of the connexiva an important feature of species in the *A. signoreti* complex.

Based on the shape of the pseudoparameres and characteristics of the ventral side of the phallosoma, the species closely related to *A. mexicanus* are: *A. arizonus*, *A. ayoyolin* **n. sp**, *A. bowlesi* **n. sp.**, *A.* contrerasi **n. sp.**, *A. guttatipennis*, *A. itsipatsari* **n.**

sp., *A. mormon*, *A. noveloi* **n. sp**., and *A. veracruzanus* **n. sp.** This species group should be referred to as the *A. guttatipennis* Stål complex because this was the first species in the complex to be described (Stål 1876).

Diagnosis: The most reliable unifying features among species in the *A. guttatipennis* complex include males with the left ventral lobe of the phallosoma lateroflexed at mid-length and the right ventral lobe lateroflexed in the proximal half (e.g., Figs. 11F, 12F), the overall similar shape of the accessory genitalic process of tergum VI (e.g., Fig. 12C), and the similar shape of the medial lobes (pseudoparameres) of abdominal tergum VIII (e.g., Fig. 15C). Females of this complex exhibit some degree of variation of a generalized shape of the subgenital plate (e.g., Figs. 5G, 11G), although these differences provide the most reliable interspecific diagnostic attributes.

Key to the species of the *Ambrysus guttatipennis* species complex

In this species complex, the female subgenital plate (SGP) is the most reliable diagnostic feature for species recognition. The accessory genitalic process (AGP) and pseudoparameres are instructive for males, although these features exhibit sufficient similarity among species in the complex that reliance on them alone can lead to misidentifications. Thus, collectors should endeavor to obtain multiple specimens at a site to maximize the likelihood that females will be represented. The key presented here relies heavily on females; males are included although clear interspecific distinctions sometimes are not possible. The female subgenital plates present five important features that are used throughout the following key and in the Annotated List of Species: 1) central lobe, 2) posterolateral lobe, 3) posterolateral corner, 4) lateral lobe, and 5) basal

lobe. The central lobe is present in all species in this complex except *A. mormon*, which is unique in having a central concavity with posterolateral lobes. All species present posterolateral corners, which can be acute or narrowly rounded. The lateral lobe is always on the left margin of the SGP (both margins in *A. ayoyolin* **n. sp.**) and its position can be at mid-length, subapical, or apical. The basal lobe on the left margin is present only in *A. ayoyolin* **n. sp**.

1. Posterolateral corner of connexiva III–IV not produced (Fig. 17D) or only slightly produced; if slightly produced, then length of posterolateral corner ≤ 1/10 the length of connexivum (Figs. 3D, 8D, 12D, 13D, 15D, 19D) 2

1'. Posterolateral corner of connexiva III–IV strongly produced; length of posterolateral corner ≥ 1/7 the length of connexivum (Figs. 1D, 5D, 11D, 16D).....8

2. Posterolateral corners of connexiva III–IV narrowly rounded and not produced (Fig. 17D). Female with central lobe of mediosternite VII (SGP) nearly parallel-sided and clearly produced posteriorly further than posterolateral corners (Fig. 17G). Male accessory genitalic process of tergum VI (AGP) evenly curved throughout (Fig. 17B). Body length < 9 mm .....*Ambrysus noveloi* **n. sp.**

2'. Posterolateral corners of connexiva III–IV slightly produced (Fig. 17D). Female with central lobe of SGP with sides clearly convergent posteriorly and shorter (Fig. 13), subequal to (Figs. 15G), or slightly longer than posterolateral corners (Figs. 8G, 12G, 19G), but if central lobe produced further than posterolateral corners then basal lobe on left margin (Fig. 3G). Male AGP evenly curved (Fig. 15B) or curved in basal half

and angled at mid-length (Figs. 8B, 12B), or curved in basal 2/3 and angled in distal 1/3 (Fig. 19B), or angled at approximately 40 degrees close to the base and angled again in distal 1/3 (Fig. 3B), or curved at approximately 90 degree angle close to the base (Fig. 13B). Body length ≥ 7.8 mm.....3

3. Female with central lobe of SGP much shorter than posterolateral corners (Fig. 13G). Male AGP curved to right at approximately 90 degree angle close to the base (Fig. 13B); pseudoparameres subtriangular, with posteromesal corner rounded, produced posteriorly, and bearing tightly arranged setae (Fig. 13C). Hemelytra light brown (Fig. 13A)..... *Ambrysus itsipatsari* **n. sp.**

3'. Female with central lobe of SGP subequal to (Figs. 15G) or longer than posterolateral corners (Figs. 3G, 8G, 12G, 19G). Male AGP curved or angled at approximately 40 degrees close to the base; pseudoparameres shaped otherwise (Figs. 3C, 8C, 12C, 15C, 19C). Hemelytra usually dark brown (Figs. 3A, 8A, 12A, 15A, 19A) 4

4. Female with left margin including lateral lobe of SGP expanded and flap-like, margin concave at mid-length (Fig. 15G); SGP with posterolateral corners and central lobe subequal in length, central lobe not deeply notched (Fig. 15G). Male AGP evenly curved throughout (Fig. 15B) ..... *Ambrysus mexicanus* Montandon

4'. Female with left margin of SGP with lateral lobe, but never expanded and flap-like (Figs. 3G, 12G, 8G, 19G); SGP with central lobe produced further than posterolateral corners. Male AGP not evenly curved throughout (Figs. 3B, 8B, 12B, 19B) 5

5. Female SGP with basal lobe on left margin and lateral lobes on both margins (Fig. 3G); wide central lobe produced further than posterolateral corners (Fig. 3G). Male pseudoparameres boot-shaped (Fig. 3C).....*Ambrysus ayoyolin* **n. sp.**

5'. Female SGP without basal lobe, lateral lobe only on left margin (Figs. 8G, 12G, 19G); central lobe and posterolateral corners subequal in length. Male pseudoparameres shaped otherwise (Figs. 8C, 12C, 19C).....6

6. Female SGP with lateral lobe subapical, right margin convex apically (Fig. 8G), concavity between central lobe and posterolateral corners rounded (Fig. 8G). Male AGP width approximately consistent throughout (Fig. 8B) .... *Ambrysus contrerasi* **n. sp.**

6'. Female SGP with lateral lobe at mid-length, right margin convex or concave apically (Figs. 12G, 19G), concavity between central lobe and posterolateral corners lanceolate (Fig. 12G) or rounded (Fig. 19G). Male AGP narrowed near base, expanded near distal angle (Figs. 12B, 19B) 7

7. Female SGP with left margin concave in apical 1/3 (Fig. 12G), concavity between central lobe and posterolateral corners lanceolate (Fig. 12G). Male tergum VIII with pseudoparameres approximately as wide as narrowest point of lateral lobes. Body length > 11.50 mm .....*Ambrysus guttatipennis* Stål

7'. Female SGP with left margin convex throughout (Fig. 19G), concavity between central lobe and posterolateral corners rounded (Fig. 19G). Male tergum VIII with

pseudoparameres approximately 2/3 as wide as narrowest point of lateral lobes (Fig. 19B). Body length < 11.00 mm ..... *Ambrysus veracruzanus* **n. sp.**

8. Female SGP with a central concavity bounded by short (Fig. 16G) or long posterolateral lobes. Male AGP evenly curved to right in basal 2/3 and angled in distal 1/3 (Fig. 16B); pseudoparameres parallel-sided and angled posterolaterad at mid-length (Fig. 16C) ..... *Ambrysus mormon* Montandon

8' Female SGP with a central lobe (Figs. 1G, 5G, 11G). Male AGP evenly curved throughout (Figs. 5B, 11B) or curved in basal 1/3 then nearly straight without distal angle (Fig. 1B); pseudoparameres not angled posterolaterad, may be widened posterolaterally (Figs. 1C, 11C) or produced posteromesally (Figs. 5C) 9

9. Female SGP with notched central lobe appearing as two separate lobes, thus, posterior margin appears tetralobate (Fig. 1G); lateral margins convex apically. Male lateral lobes of tergum VIII with apices truncate (Fig 1C); AGP curved in basal 1/3 then nearly straight without distal angle (Fig. 1B) ..... *Ambrysus arizonus* La Rivers

9'. Female SGP with central lobe shallowly concave medially, thus, posterior margin appearing trilobate (Figs. 5G, 11G); lateral margins concave apically. Male lateral lobes of tergum VIII with apices rounded (Fig. 5C, 11C); AGP evenly curved throughout (Figs. 5B, 11B) 10

10. Lateral margin of embolium expanded and clearly surpassing lateral margin of abdomen (Fig. 5A). Female SGP with left margin not expanded and flap-like, with lateral lobe subapical (Fig. 5G)..... *Ambrysus bowlesi* **n. sp.**

10' Lateral margin of embolium only slightly surpassing lateral margin of abdomen (Fig. 11A). Female SGP with left margin laterally expanded and flap-like, with lateral lobe apical (Fig. 11G) .....*Ambrysus drakei* La Rivers

Annotated List of Species

***Ambrysus arizonus* La Rivers**
(Figs. 1–2)

A. arizonus La Rivers 1951a: Univ. Calif. Publ. Entomol. 8: 320–322 (original description).

Diagnosis. This is a large species at 11.20–14.08 mm in length that can be distinguished from the other species in this complex with strongly produced, spinose posterolateral corners of the connexiva (Figs. 1A, D) by females with a tetralobate posterior margin of the SGP (Fig. 1G). In *A. bowlesi* **n. sp.** and *A. drakei*, the central lobe has a shallow concavity and thus the posterior margin appears trilobate (Figs. 5G, 11G); *A. mormon* appears bilobed with a pronounced central concavity (Fig. 16G). Males of *A. arizonus* differ from all others in the complex by truncate apices of the lateral lobes of tergum VIII (Fig. 1C). Further, males present the AGP curved to the right at an approximately 80 degree angle close to the base to continue almost straight (Fig. 1B). The

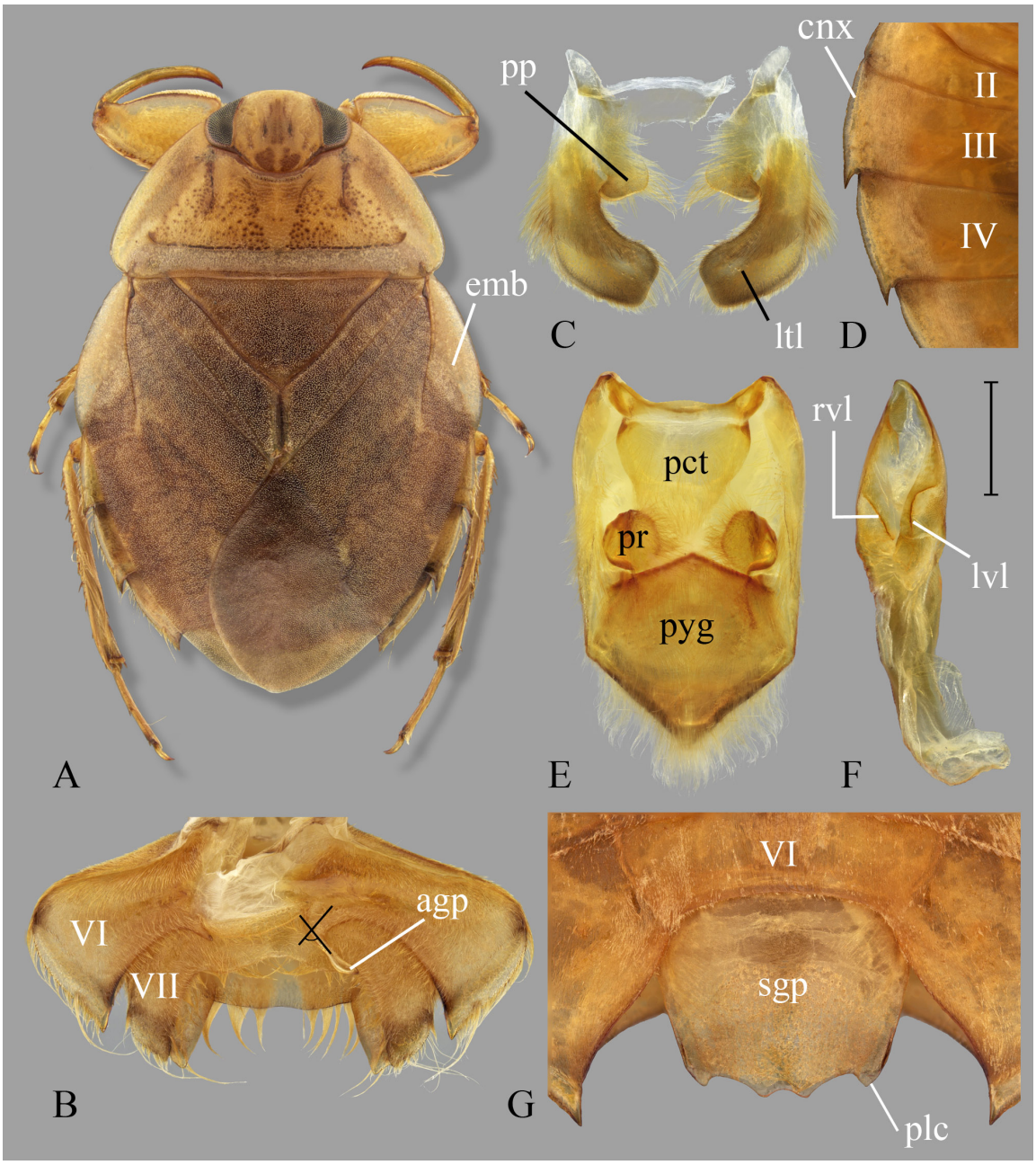

Figure 1. Structures of *Ambrysus arizonus*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, angle of curvature of the agp is determined as indicated by black lines, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed). agp = accessory genitalic process, cnx = connexivum, emb = embolium, ltl = lateral lobe, lvl = left ventral lobe, pct = proctiger, plc = posterolateral corner, pp = pseudoparamere, pr = paramere, pyg = pygophore, rvl = right ventral lobe, sgp = subgenital plate.

pseudoparameres have the posteromesal corner broadly rounded and not produced (Fig. 1C) and the parameres are rounded (Fig. 1E).

Discussion. This is a relative large species described from a small series of specimens collected in the southwestern state of Arizona, United States (La Rivers 1951a). La Rivers (1953) considered that some of the records of *A. signoreti* from the United States were actually based on misidentified specimens belonging to different species that included *A. arizonus.*

Variation. No variation was detected in the diagnostic features.

Type Locality. United States: Arizona: Pinal Co., Florence.

Repository. Holotype is housed at the SEMC.

Distribution. In the Unites States, *A. arizonus* is distributed in the southern area of the Basin and Range geophysical region of Arizona. In Mexico, this species is present only in the Sonora biogeographic province (Fig. 2).

Published Records. United States: Arizona (La Rivers 1951a, 1971; Davis 1986)

Type Material Examined. HOLOTYPE ♂: **[UNITED STATES: ARIZONA:** Pinal Co.**]**, Florence, VII-26-03, Ariz., C. R. Biederman / *Ambrysus arizonus* La Rivers HOLOTYPE / 1948 *Ambrysus arizonus* La Rivers determined by Ira La Rivers. PARATYPE: same but / [Phil. ?] / *Ambrysus signoreti* Stal / Ambrysus *arizonus* La Rivers ALLOTYPE (1♀ SEMC).

Material Examined. MÉXICO: SONORA: [Mpio. Bavicora], Río Sonora, Bavicora, ≈60 mi. (by road) S. of Arizpe, Sonora, R. G. Miller, III:11:1941, Rig. no. X6:41, Acc. 1941-V-14 Fish Div. (1♀ UMMZ); Río Altar, & [8 ?] mi. NE. of Altar flood trib. to Gulf

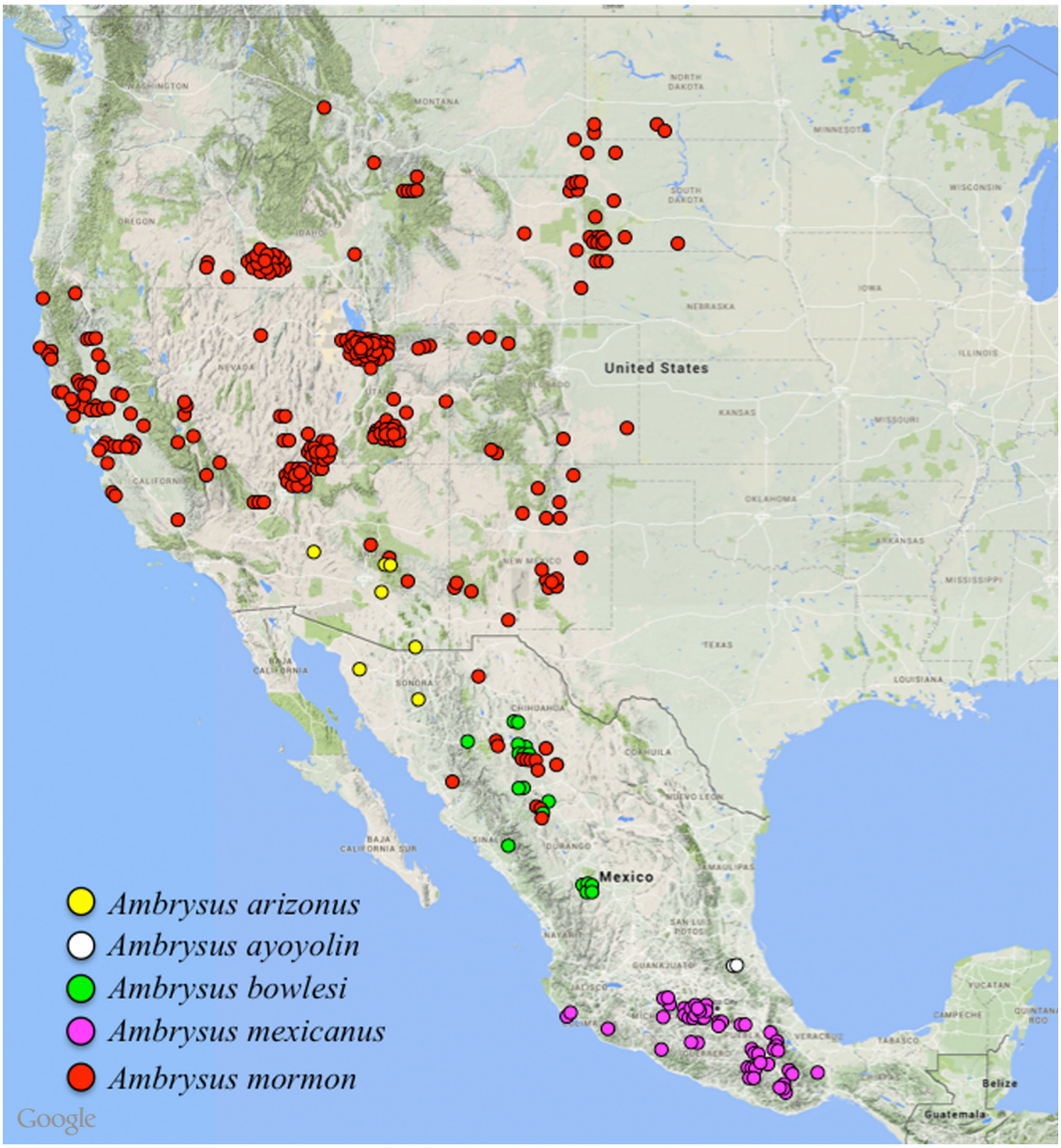

Figure 2. Distribution of *Ambrysus arizonus*, *A. ayoyolin* **n. sp.**, *A. bowlesi* **n. sp.**, *A. mexicanus,* and *A. mormon* in North America.

of California, 09 March 1941, R. G. Miller, XI-41 / *Ambrysus* sp. (Hemiptera: Naucoridae) (1♀ UMMZ). **UNITED STATES: ARIZONA:** Cochise Co., San Pedro River, ca. 8 mi. E of State Hwy 92, 25 April 1950, M50-55, coll: R. R. Miller & party / *Ambrysus arizonus* La Rivers det. R. W. Sites (9♂, 5♀ UMC); Gila Co. 5.4 mi S Jake's Corner, Hwy 188, Tonto Ck., 2 September 1990, coll: J. D. York / *Ambrysus arizonus* La

Rivers det. R. W. Sites (1♂ UMC); Gila Co. 5.4 mi S Jake's Corner, off Hwy 188, Tonto Ck., 2 September 1990, coll: D. P. Hermann (4♀ UMC); same but / *Ambrysus arizonus* La Rivers det. R. W. Sites (7♂, 5♀ UMC); same but / shallow water (3♂, 5♀ UMC); Gila Co. 5.4 mi S Jake's Corner, off Hwy 188, Tonto Ck., 2 Sept 1990, coll: D. P. Hermann, shallow water / *Ambrysus arizonus* La Rivers det. R. W. Sites (14♂, 12♀ UMC); Gila Co. Tonto Ck., 5.4 mi S Jakes Corner, hwy 188, 20 Nov. 1990, coll: J. A. Back, aquatic vegetation/algae / *Ambrysus arizonus* La Rivers det. R. W. Sites (1♀ UMC); Mohave Co., Williams River & [at ?] Silver Field Mine camp, 30 mi NE Bouse, 7 April 1950, Miller & Winn, M50-30 / *Ambrysus arizonus* La Rivers det. R. W. Sites (1♀ UMC).

Ambrysus ayoyolin **Reynoso & Sites NEW SPECIES**

(Figs. 2, 3–4)

Description. Submacropterous female. HOLOTYPE, length 9.60; maximum width 5.84. Paratypes (n = 3), length 9.44–9.92 (mean = 9.60); maximum width 5.84–6.08 (mean = 5.97). General shape elongate, parallel-sided; widest across embolia (Fig. 3A). Overall dorsal coloration of hemelytra dark brown, lighter on clavus; pronotum and head pale yellow with dark brown marks; legs light brown. Dorsal surface coarsely punctate. Ventral coloration of head pale yellow, thorax light brown to dark brown, abdomen dark brown with brown pubescence.

Head. Head length 1.72; maximum width 2.76. Mostly pale yellow with brown posteriorly; coarsely punctate. Eyes convergent anteriorly, synthlipsis 1.32; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of

eyes 8.1% of head length; posterior margin between eyes strongly convex, extending posteriorly 24.4% of head length. Labrum width 1.6× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.40 beyond labrum not including extruded stylets. Antennal proportions 3:12:15:7, length 0.74, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color pale yellow, brown markings, brown line behind eyes; transverse sulcus marking anterior border of transverse band in posterior 1/4; transverse band pale yellow; lateral margins brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.9× length; length at midline 1.76; maximum width at posterolateral corners 5.12. Prothorax ventrally pruinose throughout, except lateral 1/8; apices of propleura meeting at midline, not appressed to prosternellum; propleuron dark brown, medial 2/3 of posterior margin with golden setae. Probasisternum with sharp median carina and row of setae lateral to carina. Scutellum coarsely punctate, triangular, brown, light brown coloration along midline and on anterior and posterior apices, width 2.3× length, width 3.60, length 1.58. Hemelytra densely punctate, dark brown, length 6.84 (chord measurement). Clavus lighter in color, length 4.6× width, length 3.72, width 0.80; claval commissure dark brown, length 1.04. Embolium length 2.84, greatest width 0.94; lateral margin convex, pale yellow in anterior 2/3, dark brown posteriorly. Hind wings extending to middle of tergum VI. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina broad and narrowly

acuminate.

Legs. All legs segments light brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to five spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.32, tibia 1.84, tarsus 0.44; middle leg, femur 2.36, tibia 2.04, tarsomeres 1–3, 0.20, 0.64, 0.46; hind leg, femur 2.96, tibia 3.36, tarsomeres 1–3, 0.24, 0.76, 0.59.

Abdomen. Dorsally with connexiva of III–VI exposed, laterotergites light brown; lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners. Posterolateral corner of II (visible ventrally) narrowly rounded to right angled, III–V acute and spinose, VI–VII bluntly acute. Ventrally dark brown with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous

rounded to oval patches around spiracles on laterosternites II–VI. Mediosternite VII (subgenital plate) width 1.3× length, length at midline 1.06, maximum width 1.36; left margin with basal pointed lobe deflexed ventrad; each lateral margins with apical, pointed, lateral lobe; posterior margin with posterolateral corners pointed; wide central lobe deeply notched giving appearance of two pointed lobes bounding a concavity; central lobe produced posteriorly further than posterolateral corners (Fig. 3G).

Submacropterous male. Paratypes (n = 3), length 8.64–9.12 (mean = 8.80); maximum width 5.36–5.68 (mean = 5.54). Coloration, setation, pronotum proportions, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for holotype. Otherwise hind wings extending to middle of tergum V. Accessory genitalic process of tergum VI curved to right at approximately 40 degree angle close to base, distal 1/3 angled to right to continue almost perpendicular to the body axis, widest at angle (Fig. 3B). Medial lobes of tergum VIII (pseudoparameres) symmetrical, boot-shaped (Fig. 3C). Phallosoma elongate, linear, constricted basally; left ventral lobe lateroflexed at mid-length, right ventral lobe lateroflexed in proximal half (Fig. 3F). Parameres symmetrical, slightly longer than wide, mesal margin straight, setae emanating from distal 1/3 of dorsal surface. Proctiger almost as long as width at base. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 3E).

Variation. The pale yellow color on the pronotum and head can be light brown. Two females each presented light brown triangular and oval marks at the lateral and posterior margins of the corium, respectively. The abdomen can have medium brown coloration instead of dark brown. Females can present the left margin of the SGP with the basal

lobe and the lateral lobe rounded.

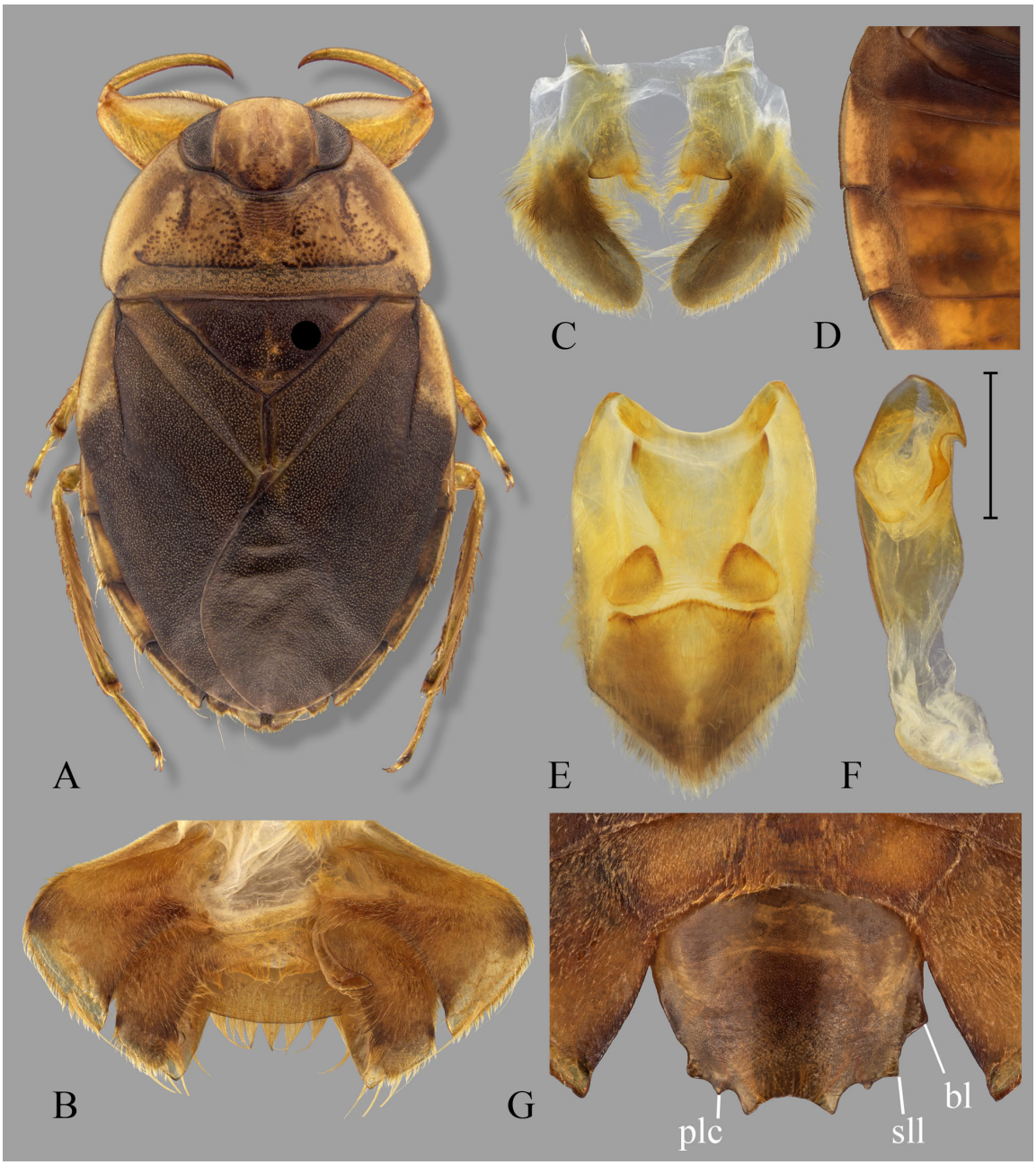

Figure 3. Structures of *Ambrysus ayoyolin* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed). bl = basal lobe, plc = posterolateral corner, sll = sublateral lobe.

Discussion. This species exhibits similar diagnostic features as those of *A. mexicanus*

and *A. veracruzanus* **n. sp.,** although it has lighter coloration on the clavus and features of the SGP support the concept of *A. ayoyolin* as a distinct species.

Diagnosis. This is a medium sized species at 8.64–9.92 mm in length that can be distinguished from the other species in this complex with posterolateral corners of the connexiva slightly produced (Figs. 3A, D) by the presence of an apical, pointed lateral lobe on both margins of the SGP and a pointed basal lobe on the left margin. The central lobe on the posterior margin of the SGP is widely concave giving the impression of two pointed lobes bounding a central concavity (Fig. 3G). Males present the AGP curved to the right at an approximately 40 degree angle close to the base and angled to the right at the distal 1/3, then continuing almost perpendicular to the body axis (Fig. 3B). The pseudoparameres are boot-shaped (Fig. 3C).

Habitat Description. The type locality (Fig. 4A) was a seepage over bedrock with algae and marginal vegetation composed mostly of grasses, which is an atypical habitat for a saucer bug. The specimens were collected from rootmats of the marginal vegetation (Fig. 4B).

Distribution. This species is only known from two localities in the municipality of Tlanchinol in the state of Hidalgo. Both localities are in the Sierra Madre Oriental biogeographic province (Fig. 2).

Etymology. The specific epithet *"ayoyolin*" is a noun in apposition derived from the Classical Nahuatl word âyôyôlin, which means "aquatic insect."

Repository. The holotype and one paratype will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the Enns Entomology Museum (University of Missouri).

Figure 4. Type locality of *Ambrysus ayoyolin* **n. sp.** in the state of Hidalgo (México). (A) general habitat, (B) specific habitat.

Type Material Examined. HOLOTYPE ♀. **MÉXICO: HIDALGO:** Mpio. Tlanchinol, ca. 2 km W of Chalchocotipa, 21° 02' 53.4" N, 98° 35' 40.5" W, 681 m, 06 June 2013, L-1523, DRV, Sites, Shepard & PRH colls. PARATYPES: same data as holotype (1♂ CNIN; 1♂, 3♀ UMC); Mpio. Tlanchinol, road to Sta. Maria Catzotipan, 0.8 km W of jct. with Hwy. 105, km 3 + 400, 528 m, 21° 02' 36.4" N, 98 36' 00.8" W, 06 June 2013, L-1522, Sites, DRV, PRH & Shepard colls. (1♂ UMC).

Ambrysus bowlesi Reynoso & Sites NEW SPECIES
(Figs. 2, 5–7)

Description. Macropterous female. HOLOTYPE, length 13.28; maximum width 9.52. Paratypes (n = 10), length 12.00–14.56 (mean = 13.35); maximum width 8.00–10.72 (mean = 9.28). General shape elongate, widest across embolia (Fig. 5A). Overall dorsal coloration of hemelytra dark brown with light brown oval and triangular marks at lateral and posterior margins of corium, respectively; pronotum and head light brown with dark brown marks; legs yellowish brown. Dorsal surface coarsely punctate. Ventral coloration of head pale yellow, thorax yellow, abdomen with yellowish pubescence.

Head. Head length 2.16; maximum width 3.44. Mostly light brown with brown medially and posteriorly; coarsely punctate. Eyes convergent anteriorly, synthlipsis 1.64; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 5.5% of head length; posterior margin between eyes strongly convex, extending posteriorly 25% of head length. Labrum width 2.1× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.52 beyond labrum not including extruded stylets. Antennal proportions 5:14:17:10, length 0.92, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color light brown, extensive brown markings, brown line behind eyes; transverse sulcus marking anterior border of transverse band in posterior 1/3; transverse band light brown anteriorly, brown posteriorly; lateral margins brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.9× length; length at midline 2.52; maximum width at posterolateral corners 7.28. Prothorax ventrally pruinose throughout, except lateral 1/8; apices of propleura meeting at midline, not appressed to prosternellum; propleuron yellow, brown posteriorly, medial 2/3 of posterior margin with golden setae. Probasisternum with sharp median carina and row of setae lateral to carina. Scutellum coarsely punctate, triangular, brown, light brown coloration along margins and middle and on anterior and posterior apices, width 2.0× length, width 4.80, length 2.36. Hemelytra densely punctate, dark brown, length 9.76 (chord

measurement); corium with light brown oval and triangular marks at lateral and posterior margins, respectively. Clavus dark brown, length 4.4× width, length 5.44, width 1.24; claval commissure black, length 1.94. Embolium length 4.48, greatest width 1.96; lateral margin convex, light brown in anterior 2/3, dark brown posteriorly. Hind wings extending to middle of tergum VI. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments yellowish brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to five spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 3.20, tibia 2.52, tarsus 0.52; middle leg, femur 3.40, tibia 3.08, tarsomeres 1–3, 0.22, 0.56, 0.58; hind leg, femur 4.48,

tibia 6.40, tarsomeres 1–3, 0.30, 1.04, 0.78.

Abdomen. Dorsally with connexiva of III–V exposed, each laterotergite light brown with dark brown at anterior and posterior ends, giving checkered appearance (Fig. 5A); lateral margin finely serrate, marginal row of intermixed short and long yellow setae, group of trichobothria near posterolateral corners. Posterolateral corner of II (visible ventrally) narrowly rounded to right angled, III–VI acute, spinose, VII bluntly acute. Ventrally yellowish, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VI. Mediosternite VII (subgenital plate) width 1.2× length; length at midline 1.44; maximum width 1.80; lateral lobe subapical, posterior margin with posterolateral corners pointed, notched central lobe produced posteriorly slightly further than posterolateral corners (Fig. 5G).

Macropterous male. Paratypes (n = 10), length 11.04–12.80 (mean = 12.20); maximum width 7.84–9.28 (mean = 8.66). Coloration, setation, pronotum proportions, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for holotype. Otherwise hind wings extending to posterior margin of tergum V. Accessory genitalic process of tergum VI evenly curved to right, not expanded distally (Fig. 5B). Medial lobes of tergum VIII (pseudoparameres) symmetrical, posteromesal corner narrowly rounded and produced, posterolateral corner broadly rounded. (Fig. 5C). Phallosoma elongate, linear, constricted basally; left ventral lobe lateroflexed at mid-length, right ventral lobe lateroflexed in proximal half (Fig. 5F). Parameres symmetrical, longer than wide, mesal margin slightly convex, setae emanating from distal 1/3 of dorsal surface. Proctiger length subequal to width at base. Pygophore with elongate setae

sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 5E).

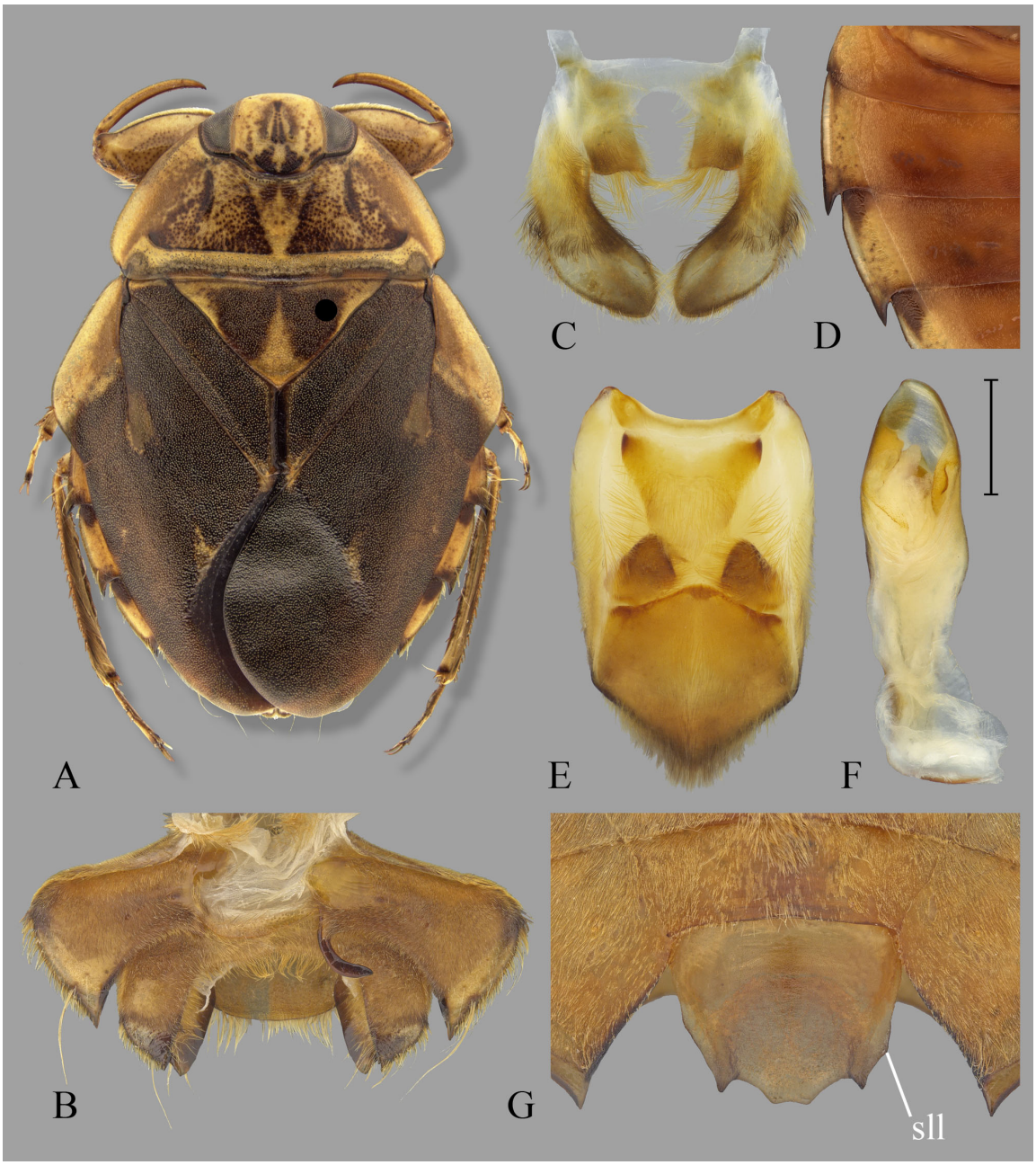

Figure 5. Structures of *Ambrysus bowlesi* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed). sll = sublateral lobe.

Variation. Males can present the AGP slightly angled to the right at mid-length to

extend almost perpendicular to the body axis in its distal half.

Discussion. This large species is similar to *A. guttatipennis*, but can be easily distinguished from the latter by the spinose posterolateral corners of the connexiva, a character shared with *A. arizonus*, *A. drakei*, and *A. mormon*. The presence of expansively wide embolia surpassing the lateral sides of the abdomen is a character present only in the two Mexican species *A. inflatus* and *A. plautus*, both of which are in different species complexes. *Ambrysus drakei* and *A. mormon* present embolia that barely surpass the lateral sides of the abdomen.

Figure 6. Specimen of *Ambrysus bowlesi* **n. sp.** in its natural habitat at Río Satevo (Chihuahua, México).

Diagnosis. This is a large species at 11.04–14.56 mm in length that can be distinguished from the other species in this complex with spinose posterolateral corners of the connexiva strongly produced by the expansively wide embolia (Figs. 5A, 6). Females have a trilobate posterior margin and small lateral lobe at mid-length of the SGP (Fig. 5G). In *A. drakei*, the posterior margin of the SGP appears trilobate but the lateral lobe is elongate and flap-like, in *A. arizonus* the SGP appears tetralobate, and in *A. mormon* the SGP appears bilobed with a pronounced central concavity. Males of *A. bowlesi* have pseudoparameres with the posteromesal corner narrowly rounded and produced (Fig. 5C), whereas it is broadly rounded in the other species with spinose posterolateral corners of the connexiva. Further, males of *A. bowlesi* present the AGP evenly curved to right (Fig. 5B). The apices of the lateral lobes of tergum VIII are rounded (Fig. 5C) and the parameres are longer than wide (Fig. 5E).

Habitat Description. Río Florido originates on the eastern slopes of the Sierra Madre Occidental in northern Durango state. This river merges with Río Conchos in the state of Chihuahua (Río Conchos Basin) to later merge with Río Grande/Bravo to finally drain into the Gulf of Mexico. The current of Río Florido is regulated by the San Miguel dam. At the type locality (Fig. 7), the river is approximately 50 meters wide; however, at the time of our collecting sections of the watercourse fluctuated from 3 to 15 meters in width and was shallow. The substratum was mainly composed of fine gravel, pebbles, and cobbles covered with algae. We collected *A. bowles*i by disturbing the substratum with the net.

Figure 7. Type locality of *Ambrysus bowlesi* **n. sp.** at Río Florido (Durango, México).

Distribution. This species is distributed along the border between the Mexican Plateau and the Sierra Madre Occidental biogeographic provinces in the Mexican states of Chihuahua and Durango. Also, it is present in the state of Sinaloa, which is in the northern part of the Mexican Pacific Coast biogeographic province (Fig. 2).

Etymology. The specific epithet "*bowlesi*" honors our colleague and friend David E. Bowles, who collected specimens of this species in the state of Chihuahua, and to whom DRV is indebted for his friendship and support before and during his doctoral studies.

Repository. The holotype and some paratypes will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the California Academy of Sciences (San Francisco), Colección Entomológica del Instituto de Ecología A.C. (Xalapa), Enns Entomology Museum (University of Missouri), Essig Museum of Entomology Collection (Berkeley), Field Museum of Natural History (Chicago), University of Michigan Museum of Zoology (Ann Arbor), and the United States National Museum of Natural History (Washington D.C.).

Type Material Examined. HOLOTYPE ♀. **MÉXICO: DURANGO:** Mpio. Villa de Ocampo, Villa de Ocampo, Río Florido, L-1710, 01 January 2014 / 1719 m, 26º 26' 07.2"

N, 105º 30' 24.3" W, DRV & PRH colls. PARATYPES: same data as holotype (2♂, 2♀ CAS; 5♂, 5♀ CNIN; 2♂, 2♀ IEXA; 37♂, 15♀ UMC; 3♂, 3♀ USNM); Arroyo el corralito, Sn. Juan Michis, 2010 m, 2-VII-1985, C. Castillo, P. Reyes (2♂, 1♀ CNIN); La Michilía, Arroyo Corralitos, 16 Abril 1987, R. Novelo col. (1♀ IEXA); La Michilía, Arroyo El Temazcal, 10 Diciembre 1987 / 23º 19' 24.22" N, 104º 09' 58.13" W, R. Novelo col. (1♀ IEXA); La Michilía, Arroyo Nana Juana, 15 Abril 1988, R. Novelo col. (1♀ IEXA); Mpio. San Bernardo, San Bernardo, Río Sextín (Río Nazas), 01 Jan. 2014, L-1711 / 1607 m, 26° 00' 05.0" N, 105° 30' 17.6" W, DRV & PRH colls. (1♂, 2♀ UMC); Mpio Súchil, Corralitos, Arroyo Corralitos, 04 Jan. 2014, L-1720 / 2091 m, 23° 31' 11.1" N, 104° 08' 13.3" W, DRV & PRH colls. (17♂, 3♀ UMC); Mpio. Súchil, Corralitos, Arroyo Paso de San Juan, 04 Jan. 2014, L-1719 / 2093 m, 23° 30' 50.3" N, 104° 08' 13.9" W, DRV & PRH colls. (1♀ UMC). **CHIHUAHUA:** Chihuahua, VI:20:01, Mex. / Mus. Expd. FELutz, Col. / Field Museum Coll. (1♂, 1♀ FMNH); Mpio. Chihuahua, El Puente, Pte. Santa Isabel, Río Santa Isabel, 31 Dec. 2013 / 1469 m, 28° 11' 12.2" N, 106° 13' 50.2" W, DRV & PRH colls. (2♂, 2♀ UMC); Mpio. Chihuahua, W of Agua Caliente, ca. 16.5 km on road 160 to Namiquimipa, Arroyo El Potrero, 31 Dec. 2013, L-1709 / 1777 m, 29° 05' 34.8" N, 106° 28' 42.8" W, DRV & PRH colls. (1♂ UMC); Mpio. Balleza, Balleza, Río de Balleza, 30 Dec. 2013, L-1703 / 1574 m, 26° 55' 20.8" N, 106° 19' 50.1" W, DRV & PRH colls. (1♀ UMC); Mpio. Balleza, El Padre, 6 km W of Balleza, Río de Agujas, 29 Dec. 2013, L-1701 / 1572 m, 26° 57' 01.8" N, 106° 24' 00.8" W, DRV & PRH colls. (5♂, 2♀ UMC); [Mpio. Santa Isabel], G[ene]ral Trias, [28º 21' 00" N, 106º 22' 00" W], 19-IX-84, A. Ibarra (1♀ CNIN); Mpio. Satevo, Satevo, Río Satevo, L-1706, 30 December 2013 / 1377 m, 27° 57' 44.7" N, 106° 07' 35.6" W, DRV & PRH colls. (5♂,

4♀ UMC); same but L-1707, 31 December 2013 (9♂, 16♀ UMC); Mpio. Temósachic, Las Gallinas, Arroyo Gallinas, 28 December 2013, L-1694 / 1494 m, 28° 26' 13.1" N, 108° 28' 42.3" W, DRV & PRH colls. (1♀ UMC); Río Chuviscar, off road to Namisquipa [Namiquimipa], Hwy 160, 22 October 1995 / 29º 05' 30.4" N, 106º 28' 51.4" W, coll. D. E Bowles (4♂, 4♀ UMC); Río San Pedro just above Satevó, M78-9, 23–24 May 1978, Miller, Smith & Marsh (2♂, 1♀ UMMZ). **SINALOA:** [Mpio. Culiacán], Los Mayos, 24 July 1952, John D. Lattin, Cal.Acad.Sci.Coll. / looks like *inflatus* but has different male process [note] / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂ CAS).

Ambrysus contrerasi Reynoso & Sites NEW SPECIES
(Figs. 8–10)

Description. Macropterous female. HOLOTYPE, length 11.04; maximum width 7.04. Paratypes (n = 10), length 11.36–12.96 (mean = 12.18); maximum width 7.04–7.84 (mean = 7.39). General shape elongate, parallel-sided; widest across embolia (Fig. 8A). Overall dorsal coloration of hemelytra dark brown with light brown oval and triangular marks at lateral and posterior margins of corium, respectively; pronotum and head light brown with dark brown marks; legs yellowish brown. Dorsal surface coarsely punctate. Ventral coloration of head and thorax light brown to medium brown, abdomen with yellowish brown pubescence.

Head. Head length 1.92; maximum width 3.08. Mostly light brown with brown medially and posteriorly; coarsely punctate. Eyes convergent anteriorly, synthlipsis 1.40; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly

in front of eyes 7.2% of head length; posterior margin between eyes strongly convex, extending posteriorly 27% of head length. Labrum width 2.0× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.42 beyond labrum not including extruded stylets. Antennal proportions 3:13:16:9, length 0.82, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color light brown, extensive brown marking, brown line behind eyes; transverse sulcus marking anterior border of transverse band in posterior 1/3; transverse band pale yellow anteriorly, brown posteriorly; lateral margins light brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.9× length; length at midline 2.12; maximum width at posterolateral corners 6.08. Prothorax ventrally pruinose throughout, except lateral 1/10; apices of propleura meeting at midline, not appressed to prosternellum; propleuron light brown, medium brown posteriorly, medial 2/3 of posterior margin with golden setae. Probasisternum with sharp median carina and row of setae lateral to carina. Scutellum coarsely punctate, triangular, brown, light brown coloration on anterior and posterior apices, width 2.3× length, width 4.44, length 1.96. Hemelytra densely punctate, dark brown, length 8.28 (chord measurement); corium with light brown oval and triangular marks at lateral and posterior margins, respectively. Clavus dark brown, length 4.5× width, length 4.64, width 1.04; claval commissure dark brown, length 1.56. Embolium length 3.60, greatest width 1.06; lateral margin convex, light brown in anterior 2/3, dark brown posteriorly. Hind wings extending to posterior

margin of tergum VI. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments light brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to five spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.84, tibia 2.34, tarsus 0.50; middle leg, femur 2.80, tibia 2.56, tarsomeres 1–3, 0.25, 0.51, 0.48; hind leg, femur 3.56, tibia 4.08, tarsomeres 1–3, 0.34, 0.96, 0.64.

Abdomen. Dorsally with connexiva of III–VI exposed, each laterotergite medium brown in anterior 1/3 and light brown posteriorly (Fig. 8A); lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners.

Posterolateral corner of II (visible ventrally) narrowly rounded to right angled; III–V acute, spinose; VI–VII bluntly acute. Ventrally medium brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VII. Mediosternite VII (subgenital plate) width 1.3× length; length at midline 1.24; maximum width 1.58; lateral lobe subapical, left margin convex apically, posterior margin with posterolateral corners pointed, truncate central lobe produced posteriorly slightly further than posterolateral corners (Fig. 8G).

Macropterous male. Paratypes (n = 10), length 9.92–11.68 (mean = 10.70); maximum width 6.08–7.04 (mean = 6.52). Coloration, setation, pronotum proportions, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for holotype. Otherwise hind wings extending to posterior margin of tergum V. Accessory genitalic process of tergum VI evenly curved to right, angled to right at mid-length (Fig. 8B). Medial lobes of tergum VIII (pseudoparameres) symmetrical, posteromesal corner produced, posterolateral corner broadly rounded (Fig. 8C). Phallosoma elongate, linear, constricted basally; left ventral lobe lateroflexed at mid-length, right ventral lobe lateroflexed in proximal half (Fig. 8F). Parameres symmetrical, longer than wide, mesal margin straight, setae emanating from distal 1/4 of dorsal surface. Proctiger length subequal to width at base. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 8E).

Variation. Some females from the state of Jalisco exhibited the SGP with the left margin concave apically. Also, the lateral lobe on the left margin of the SGP can be more produced, similar to that of *A. guttatipennis*. The central lobe on the posterior margin of the SGP can be shallowly notched. The male AGP can be evenly curved to right from

base to apex.

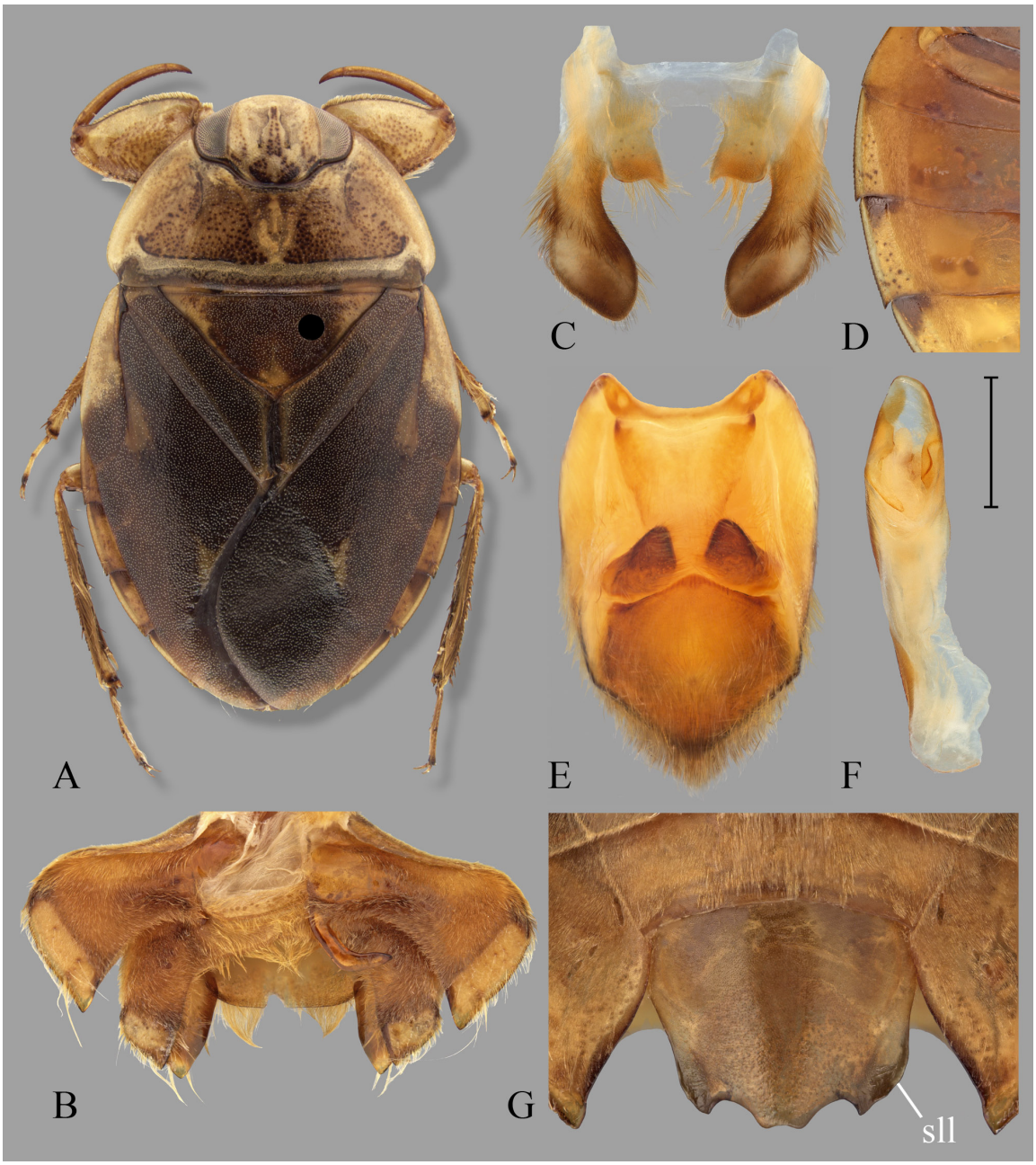

Figure 8. Structures of *Ambrysus contrerasi* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed). sll = sublateral lobe.

Discussion. This species is similar to the closely related *A. guttatipennis,* which has

created confusion in the past as species of *A. contrerasi* have been erroneously identified as *A. guttatipennis.* A source of the confusion is the work of Champion (1901) in which he stated that *A. guttatipennis* was easily identifiable based on its large size and the two flavous marks on the corium (feature present in most of the species in this complex), but also that the holotype of *A. guttatipennis* was housed in an European collection and entomologists only had the brief and uninformative original description of the species. Although *A. contrerasi* is slightly smaller than *A. guttatipennis*, this species also presents the two light brown marks on the corium that would lead to a misidentification. Even the expertise of La Rivers failed to recognize that specimens of *A. contrerasi* were actually different from those of *A. guttatipennis* and he based his supplemental description of *A. guttatipennis* (La Rivers 1953) on at least two female specimens of *A. contrerasi* from the Robert L. Usinger collection (housed at EMEC) that were collected in central Mexico.

When comparing specimens of *A. contrerasi* and *A. guttatipennis,* a few subtle but informative features become evident. Specimens of *A. contrerasi* have a definite oval body shape because the lateral margins are less convex (more parallel-sided), whereas specimens of *A. guttatipennis* present a more rounded shape with more convexity in the lateral margins. The left margin of the SGP in *A. contrerasi* is almost evenly convex because of a low, subapical, lateral lobe. In *A. guttatipennis* the left margin of the SGP is not evenly convex because of the presence at mid-length of a conspicuous lateral lobe and the left margin of the SGP is concave apically. Finally, the concavity between the posterolateral corners and the central lobe on the posterior margin of the SGP of *A. contrerasi* is evenly curved, whereas in *A. guttatipennis* the concavity is lanceolate.

Diagnosis. This is a medium size species at 9.92–12.96 mm in length that can be

distinguished from the other species in this complex with slightly produced spinose posterolateral corners of the connexiva (Figs. 8A, D) by the left margin of the SGP convex apically and the lateral lobe subapical (Fig. 8G). Males present the AGP evenly curved to the right in the basal half and angled to the right at mid-length to extend almost perpendicular to the body axis in its distal half (Fig. 8B). The pseudoparameres have the posteromesal corner produced (Fig. 8C).

Figure 9. Type locality of *Ambrysus contrerasi* **n. sp.** at Arroyo El Aguayabal (Michoacán, México).

Habitat Description. The type locality is in the western part of the state of Michoacán, on the border between the Balsas Basin and the Mexican Pacific Coast biogeographic provinces. The type locality of Arroyo El Aguayabal is a small stream with a maximum width of approximately 6 meters and shallow waters (Fig. 9). The substratum is mainly composed of sand and gravel but it also has areas with pebbles and cobble (Fig. 9). Specimens of *A. contrerasi* were collected from marginal vegetation and by disturbing the substratum with the net.

Distribution. This species is distributed in the Balsas Basin (Guerrero, Michoacán, Morelos), Mexican Plateau (Jalisco), and Transmexican Volcanic Belt (Estado de

México, Jalisco) biogeographic provinces (Fig. 10). *A. contrerasi* was found syntopically with *A. mexicanus* in the state of Jalisco (L-1581).

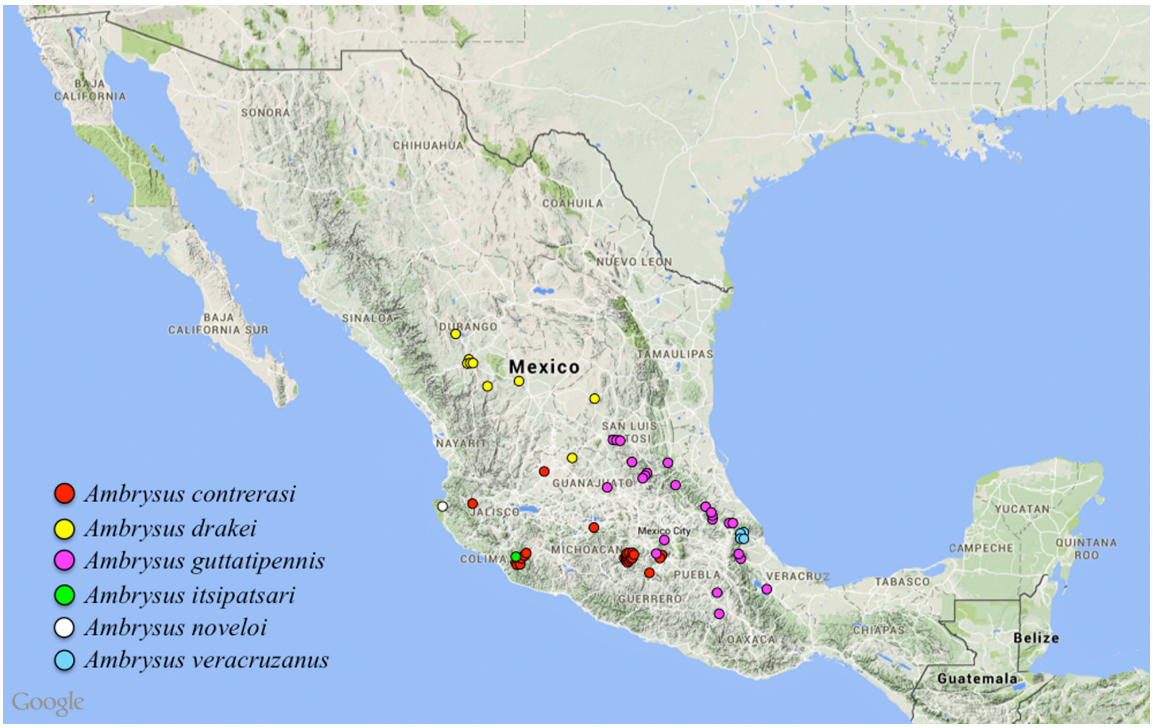

Figure 10. Distribution of *Ambrysus contrerasi* **n. sp.**, *A. drakei*, *A. guttatipennis*, *A. itsipatsari* **n. sp.**, *A. noveloi* **n. sp.**, and *A. veracruzanus* **n. sp.** in Mexico.

Etymology. This species is dedicated to Atilano Contreras Ramos, who advised me during my undergraduate and master's degree studies, and to whom I am extremely grateful for support and encouragement to study entomology.

Repository. The holotype and some paratypes will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the California Academy of Sciences (San Francisco), Enns Entomology Museum (University of Missouri), Essig Museum of Entomology Collection (Berkeley), Field Museum of Natural History (Chicago), and the United States National Museum of Natural History (Washington D.C.).

Type Material Examined. HOLOTYPE ♀: **MÉXICO: MICHOACÁN:** Mpio. Coalcomán, El Salitre de Maruata, Río El Gauyabal, 25 Dec. 2012, L-1486 / 1143 m, 18º 52' 50.4" N, 103º 08' 44.5" W, DRV & PRH colls. PARATYPES: same data as holotype (4♂, 6♀); La Chichihua, 19 Febrero 2005, R. Novelo, J. A. Gómez (1♂, 1♀ UMC); La Chichihua, 2 April 2005, coll: R. Novelo (1♀ UMC); Morelia, Michoacán, 9-6-38, H. D. Thomas / *Ambrysus guttatipennis* Stål 1876 (Ira La Rivers) (1♂ EMEC); Mpio. Chinicuila, La Nuez, Cañada El Colorín, 17 Mayo 2002, R. Novelo col. (2♀ UMC); same but 15-Sep-2003 (1♀); same but 11 Julio 2006 (3♂, 3♀ UMC); Mpio. Coalcomán, El Salitre de Maruata, 25 Dec. 2012, L-1485 / 1149 m, 18º 53' 00.6" N, 103º 08' 40.5" W, DRV & PRH colls. (1♂, 3♀ CNIN; 5♂, 3♀ UMC; 2♂, 2♀ USNM); Sierra de Coalcomán, La Chinicuila, 04 Junio 2005, R. Novelo col. (2♀ UMC); Sierra de Coalcomán, La Nuez, 9-Ago-2006, R. Novelo col. (2♂ UMC). **GUERRERO:** Taxco, Gro., Mexico, VII-9-1962 / D. H. Janzen Collector (1♀ EMEC). **JALISCO:** Mpio. Atenguillo, El Bajío, km 55 carr. Mascota-Ayutla, ca. 2 km NW of Los Volcanes, 27 June 2013, L-1581 / 1509 m, 20° 20' 08.2" N, 104° 34' 19.2" W, DRV & PRH colls. (8♂, 5♀ UMC); Mpio. Jalostotitlán, San Nicolás de las Flores, carr. Jalostotitlán-Teocaltiche 280June 2013, L-1585 / Río Verde, 1653 m, 21° 17' 32.7" N, 102° 33' 15.4" W, DRV & PRH colls. (2♂ UMC). **MÉXICO:** Mpio. Tejupilco, Río Chilero, 02 Mayo 2008, R. Novelo & K. Cuevas (1♂ UMC); same locality information but 19 Sep. 2009, R. Novelo & Sites colls. (2♀ UMC); Mpio. Temascaltepec, San Andrés de Los Gama, road to Mina del Rincón, 19 Dec. 2012, L-1456 / 1897 m, 19º 02' 07.8" N, 99º 59' 37" W, DRV & PRH colls. (1♂ UMC); Real de Arriba, Temescaltepec [Temascaltepec], Mex., V-21-33 / H. E. Hinton, R. L. Usinger Collectors (2♀ EMEC); Real de Arriba, Temescaltepec

[Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / *Ambrysus guttatipennis* Stål (Ira La Rivers) (1♀ EMEC); Real de Arriba, Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / Homotype (1♀ EMEC); Real de Arriba, Temescaltepec [Temascaltepec], Mex., V-25-33 / H. E. Hinton, R. L. Usinger Collectors / 17 / *Ambrysus guttatipennis* Stål determined by Ira La Rivers 1948 / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂ CAS); San Martín Otzoloapan, 27-II-1993, H. Brailovsky, E. Barrera (1♀ UMC); Tejupilco, Mex. Temescaltepec [Temascaltepec], VII-13-1932 [1933 ?], (1♀ EMEC); Tejupilco, Mex. Temescaltepec [Temascaltepec], VI-19-33 / H. E. Hinton, R. L. Usinger Collectors (4♂ EMEC); same but VI-21-33 (1♀ EMEC); Tejupilco, Mex. Temescaltepec [Temascaltepec], June 1933 / R. L. Usinger Collector / *guttatipennis* / *Ambrysus* sp. nr. *signoretii* (sic) (1♀ CAS); Temescaltepec [Temascaltepec], Mex., 11-5-33 / H. E. Hinton, R. L. Usinger Collectors / 16 / *Ambrysus guttatipennis* Stål 1876 (Ira La Rivers) / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂ CAS); Temescaltepec [Temascaltepec], Mex., V-28-33 / H. E. Hinton, R. L. Usinger Collectors (1♀ EMEC); Temescaltepec [Temascaltepec], Mex., VI-1-33 / Timbres / H. E. Hinton, R. L. Usinger Collectors (1♀ EMEC); same but / *Ambrysus guttatipennis* Stål determined by Ira La Rivers '50 (1♀ EMEC); Temescaltepec [Temascaltepec], Mex., VI-5-33 / Exchanged with California Academy of Science[s] (1♂ FMNH); Temescaltepec [Temascaltepec], Mex., VI-5-33 / H. E. Hinton, R. L. Usinger Collectors (2♂, 1♀ EMEC). **MORELOS:** Colección Com.Geogr.Explor. Cuernavaca, Mor., [no date], *Ambrysus signoreti* A.S. (1♂ CNIN); Cuernavacas [Cuernavaca], Mex., XI / *Ambrysus guttatipennis* Stål 1876 (Ira La Rivers) / Ira La Rivers collection

bequeathed to the California Academy of Sciences - 1978 (1♂, 1♀ CAS); Loc[ality] Cuernavaca, Mor., 10-V-50 / *Ambrysus signoretti* (sic) Stal (1♂ CNIN); Mpio. Xochitepec, Xochitepec, Río Sabinos, 24-Abr-2003, R. Novelo col. (1♂ UMC).

***Ambrysus drakei* La Rivers**
(Figs. 10, 11)

A. drakei La Rivers 1957a: Entomol. News 68: 232–237 (original description).

Diagnosis. This is a medium size species at 9.92–12.00 mm in length that can be distinguished from the other species in this complex with strongly produced, spinose posterolateral corners of the connexiva (Figs. 11A, D) by females with a trilobate posterior margin of the SGP and the lateral lobe elongate and flap-like (Fig. 11G). In *A. bowlesi*, the posterior margin of the SGP appears trilobate but the lateral lobe is small and at mid-length, in *A. arizonus* the SGP appears tetralobate, and in *A. mormon* the SGP appears bilobed with a pronounced central concavity. Further, males of *A. drakei* have the AGP evenly curved to the right in a semicircle (Fig. 11B), the apices of the lateral lobes of tergum VIII are rounded (Fig. 11C), the pseudoparameres have the posteromesal corner broadly rounded (Fig. 11C), and the parameres are longer than wide (Fig. 11E).

Discussion. This is perhaps the most closely related species to *A. mexicanus*; both species exhibit similar diagnostic features. The most significant differences between the two species are the slightly larger size, wider embolia, and posteriorly produced corners of the connexiva in *A. drakei*. This species originally was considered a member of the *A. signoreti* complex based on the posteriorly produced corners of the connexiva, but with an "aberrant" shape of the SGP similar to that of *A. mexicanus* (La Rivers 1957a).

Contrary to the evidence of a similar shape of the AGP and the SGP between *A. drakei* and *A. mexicanus*, La Rivers (1957a) considered *A. drakei* more closely related to *A. signoreti.* This species was described from the northwestern Mexican state of Durango (La Rivers 1957a). La Rivers named the species after the Hemiptera systematist Dr. C. J. Drake.

Variation. Some females present the left margin of the SGP not expanded laterally. Males sometimes exhibit the AGP angled to the right at mid-length to extend almost perpendicular to the body axis.

Type Locality. Mexico: Durango.

Repository. Holotype is housed at the USNM.

Distribution. This species is distributed in the central (Durango) and southern (Jalisco, San Luis Potosí, Zacatecas) parts of the Mexican Plateau biogeographic province. The localities in the state of Durango are on the border of the Mexican Plateau and the Sierra Madre Occidental biogeographic provinces (Fig. 10).

Published Records. Mexico: Durango (La Rivers 1957a, 1971)

Type Material Examined. HOLOTYPE ♂: **MÉXICO: DURANGO:** Durango, Aug. 6, 1950, Drake & Hottes / *Ambrysus drakei* La Rivers HOLOTYPE / C.J. Drake Coll. 1956 / Mex. PARATYPE: Mex. / Durango, Aug. 6, 1950, Drake & Hottes / PARATYPE *Ambrysus drakei* La Rivers / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (3♂ CAS).

Material Examined. MÉXICO: DURANGO: Durango City / JD Lattin, 1952 Jul 9, / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂, 1♀ CAS); Durango City, JD Lattin, 1952 Jul 9, / Ira La Rivers collection bequeathed to

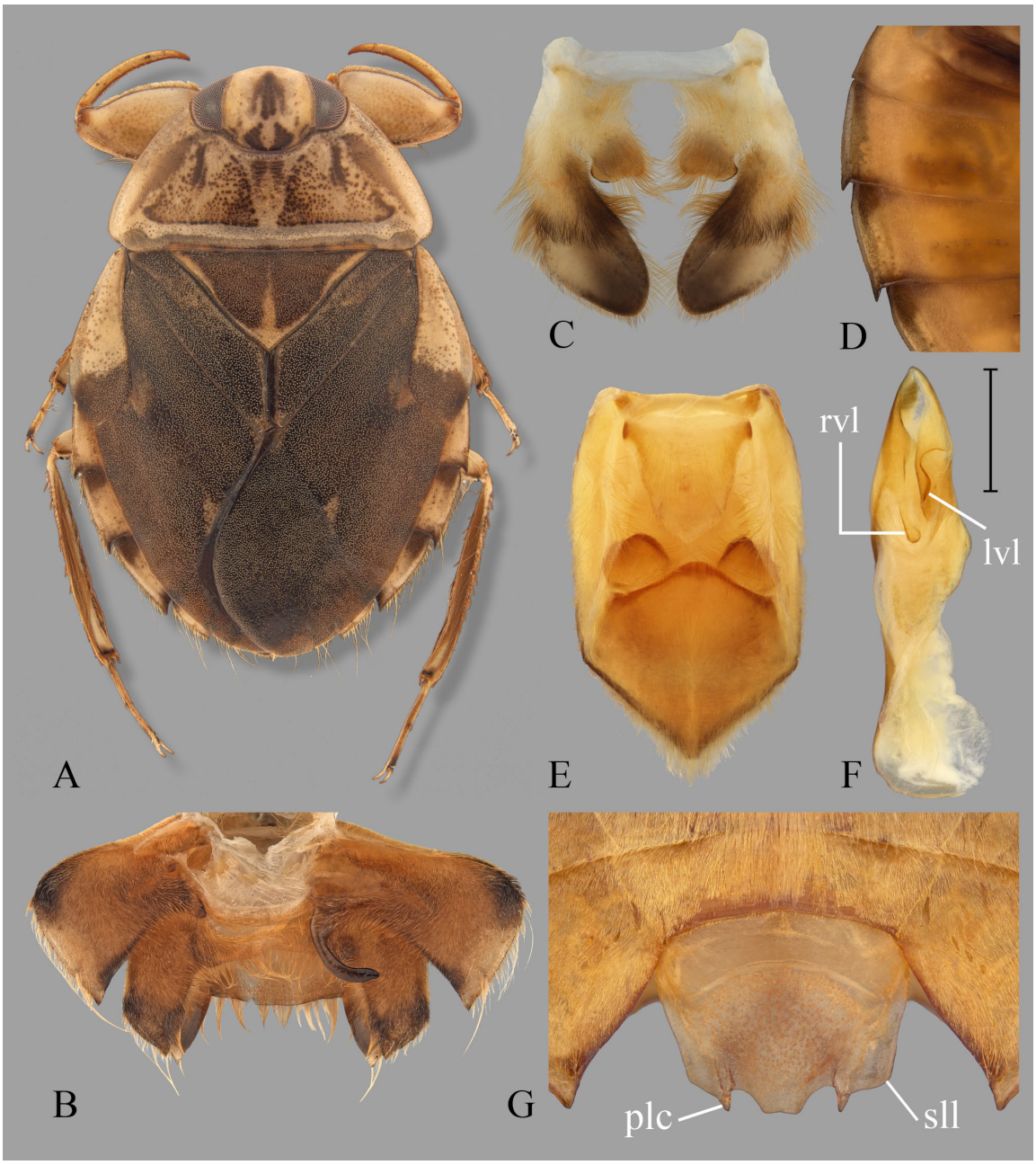

Figure 11. Structures of *Ambrysus drakei*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II– IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed). lvl = left ventral lobe, plc = posterolateral corner, rvl = right ventral lobe, sll = sublateral lobe.

the California Academy of Sciences - 1978 (7♂, 9♀ CAS); same but / H. Brailovsky A.

det. *Ambrysus drakei* La Rivers (1♀ CNIN); Durango City, 14 mi. N, 1952 Jul 9, JD

Lattin / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978

(2♀ CAS); Mpio. Canatlán [Nuevo Ideal], Guatimapé, Pte. Guatimapé, 24° 48' 41.7" N, 104° 55' 15.8" W, 1966 m, 03-Jan-2014, L-1718, DRV & PRH colls. (30♂, 20♀ UMC); Mpio. Súchil, Corralitos, Arroyo Corralitos, 23° 31' 11.1" N, 104° 08' 13.3" W, 2091 m, 04-Jan-2014, L-1720, DRV & PRH colls. (1♂ UMC); 10 mi W Durango, Dgo. VIII-23-69 / Río Chico / J. Haddock Collector (1♀ EMEC). **JALISCO:** [Mpio. Lagos de Moreno], Verde at Cuarenta, ≈15 mi NE of Lago[s] de Moreno, 20 March 1955, M55-62, R. R. Miller (2♂, 1♀ UMMZ). **SAN LUIS POTOSÍ:** Mpio. Charcas, Ojito Santa Cruz, 2 km S of Charcas, 23° 06' 56" N, 101° 06' 16.4" W, 2017m, 15-May-2014, L-1762, DRV & PRH colls. (4♂, 3♀ UMC). **ZACATECAS:** Mpio. Sain Alto, Sain Alto, Arroyo Frío, 23° 33' 36.3" N, 103° 15' 50" W, 2034m 05-Jan-2014, L-1722, DRV & PRH colls. (5♂, 2♀ UMC).

***Ambrysus guttatipennis* Stål**
(Figs. 10, 12)

A. guttatipennis Stål 1876: K. Svens. Vet.-Akad. Handl. 14: 143 (original description).

A. guttatipennis: Montandon 1897, Verh. Zool.-Bot. Ges. Wien 47: 22–23 (supplemental description).

A. guttatipennis: Hungerford 1919, Univ. Kans. Sci. Bull. 11: 203 (translation of Montandon's supplemental description).

A. guttatipennis: La Rivers 1953, Univ. Kans. Sci. Bull. 35: 1331–1333 (supplemental description based on at least two misidentified female specimens that belongs to *A. contrerasi* **n. sp.**).

Supplemental Redescription. HOLOTYPE ♀: length 12.64; maximum width 8.16.

General shape elongate, parallel-sided; widest across embolia. Overall dorsal coloration of hemelytra dark brown with light brown oval and triangular marks at lateral and posterior margins, respectively; head, pronotum, and legs brown. Dorsal surface coarsely punctate. Ventral coloration of head and thorax brown, abdomen with golden brown pubescence.

Head. Head length 2.20; maximum width 3.44. Mostly medium brown with dark brown medially and posteriorly; coarsely punctate. Eyes convergent anteriorly, synthlipsis 1.48; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 5.4% of head length; posterior margin between eyes strongly convex, extending posteriorly 23.6% of head length. Labrum width 2.0× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.44 beyond labrum not including extruded stylets. Antennal proportions 4:12:19:13, length 0.92, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color brown; transverse sulcus marking anterior border of transverse band in posterior 1/4; transverse band pale yellow; lateral margins brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 3.1× length; length at midline 2.20; maximum width at posterolateral corners 6.76. Prothorax ventrally pruinose throughout, except lateral 1/9; apices of propleura meeting at midline, not appressed to prosternellum; propleuron brown, medial 2/3 of posterior margin with elongate golden setae.

Probasisternum with sharp median carina and row of setae lateral to carina. Scutellum coarsely punctate, triangular, brown, light brown coloration at apex, width 1.9× length, width 4.80, length 2.52. Hemelytra densely punctate, dark brown, length 9.12 (chord measurement); corium with light brown oval and triangular marks at lateral and posterior margins, respectively. Clavus pale brown, length 4.3× width, length 4.88, width 1.12; claval commissure light brown, length 1.60. Embolium length 3.92, greatest width 1.44; lateral margin convex, pale brown in anterior 2/3, dark brown posteriorly. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to five spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws

slender, gently curved, with small basal tooth (holotype is missing right metatibia). Leg measurements as follows: foreleg, femur 2.92, tibia 2.30, tarsus 0.54; middle leg, femur 3.04, tibia 2.80, tarsomeres 1–3, 0.38, 0.56, 0.54; hind leg, femur 4.0, tibia 4.40, tarsomeres 1–3, 0.32, 0.96, 0.64.

Abdomen. Dorsally with connexiva of III–VI exposed, each laterotergite dark brown in anterior 1/3 and lighter brown posteriorly; lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners. Posterolateral corner of II (visible ventrally) narrowly rounded to right angled; III–VI acute, spinose; VII bluntly acute. Ventrally yellowish brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VII. Mediosternite VII (subgenital plate) width 1.1× length; length at midline 1.46; maximum width 1.66; lateral lobe at mid-length, left margin concave apically, posterolateral corners pointed, notched central lobe produced slightly further posteriorly than posterolateral corners.

Male. The following is based on specimens collected during this study and measurements were taken from 10 specimens. Length 11.68–12.64 (mean = 12.14); maximum width 7.52–8.16 (mean = 7.85). Coloration, setation, pronotum proportions, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for holotype. Otherwise accessory genitalic process of tergum VI gently curved to right in proximal 2/3, then angles to almost perpendicular to the body axis in distal 1/3 (Fig. 12B). Medial lobes of tergum VIII (pseudoparameres) symmetrical, posteromesal corners produced (Fig. 12 C). Phallosoma elongate, linear, constricted basally; left ventral lobe lateroflexed at mid-length, right ventral lobe lateroflexed in proximal half

(Fig. 12F). Parameres symmetrical, longer than wide, mesal margin slightly convex, setae emanating from distal 1/3 of dorsal surface. Proctiger slightly longer than width at base. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 12E).

Variation. The scutellum sometimes presents light brown coloration on the anterolateral corners. Specimens can have an oblique light brown line at the middle of the corium that connects the oval and triangular marks at the lateral and posterior margins, respectively. The posterolateral corners and central lobe of the female SGP can be subequal in length. The male AGP sometimes is evenly curved from base to apex.

Discussion. This species was described from a single female specimen collected in Mexico (Stål 1876); however, no specific locality data was provided in the original description. *Ambrysus guttatipennis* has remained a species difficult to identify because the original description was brief and only considered gross morphological features (e.g., size, color). As a result, some authors (e.g., Hungerford 1919) reported the species from the southwestern United States based on misidentified specimens probably belonging to *A. arizonus*, *A. mormon*, and *A. occidentalis* (La Rivers 1953). Also, although La Rivers (1953) was not able to examine the holotype of *A. guttatipennis*, he further contributed to the confusion by providing a supplemental description and line drawings of the male AGP and the posterior margin of the female SGP. The female specimens (housed at the EMEC) that La Rivers examined to provide the supplemental description of *A. guttatipennis* actually were the (at that time) undescribed *A. contrerasi* **n. sp.**, which is similar but has subtle differences in the shape of the SGP. Another source that has lead to erroneous identifications of the species comes from the work of Champion (1901) in

which he stated that *A. guttatipennis* was easily distinguishable by the two flavous spots on the corium, which also are present in *A. contrerasi* **n. sp.** and other species. In order to avoid confusion about the identity of this species, we have provided a supplemental redescription based on the female holotype and included figures of specimens collected during our study that were positively identified as *A. guttatipennis*.

Diagnosis. This is a large species at 11.68–13.44 mm in length that can be distinguished from the other species in this complex with slightly produced, spinose posterolateral corners of the connexiva (Figs. 12A, D) by the left margin of the SGP concave apically and the lateral lobe at mid-length (Fig. 12G). The male AGP is gently curved to the right in the basal 2/3, then angled to the right at the distal 1/3 to continue almost perpendicular to the body axis (Fig. 12B). The pseudoparameres have the posteromesal corner narrowly rounded and produced (Fig. 12C).

Distribution. This species is distributed in the Balsas Basin (Morelos), Mexican Plateau (Querétaro, Guanajuato, San Luis Potosí), Sierra Madre Oriental (Hidalgo, Puebla), and the Transmexican Volcanic Belt (Mexico City) biogeographic provinces. Also, this species is present in the transition zone between the Transmexican Volcanic Belt and Mexican Gulf (Veracruz), as well as the transition zone between the Sierra Madre del Sur and Mexican Gulf (northern Oaxaca) biogeographic provinces (Fig. 10). Based on our extensive collecting and the fact that specimens from different species have been incorrectly identified as *A. guttatipennis*, we consider the record of this species from the northwestern state of Sonora (Davis 1986) to be erroneous. This species was found syntopically with *A. mexicanus* in two localities in the state of Oaxaca (San Francisco Huapanapa and Río de Arenas).

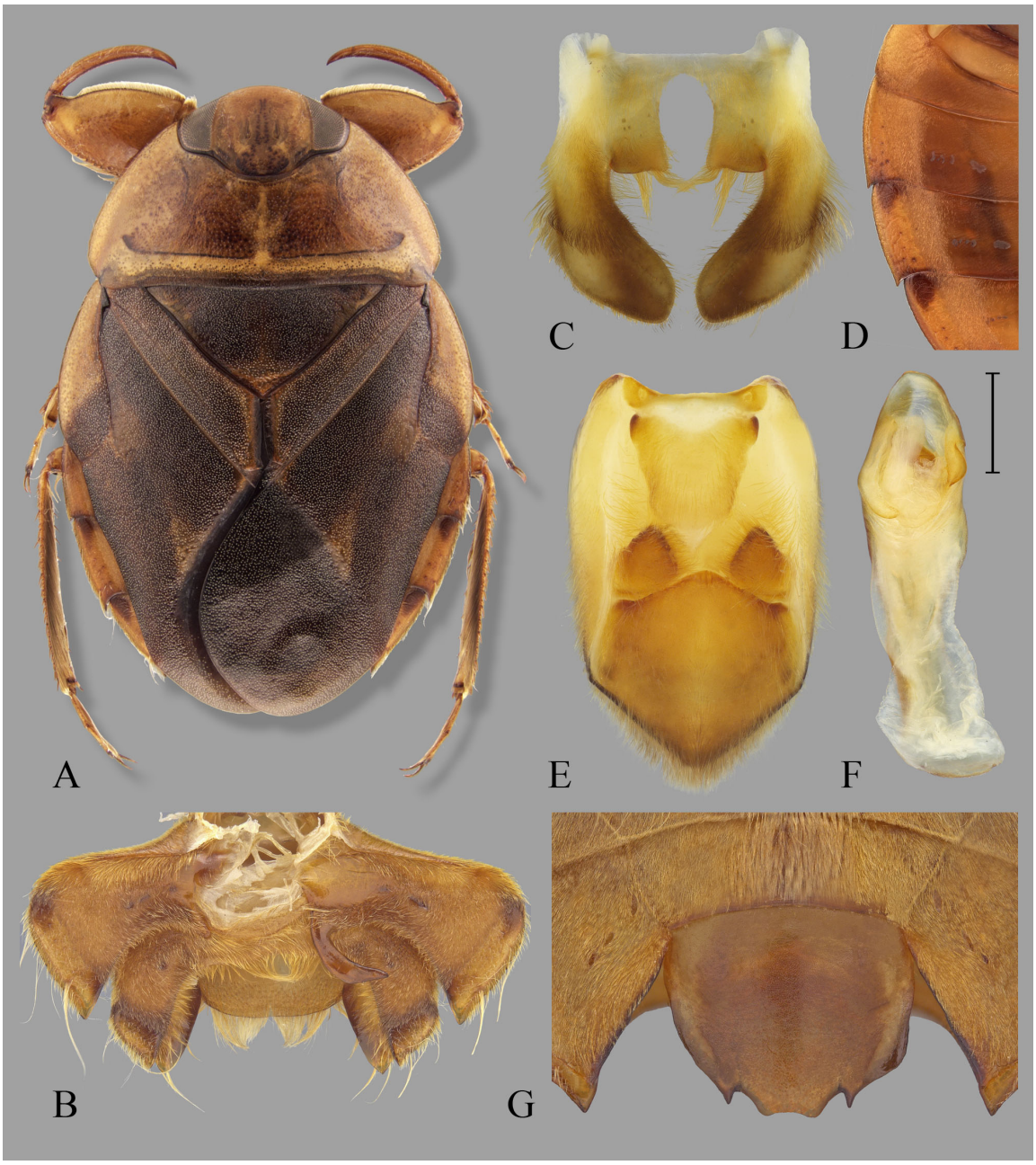

Figure 12. Structures of *Ambrysus guttatipennis*. (A) dorsal habitus of male, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Published Records. Mexico: Estado de México, San Luis Potosí, Sonora, Veracruz (Stål 1876; Champion 1901; La Rivers 1953, 1971; Davis 1986). United States: Arizona (Van Duzee 1917, Hungerford 1919, La Rivers 1948). La Rivers (1953) considered the

records of *A. guttatipennis* from the United States to be erroneous and suggested that those records were probably based on specimens of *A. arizonus*, *A. occidentalis*, or *A. mormon*. The record from Estado de México (La Rivers 1953) was based on misidentified specimens that belong to the species *A. contrerasi* **n. sp.** Although Davis (1986) indicated that this species occurred in Sonora, he did not list any material examined from that state or provide the source for that record.

Repository. The holotype is housed at the SMNH.

Type Material Examined. HOLOTYPE ♀. **MÉXICO:** Mexico / Stål / *guttatipennis* Stål / Sp. figured / ♀ / Typus / NHRS-JLKB 000023185.

Material Examined. MÉXICO: GUANAJUATO: San Isidro [de las Palmas], (arroyo) at 1,000 msnm [1200 m], [21º27'32" N, 100º06'26" W], 04-Agosto-2002, R. Novelo (1♂ UMC); San Miguel de Allende, Mex., / Mus. Expd. FELutz, Col. / Field Museum Coll. (1♀ FMNH). **HIDALGO:** Mpio. Molango, Molango, tributary of Laguna Atezca, 6 June 2013, L-1520, Sites, DRV, Shepard, PRH / 1289 m, 20° 48' 30.1" N, 98° 44' 56.2" W, slow, muddy-bottomed stream w/ veg margins (1♂, 1♀ UMC).

MEXICO CITY: Xochimilco, Mex. D. F., VI-[no day] 33 / Ancona Collector / to be compared with *Ambrysus guttatipennis* Stål [note] (1♀ EMEC). **MORELOS:** Cuernavaca, Mex, VI-1933 / H. E. Hinton / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♀ CAS). **OAXACA:** Papalupan [Papaloapan River], Oax, IV.32 Mex. / J. R. de La Torre Bueno Collection K. U. / *Ambrysus guttatipennis* Stål det. J. R. Davis 94 (1♂ UMC); San Fco. Huapanapan [Huapanapa], Rt. 125, shallow stream, 14 Oct 1989, R. S. Zack col. (2♂, 2♀ UMC; 1♂, 4♀ WSUC); km 31 carr. Tlaxiaco-San Juan Teposcolula, Río de Arena, 17º 25' 37.1" N, 97º 35' 24.7" W,

2098 m, 31-May-2012, L-1403, DRV & PRH colls. (1♀ UMC). **PUEBLA:** carr. Tepango-Amixtlán, 7 km SW of Amixtlán, 20º 00' 38.7" N, 97º 49' 37" W, 1231 m, 04-Jun-2012, L-1414, DRV & PRH colls. (21♂, 17♀ UMC); Mpio. San Felipe Tepatlán, carr. San Felipe Tepatlán-Xochicutla, 20º 05' 45.4" N, 97º 48' 15.5" W, 364 m, 04-Jun-2012, L-1415, DRV & PRH colls. (1♂, 1♀ UMC); Mpio. Tlaxco, carr. Tlaxco-Cuaxtla, ca. 2 km S of Acalman, Río Los Cajones, 20º 24' 26.8" N, 98º 03' 51.5" W, 785 m, 05-Jun-2012, L-1418, DRV & PRH colls. (2♂, 2♀ UMC); Mpio. Zapotitlán de Méndez, Zapotitlán, Río Zempoala, 20º 00' 13.6" N, 97º 43' 26.3" W, 671 m, 03-Jun-2012, L-1413, DRV & PRH colls. (1♂, 1♀ UMC). **QUERÉTARO:** Mpio. Peñamiller, Peña Blanca, Río Extoraz, 21° 01' 52.7" N, 99° 44' 25.8" W, 1256m, 13-May-2014, L-1752, DRV & PRH colls. (1♀ UMC); Mpio. Peña Miller, 1 km S Sn Miguel Palmas, 21º 05' 13" [N], 99º 57' 10" [W], 9-VII-00, R. Jones (1♂ UAQE); Mpio Pinal de Amoles, Cañón de la Angostura, Río Escanela, 13 May 2014, L-1753 / elev. 1241 m, 21º 11' 47.6" N, 99º 36' 19.1" W, DRV & PRH Colls. (1♂ UMC). **SAN LUIS POTOSÍ:** km 66 San Luis Potosí-Cd. Valles, Puente El Charco, 22º03'38" N, 100º29'47" W, 1224 msnm, 02-VII-2006, L. Cervantes, D. Brzoska (1♂, 1♀ CNIN); Mpio. San Nicolas Tolentino, Pte. El Charco, 22º 03' 34.6" N, 100º 29' 47.1" W, 1235 m, 20-Jul-2011, L-1312, DRV coll. (1♂ UMC); Mpio. San Nicolás Tolentino, carr. Río Verde-San Luis Potosí, Pte. El Charco, 22° 03' 36.3" N, 100° 29' 47.1" W, 1182 m, 15-May-2014, L-1760, DRV & PRH colls. (2♂, 1♀ UMC); Xilitla, S.L.P., Mex., VII-23-54, 1450 ft. / Univ. Kans. Mex. Expedition / *Ambrysus guttatipennis* Stal 1876 (Ira La Rivers) / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂ CAS). **VERACRUZ:** Coscomatepec, Veracruz, 11-VII-75, H. Brailovsky A. Col. (1♂ CNIN); Mpio. Atzalán, Pte. Tomata, Río

Alseseca, 19° 55' 15.7" N, 97° 13' 28.2" W, 514 m, 13-Jun-2013, L-1549, DRV, Sites, Shepard, Novelo & PRH colls. (1♀ UMC); Fortín de las Flores / R. E. Woodruff (1♀ UMC); Municip. Tlapacoyan, Rio Filibobos [Filobobos], 267 m, 19º55.662'N, 97º09.764'W, 8 November 2009, L-1124, Sites, Cervantes, Novelo (7♂, 2♀UMC).

Ambrysus itsipatsari Reynoso & Sites NEW SPECIES
(Figs. 10, 13–14)

Description. Macropterous male. HOLOTYPE, length 8.72; maximum width 5.28. Paratypes (n = 6), length 7.84–8.72 (mean = 8.32); maximum width 5.12–5.32 (mean = 5.24). General shape elongate, widest across embolia (Fig. 13A). Overall dorsal coloration of hemelytra light brown with dark brown membrane; almost indistinguishable light brown oval and triangular marks at lateral and posterior margins of corium, respectively; pronotum and head pale yellow with brown marks; legs pale yellow. Dorsal surface coarsely punctate. Ventral coloration of head pale yellow, thorax pale yellow to brown, abdomen brown with yellowish pubescence.

Head. Head length 1.60; maximum width 2.60. Mostly pale yellow with brown medially and posteriorly; coarsely punctate. Eyes convergent anteriorly, synthlipsis 1.16; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 6.2% of head length; posterior margin between eyes strongly convex, extending posteriorly 28.7% of head length. Labrum width 2.0× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.46 beyond labrum not including extruded stylets. Antennal proportions 2:11:15:7, length 0.70, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half

of 3.

Thorax. Pronotum coarsely punctate, ground color pale yellow, extensive brown marking, brown line behind eyes; transverse sulcus marking anterior border of transverse band in posterior 1/4; transverse band pale yellow; lateral margins light brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.9× length; length at midline 1.60; maximum width at posterolateral corners 4.64. Prothorax ventrally pruinose throughout, except lateral 1/12; apices of propleura meeting at midline, not appressed to prosternellum; propleuron brown, light brown posterolaterally, medial 2/3 of posterior margin with elongate golden setae. Probasisternum with sharp median carina and row of setae lateral to carina. Scutellum coarsely punctate, triangular, brown, light brown coloration along lateral margins, width 2.2× length, width 3.04, length 1.38. Hemelytra densely punctate, light brown, length 5.92 (chord measurement); corium with dark brown narrow oblique line at middle and posterior margins, with light brown oval and triangular marks at lateral and posterior margins, respectively. Clavus dark brown, with light brown along margins, length 4.4× width, length 3.32, width 0.76; claval commissure dark brown, length 1.00. Embolium length 2.60, greatest width 0.78; lateral margin convex, pale yellow in anterior 2/3, dark brown posteriorly. Hind wings extending to posterior margin of tergum V. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments pale yellow. Profemur posterior margin with row of

tightly arranged setae in basal 2/3, row of short brown spines along middle third; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to six spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.12, tibia 1.60, tarsus 0.40; middle leg, femur 2.00, tibia 1.80, tarsomeres 1–3, 0.16, 0.40, 0.40; hind leg, femur 2.60, tibia 2.84, tarsomeres 1–3, 0.24, 0.68, 0.55.

Abdomen. Dorsally with connexiva of III–V exposed, each laterotergite dark brown in anterior 1/3 and light brown posteriorly (Fig. 13A); lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners. Posterolateral corners of II (visible ventrally) narrowly rounded; III–IV almost right angled; V–VI acute, spinose; VII bluntly acute. Ventrally brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VII. Accessory genitalic process of tergum VI curved to

right at approximately 90 degree angle close to the base, slightly expanded at mid-length (Fig. 13B). Medial lobes of tergum VIII (pseudoparameres) symmetrical, subtriangular, posteromesal corners produced posteriorly, with group of thick setae on posteromesal corner (Fig. 13C). Phallosoma elongate, linear, constricted basally; left ventral lobe lateroflexed at mid-length, right ventral lobe lateroflexed in proximal half (Fig. 13F). Parameres symmetrical, longer than wide, mesal margin straight, setae emanating from distal 1/3 of dorsal surface. Proctiger almost as long as width at base. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 13E).

Macropterous female. Paratypes (n = 8), length 8.56–9.28 (mean = 8.96); maximum width 5.52–5.92 (mean = 5.66). Coloration, setation, pronotum proportions, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for holotype. Otherwise hind wings extending to posterior margin of tergum VI. Mediosternite VII (subgenital plate) width 1.5× length; length at midline 0.98; maximum width 1.46; acuminate posterolateral corners produced further posteriorly than notched central lobe (Fig. 13G).

Variation. The male AGP can be curved to right at approximately 100–110 degree angle close to the base or continuously evenly curved from base to apex.

Discussion. This small species is slightly different than the other species in this complex and is comparable in size only with *A. noveloi* **n. sp.** The overall color of the species is lighter that that of any of the other species. Also, this is the only species in the complex with the posteromesal corner of the pseudoparameres produced posteriorly with a brush of tightly arranged setae.

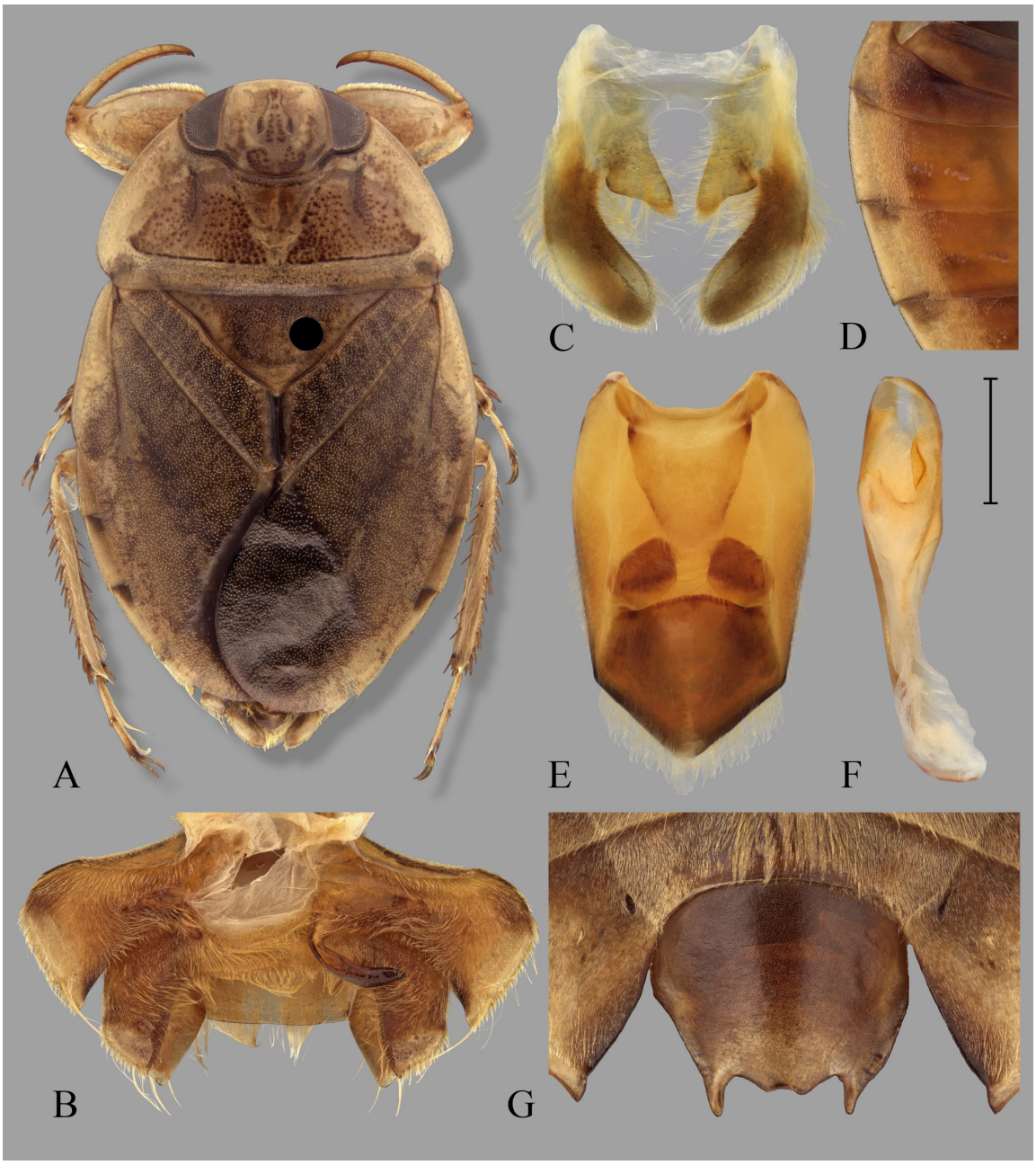

Figure 13. Structures of *Ambrysus itsipatsari* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Diagnosis. This is a small species at 7.84–9.28 mm in length that can be distinguished from the other species in this complex with slightly produced posterolateral corners of the connexiva (Figs. 13A, D) by the posterior margin of the SGP with acuminate

posterolateral corners that are produced further posteriorly than the central notched lobe (Fig. 13G). Males present the AGP curved to the right at an approximately 90 degree angle close to the base (Fig. 13B). The pseudoparameres are subtriangular with a brush of tightly arranged setae on the posteromesal corner (Fig. 13C). Specimens present an overall lighter dorsal coloration than that of the other species in this complex (Fig. 13A).

Habitat Description. At the type locality, the stream is third-order with the channel width ranging from 2–15 meters and the substratum is limestone cobble and bedrock (Fig. 14). Along its course through a deciduous forest the depth is variable (up to approximately 2 meters), but at the study site the stream is 30–50 cm deep (Novelo-Gutiérrez, per. comm.). The stream runs through the western part of the state of Michoacán where the Balsas Basin and Mexican Pacific Coast biogeographic provinces come together.

Figure 14. Type locality of *Ambrysus itsipatsari* **n. sp.** at Villa Victoria (Michoacán, México).

Distribution. This species has been only collected from the type locality in the state of Michoacán, on the border of the Balsas Basin and the Mexican Pacific Coast biogeographic provinces (Fig. 10).

Etymology. The specific epithet *"itsipatsari*" is a noun in apposition derived from the Purépecha *its'ï patsari*, which means "guardian of the water". The Purépecha, also known as Tarascan, is a language spoken in the Mexican state of Michoacán where this species was collected.

Repository. The holotype and some paratypes will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the Enns Entomology Museum (University of Missouri) and the United States National Museum of Natural History (Washington D.C.).

Type Material Examined. HOLOTYPE ♂. **MÉXICO: MICHOACÁN:** Mpio. Chinicuila, Villa Victoria, 740 m, 17 Mayo 2002, R. Novelo col. PARATYPES: same data as holotype (2♀ CNIN; 1♂, 2♀ UMC); Mpio. Chinicuila, Villa Victoria, 750 m, 10 Agosto 2000, R. Novelo col. (1♂ CNIN); Mpio. Chinicuila, Villa Victoria, 740 m, 03 Junio 2003, R. Novelo col. (2♂, 1♀ USNM); Mpio. Chinicuila, Villa Victoria, 740 m, 16 Septiembre 2003 (1♀ USNM); Mpio. Chinicuila, Villa Victoria, 740 m, 18 Febrero 2005, R. Novelo col. (1♂, 1♀ UMC); Mpio. Chinicuila, Villa Victoria, 740 m, 31 Marzo 2005, R. Novelo col. (1♂, 1♀ UMC).

Ambrysus mexicanus **Montandon**
(Figs. 2, 15)

A. mexicanus Montandon 1897: Verh. Zool.-Bot. Ges. Wien 47: 21–22 (original description).

A. dilatus Montandon 1910: Bull. Soc. Stiinte 18: 190–191 (original description).

A. hintoni Usinger 1946: Univ. Kans. Sci. Bull. 31: 206–207 (original description).

A. dilatus: La Rivers 1953, Univ. Kans. Sci. Bull. 35: 1327–1329 (supplemental description).

A. hintoni: La Rivers 1953, Univ. Kans. Sci. Bull. 35: 1329 (synonym of *A. dilatus*).

A. mexicanus: La Rivers 1957b, Wasmann J. Biol. 15: 103–106 (redescription).

A. dilatus: La Rivers 1958, Proc. Ent. Soc. Wash. 60: 73 (synonym of *A. mexicanus*).

Diagnosis. This is a medium sized species at 8.64–11.04 mm in length that can be distinguished from the other species in this complex with slightly produced posterolateral corners of the connexiva (Figs. 15A, D) by the left margin of the SGP expanded, flap-like, and concave at mid-length; the apical lateral lobe is broadly rounded (Fig. 15G). Males present the AGP evenly curved to right in a semicircle (Fig. 15B). The pseudoparameres are boot-shaped (Fig. 15C).

Discussion. When Montandon (1897) described this species, he compared it with *A. guttatipennis* and reported that *A. mexicanus* was smaller, narrower, and had lighter coloration. Montandon (1897) also noticed that the posterior corners of the connexiva were not produced in *A. mexicanus*. La Rivers (1953) was not able to include *A. mexicanus* in his work on the *Ambrysus* of Mexico because he did not have access to the type material housed at the SMNH; nevertheless, he indirectly treated the species by including *A. dilatus* in his work since he later determined it to be a junior synonym of *A. mexicanus* (La Rivers 1958). La Rivers (1957b) provided a redescription of *A. mexicanus* based on the holotype and designated a homotype from the Mexican state of Oaxaca.

Variation. Some females present the left margin of the SGP convex (expanded at mid-length). Also, the posterolateral corners of the SGP can be produced slightly further than the central lobe. The male AGP can be angled at mid-length to extend almost perpendicular to the body axis.

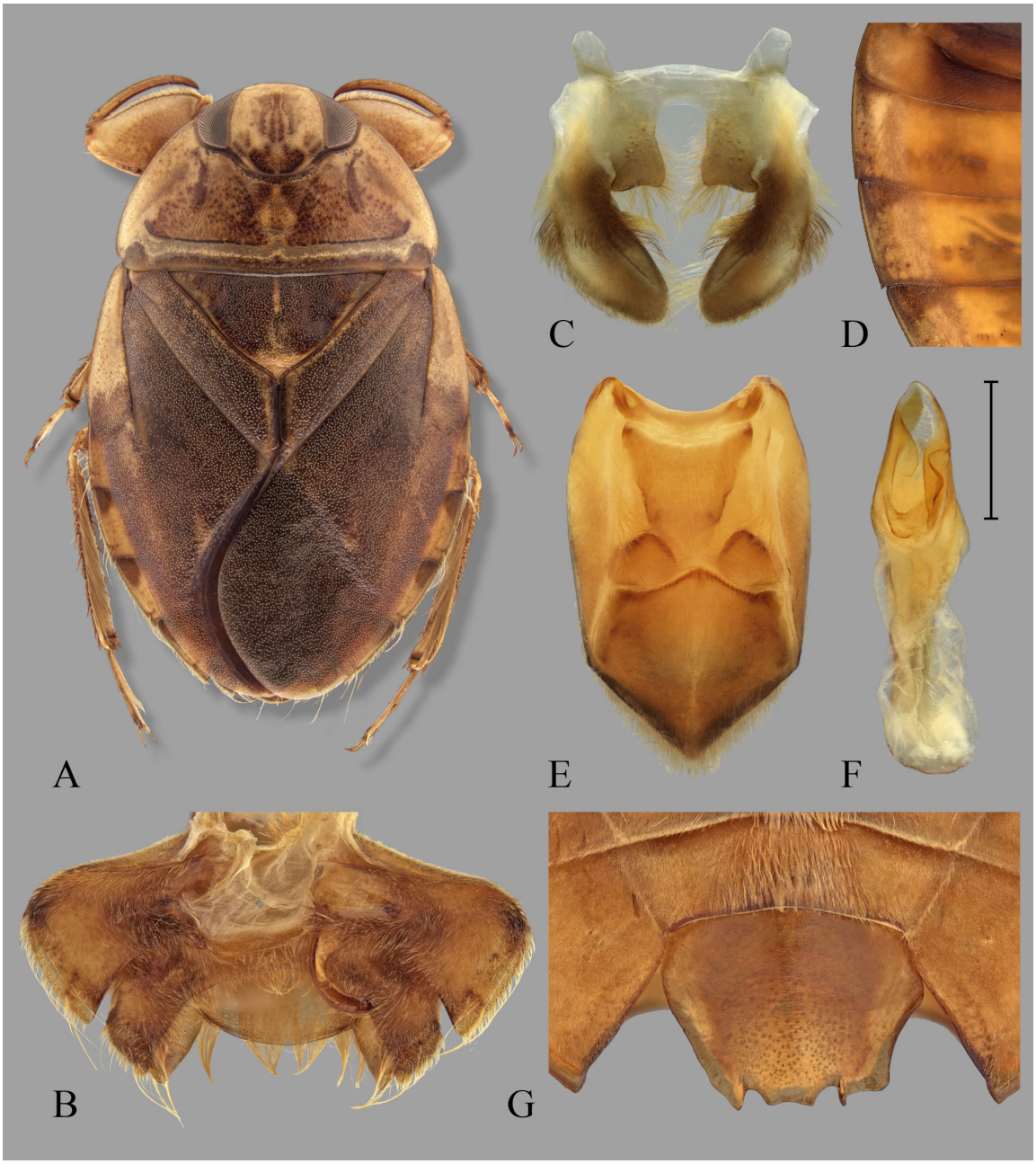

Figure 15. Structures of *Ambrysus mexicanus*. (A) dorsal habitus of female, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings

removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Type Locality. Mexico.

Repository. Holotype is housed at the SMNH.

Distribution. This species is distributed in the Balsas Basin (Guerrero, Michoacán, Morelos), Sierra Madre del Sur (Oaxaca), and Transmexican Volcanic Belt (Jalisco, México, Michoacán, Puebla) biogeographic provinces (Fig. 2). *Ambrysus mexicanus* was collected syntopically with *A. hydor* and *A. scalenus* at Paso de Vigas in Estado de México (L-1909) and with *A. contrerasi* **n. sp.** in the state of Jalisco (L-1581). Also, it was found syntopically with *A. guttatipennis* at San Francisco Huapanapa and Río de Arenas (Oaxaca).

Published Records. Mexico: Estado de México, Michoacán, Oaxaca, Puebla (Montandon 1897, 1910; Champion 1901; Usinger 1946; La Rivers 1953, 1957, 1958, 1971). As *A. dilatus,* the species was reported from Mexico with no specific locality (Montandon 1910), and from Estado de México and Michoacán in central Mexico (La Rivers 1953). As *A. hintoni,* the species was reported from Tejupilco (type locality) in Estado de México (Usinger 1946).

Type Material Examined. HOLOTYPE ♂: **MÉXICO:** Mexico / Boucard / *Ambrysus mexicanus* Montand (sic) Type ♂ / Typus / 170, 53 / NHRS-JLKB 000023187. PARATYPES: Mexico / Boucard / *Mexicanus* Montand (sic) /Paratypus / NHRS-JLKB 000023188 (1♀ SMNH); Mexico / Boucard / Sp. figured / Paratypus / NHRS-JLKB 000023189 (1♀ SMNH); Mexico / Boucard / Paratypus / NHRS-JLKB 000023190 (1♀ SMNH). HOLOTYPE ♂: [**MÉXICO:**] Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-30-33 / H. E. Hinton, R. L. Usinger Collectors / HOLOTYPE

Ambrysus hintoni Usinger / California Academy of Sciences Type No. 7163 (CAS). PARATYPES: Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-15-33 / H. E. Hinton, R. L. Usinger Collectors / ALLOTYPE *Ambrysus hintoni* Usinger / Homotype / Collection of the California Academy of Sciences, San Francisco, California (1♀ CAS); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-15-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus hintoni* Usinger (1♂, 1♀ EMEC); same but / 7, 8, 12, 13 [without terminal segments] (4♂ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-15-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus hintoni* Usinger / *Ambrysus dilatus* Montandon determined by Ira La Rivers '50 (1♀ EMEC); same but / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♀ CAS); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-15-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus hintoni* Usinger / *Ambrysus hintoni* Usinger Ms. (1♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-15-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus hintoni* Usinger / to be compared with *Ambrysus mexicanus* Montd. #2 (1♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-16-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus hintoni* Usinger (1♂ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-20-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus hintoni* Usinger (1♂ EMEC); same but / *Ambrysus hintoni* Usinger 1946 (Ira La Rivers [without terminal segments (1♂ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-15-33 / H. E. Hinton, R. L. Usinger Collectors / PARATYPE *Ambrysus hintoni* Usinger / *Ambrysus dilatus* Montandon 1910 (Ira La Rivers) / Ira La Rivers collection bequeathed to the California Academy of Sciences -

1978 (1♂ CAS). **OAXACA:** Oaxaca, Aug 25, 1937, H. D. Thomas / This agrees well with both Wien & Stockholm types: both sexes were compared with my material (*mexicanus*) / Homotype / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂ CAS).

Material Examined. MÉXICO: Boucard / collectio Haglund / NHRS-JLKB 000023191 (1♀ SMNH). **GUERRERO:** Mpio. Teloloapan, km 20 carr. Teloloapan-Apaxtla de Castrejón, nr. Tepozanalquillo, 18º 14' 26.8" N, 99º 54' 51" W, 1083 m, 29-Dec-2012, L-1497, DRV & PRH colls. (6♂, 1♀ UMC); km 102 carr. Cd. Altamirano-Zihuatanejo, 22-VI-1990, H. Brailovsky, E. Barrera (1♂ CNIN); 10 km al Oeste de Teloloapan, 23-VI-1990, H. Brailovsky [&] E. Barrera (1♂, 1♀ CNIN). **JALISCO:** [Mpio. Atenguillo], Los Volcanes, Río Atenguillo, 27 June 2013, L-1582, DRV & PRH / 1459 m, 20º 19' 16.5" N, 104º 31' 41.1" W (8♂, 14♀ UMC); El Bajio, km 55 carr. Mascota-Ayutla, ca. 2 km NW of Volcanes, 27 June 2013, L-1581 / 1509 m, 20º 20' 08.2" N, 104º 34' 19.2" W, DRV & PRH (39♂, 22♀ UMC); Río San Rafael at San Rafael bridge, III:8:1955, M55-51 (1♀ UMMZ). **MÉXICO:** Acamochitlan, El Zapote, 21-XI-84, H. Brailovsky (1♂ CNIN); Corrientes, Mex., 8-24-37, H. D. Thomas / *Ambrysus dilatus* Montandon determined by Ira La Rivers '50 (1♂ SEMC); same locality information but / *Ambrysus dilatus* Montandon 1910 (Ira La Rivers) (1♀ SEMC); same but / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂, 1♀ CAS); Mpio. Santo Tomás de los Plátanos, Santa Bárbara, in front of Sta. Bárbara hydroelectric plant, 19º 10' 29.4" N, 100º 17' 20.4" W, 1051 m, 20-Dec-2012, L-1463, DRV & PRH colls. (1♂, 2♀ UMC); Mpio. Tejupilco, Paso de Vigas, Arroyo Paso de Vigas, 18º 53' 32.6" N, 100º 13' 57.0" W, 1107 m, 19-Dec-2012, L-1459, DRV & PRH

colls. (1♀ UMC); same locality information but 05-Apr-2015, DRV, Sites, Shepard, Barr & PRH colls., L-1909 (3♂, 5♀ UMC); Mpio. Tejupilco, Pte. Acamuchitlán, 03-Mayo-2008, R. Novelo col. (1♂ UMV); Mpio. Zacazonapan, Zacazonapan, Independencia dam, 19º 05' 03.4" N, 100º 14' 27.8" W, 1468 m, 20-Dec-2012, L-1461, DRV & PRH colls. (2♀ UMC); Real de Arriba, Temescaltepec [Temascaltepec], Mex., VI-8-1933 / H. E. Hinton, R. L. Usinger Collectors (3♂, 1♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-16-33 / H. E. Hinton, R. L. Usinger Collectors (1♀ EMEC); same but VI-19-33 (1♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-20-33 / H. E. Hinton, R. L. Usinger Collectors (4♂, 3♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-25-33 / H. E. Hinton, R. L. Usinger Collectors (1♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VI-30-33 / H. E. Hinton, R. L. Usinger Collectors (1♀ EMEC); Tejupilco, Mex., Temescaltepec [Temascaltepec], VII-[no day]-34 / H. E. Hinton, R. L. Usinger Collectors (5♂, 8♀ EMEC); Temescaltepec [Temascaltepec] 11 July 1933, Robert L. Usinger, Cal.Acad.Sci.Coll. / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (13♂, 17♀ CAS); Temescaltepec [Temascaltepec], [no date], #880, R. L. Usinger, H. H. Hinton (sic) / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (11♂, 12♀ CAS). **MICHOACÁN:** carr. San Antonio de la Huerta-Tacámbaro de Codallos, Rió Frío, 19º 12' 50.4" N, 101º 20' 47.1" W, 1297 m, 23-Dec-2012, L-1476, DRV & PRH colls. (1♂, 2♀ UMC); Morelia, 9-4-38, H. D. Thomas / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂, 1♀ CAS); same but 9-6-38 (2♂, 1♀ CAS); near Chinapa, 9-5-38, H. D. Thomas / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (2♀ CAS). **MORELOS:**

carretera Cuer[navaca]-Cuautla, 22-X-72, M. T. Mancera (Lagunas) (1♀ CNIN); Tepoztlán, 12-IV-70, Harry Brailovsky col. (1♀ CNIN); Cuautla, 8-V-70, Harry Brailovsky col. (1♂ CNIN). **OAXACA:** Huajuapan, 13 mi. S.E. Oax. Mex. VII-4-53, 6000 ft / Univ. Kans. Mex. Expedition / Slesnick Field No. 33 / *Ambrysus mexicanus* Montandon 1897 (Ira La Rivers) (5♂, 12♀ SEMC); same but / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂, 1♀ CAS); Mpio. Guelatao de Juárez, carr. Tuxtepec-Oaxaca, 6 km W of Guelatao, Pte. Xia, 17º 18' 18.3" N 96º 31' 33.8" W, 1497 m, 24-May-2012, L-1373, DRV & PRH colls. (9♂, 8♀ UMC); Mpio. Putla Villa de Guerrero, Putla de Guerrero, Pte. La Cuchara, 17º 01' 06.7" N, 97º 55' 11.8" W, 711 m, 30-May-2012, L-1396, DRV & PRH colls. (1♂, 1♀ UMC); Mpio. Putla Villa de Guerrero, Pluta de Guerrero, 17º 02' 21.5" N, 97º 54' 42.9" W, 767 m, 30-May-2012, L-1397, DRV & PRH colls. (1♂ UMC); Mpio. San Andrés Sinaxtla, carr. Huajuapán de León-Oaxaca, San Andrés Sinaxtla, Río Grande, 17º 28' 03.8" N, 97º 16' 06.1" W, 2045 m, 01-Jun-2012, L-1404, DRV & PRH colls. (7♂, 4♀ UMC); San Antonio Nanahuatipam, San Antonio Nanahuatipam, Río Salado, 18° 07' 59.4" N, 97° 07' 42.6" W, 790 m, 24-Mar-2015, L- 1877, DRV, Sites, Shepard, Barr & PRH colls. (9♂, 12♀ UMC); San Antonio Nanahuatipam , 24 III 2015, 775 m, Río Salado, N 18º 07.99', W 97º 07.71' / William D. Shepard, leg. (1♂ UMC); Mpio. San Sebastián Tecomaxthahuaca, Tecomaxthahuaca, Laguna Encantada (lateral channel), 17º 21' 57.5" N, 98º 01' 13.3" W, 1662 m, 30-May-2012, L-1399, DRV & PRH colls. (4♂, 3♀ UMC); Mpio. Santiago Juxtlahuaca, Santiago Naranjas, S of Juxtlahuaca, 17º 16' 04.5" N, 98º 00' 24.1" W, 1735 m, 30-MAY-2012, L-1398, DRV & PRH colls. (1♀ UMC); Mpio. Tlaxiaco, km 81 carr. Putla-Tlaxiaco, San Juan del Río (Río de Ocotepec), Río Ocotepec,

17º 10' 27" N, 97º 46' 17.8" W, 1967 m, 31-May-2012, L-1400, DRV & PRH colls. (2♂ UMC); San Fco. Huapanapan [Huapanapa], Rt. 125, shallow stream, 14 Oct 1989, R. S. Zack col. (4♂, 4♀ UMC; 9♂, 5♀ WSUC); 2 mi. E. Huajuapan de León 1956 Aug 15, A. A. Alcorn / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♀ CAS); 4 mi. SE Tlacolula, Oax., VIII-21-1959 / A. E. Menke Collector / *Ambrysus mexicanus* Montandon 1897 (Ira La Rivers) / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♀ CAS); 5 mi. S. of Tutla, XII-13-1948 / H. B. Leech Collector / *Ambrysus mexicanus* Montandon 1897 (Ira La Rivers) (1♀ CNIN); 9 mi. S. W. Oax., Oax. Mex. 7-5-53 / Univ. Kans. Mex. Expedition / Slesnick Field No. 33 / *Ambrysus mexicanus* Montandon 1897 (Ira La Rivers) (5♂, 6♀ SEMC); same but / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂, 1♀ CAS); 9 mi. N. Oaxaca, 12-XII-1948, clear stream / H. B. Leech Collector / Collecting stop No. 57 (1♀ CAS); 10 mi NW Tamazulapan, VII-22-1959 / A. S. Menke, L. A. Stange Collectors / *Ambrysus mexicanus* Montandon1897 (Ira La Rivers) / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂, 1♀ CAS); km 31 carr. Tlaxiaco-San Juan Teposcolula, Río de Arena, 17º 25' 37.1" N, 97º 35' 24.7" W, 2098 m, 31-May-2012, L-1403, DRV & PRH colls. (9♂, 16♀ UMC); km 89 Tehuacan-Huajuapan, 5-IX-90, E. Barrera [&] A. Cadena (1♂ CNIN). **PUEBLA:** Garci-Crespo, Dec. 27, 1958, Menke & Stange / *Ambrysus mexicanus* Montandon 1897 (Ira La Rivers) (1♀ CNIN); same but / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (2♂, 2♀ CAS); [Mpio. Vicente Guerrero], San Bernardino Lagunas, El Calvario, 2-XI-1988, R. Barba, E. Barrera, L. Cervantes (6♂, 8♀ CNIN); Puebla, July 18, 1937, H. D. Thomas / Ira La Rivers

collection bequeathed to the California Academy of Sciences - 1978 (2♂ CAS); Puebla, Colleción Com, Geogr. Explor., [no date] (1♀ CNIN); Puebla, Mex. July, 20 1951, Drake & Hottes / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♂ CAS); same but / *Ambrysus dilatus* Montandon 1910 (Ira La Rivers) (2♂, 2♀ CAS; 1♀ CNIN); Puebla, Mex. July, 20 1951, Drake & Hottes / *Ambrysus dilatus* Montandon 1910 (Ira La Rivers) / *Ambrysus dilatus* Mont. det. RISailer comp. with cotype / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♀ CAS).

Ambrysus mormon **Montandon**
(Figs. 2, 16)

A. mormon Montandon 1909: Bull. Soc. Stiinte 18: 48–49 (original description).

A. heidemanni Montandon 1910: Bull. Soc. Stiinte 18: 188–189 (original description)

A. mormon heidemanni Montandon: La Rivers 1951a: Univ. Calif. Publ. Entomol. 8: 316–317 (considered a subspecies of *A. mormon*) (**new synonym**).

A. mormon australis La Rivers 1953: Univ. Kans. Sci. Bull. 35: 1311–1313 (original description) (**new synonym**).

A. mormon minor La Rivers 1963: Biol. Soc. Nev. Occas. Pap. 1: 6 (original description) (**new synonym)**.

Diagnosis. This species can be distinguished from the other species in this complex with strongly produced, spinose posterolateral corners of the connexiva (Figs. 16A, D) by females with the posterior margin of the SGP bilobed and with a pronounced central concavity (Fig. 16G). The other three species with strongly produced, spinose posterolateral corners of the connexiva have a central lobe on the posterior margin of the

SGP. Males of *A. mormon* have the pseudoparameres parallel-sided and angled posterolaterad at mid-length (Fig. 16C). The remaining species with produced posterolateral corners of the connexiva present the pseudoparameres parallel-sided without an angle or are widened posterolaterally. Further, males of *A. mormon* have the AGP evenly curved to the right in the proximal 2/3, then angled to the right to continue perpendicular to the body axis (Fig. 16B). The apices of the lateral lobes of tergum VIII are rounded (Fig. 16C) and the parameres longer than wide (Fig. 16E).

Discussion. This species originally was described from St. Georges in the state of Utah, United States and the length was reported to be 9.30–10.60 mm (Montandon 1909). In the following year, Montandon (1910) described *A. heidemanni* from Yellowstone and named it after Mr. Otto Heidemann, stating that it was similar to *A. mormon* but smaller in size (8.60–10.00 mm). This species was later considered by La Rivers (1951a) to be a subspecies of *A. mormon*. La Rivers (1951a) considered *A. heidemanni* a diminutive replica of *A. mormon* with only a longer and narrower embolium, and small and insignificant variation in the shape of the posterior margin of the SGP and the shape of the male AGP. La Rivers (1951a) considered it possible that *A. m. heidemanni* represented a subspecies isolated in the warm mineral waters of Yellowstone, but he recognized that the evidence did not support subspecific recognition because specimens collected from different sites of the western Great Basin showed similar characteristics, particularly the small size, to those present in specimens of *A. mormon heidemanni* from the type locality. It was apparent that the smaller size was a character present in different populations of the widespread *A. mormon*. Nevertheless, La Rivers (1951a) preferred to recognize the subspecies arguing that additional fieldwork was necessary. Later, La

Rivers (1963) described the subspecies *A. mormon minor* from Hot Creek Falls in the state of Idaho, United States. La Rivers (1963) reported that this species also was similar to *A. m. mormon* but smaller in size. The main features distinguishing *A. m. minor* from the other two subspecies were an almost straight male AGP and a somewhat different shape of the posterior margin of the SGP (La Rivers 1963). Davis (1986) later suggested that high water temperature could induce small size in specimens of *A. thermarum* La Rivers *(A. hybridus* Montandon species complex). La Rivers (1953) described the subspecies *A. m. australis* from the northern Mexican state of Chihuahua. The feature distinguishing *A. m. australis* from the other subspecies was the posterolateral corners of the SGP were more strongly produced posteriorly (several times longer than wide). This subspecies was later reported from New Mexico in the southwestern United States (Davis 1986).

Sites and Willig (2000) analyzed the morphometric variation of 15 external mensural characters (e.g., body length and width, head length and width, synthlipsis) among 13 populations of *A. mormon* (California, Colorado, Idaho, Nevada, New Mexico, South Dakota, Utah, Wyoming) and found that the position of populations of *A. mormon* in multidimensional morphometric space did not reflect the established subspecific designations within the species. *Ambrysus m. heidemanni* and *A. m. minor* were in close proximity to members of the nominate subspecies and occurred within the range of variability encompassed by the nominate subspecies. This study has shown how populations in the United States of the three subspecies present variation in the size of different external structures that is not correlated with the current subspecific recognition. Further Sites et al. (1996) demonstrated that environmental temperature during

ontogenetic development is related to adult size, with smaller adults resulting from development in warmer water.

A subspecies is a geographical variety (Mayr 1982) with morphological uniformity in one or a few diagnostic characters (Wilson & Brown 1953). However, two of the subspecies are thermal isolates within the range of the nominate subspecies and were reported to be characterized by size (*A. m. heidemanni*), or size and shape of the male AGP and female SGP (*A. m. minor*). The southern populations were distinguished only by the shape of the SGP (*A. m. australis*). From the studies by Sites and Willig (2000) and Sites et al. (1996), body size is not a discrete character useful to distinguish among subspecies of *A. mormon.* We examined topotypic specimens of *A. m. heidemanni* and found subtle differences in the diagnostic features when compared with the nominate subspecies. Because of this and evidence provided by Sites and Willig (2000), subspecific recognition of *A. m. heidemanni* is not justified. Thus, we propose *A. m. heidemanni* as a junior synonym of *A. m. mormon.* In the case of *A. m. australis,* we collected specimens within the same population (L-1711 in the state of Durango) that exhibit characteristics of both *A. m. australis and A. m. mormon.* More specifically, the SGP of different females had short or long posterolateral corners. Some posterolateral corners were several times as long as wide. Thus, because both character states are present in the same population, the subspecific designation based solely on longer posterolateral corners is not valid and we hereby propose the synonymy *of A. mormon australis* with the nominate subspecies. Similarly, we examined topotypic specimens of *A. m. minor* and found that the shape of the posterior margin of the female SGP is variable, as was reported by La Rivers (1963). Most males exhibited an AGP that curves

to the right close to the base and continues almost straight to apex, although this shape was not consistent among all specimens examined. The shape of the AGP also exhibits intraspecific variation within other species of this complex. Further, the shape of the pseudoparameres in *A. m. minor* was indistinguishable from those of *A. m. mormon*. La Rivers (1963) also reported a less contrasting color pattern and narrower embolium; however, these features also exhibit intraspecific variation. Because the features presented by La Rivers (1963) fall within the range of variation encountered within the nominate subspecies, and overall body size is not a valid characteristic upon which to support subspecific recognition, we propose *A. m. minor* as a junior synonym of *A. m. mormon*.

Variation. The dark coloration on the prothorax and hemelytra on specimens from the United States is lighter in specimens from Mexico. Specimens collected from warm water present the posterolateral corners of the connexiva only slightly produced. Some females, especially those from the southernmost part of the range, present long (several times as long as wide) posterolateral lobes of the SGP, whereas those from the central and northernmost parts of the range can present lobes that are short or rounded-off and inconspicuous. *Ambrysus mormon* apparently presents a progressive reduction in the size of the posterolateral lobes of the SGP that corresponds to its south-north distribution. Also, the examined females from Idaho presented an extremely shallow central concavity on the posterior margin of the SGP. Males, especially those from the north, can present the AGP curving to the right close to the base to continue almost straight to apex. Some males present the AGP evenly curved throughout its length. The high degree of intraspecific variation exhibited by specimens of *A. mormon* reflects the wide distribution

of the species and that it occurs in environments with a wide range of environmental temperatures.

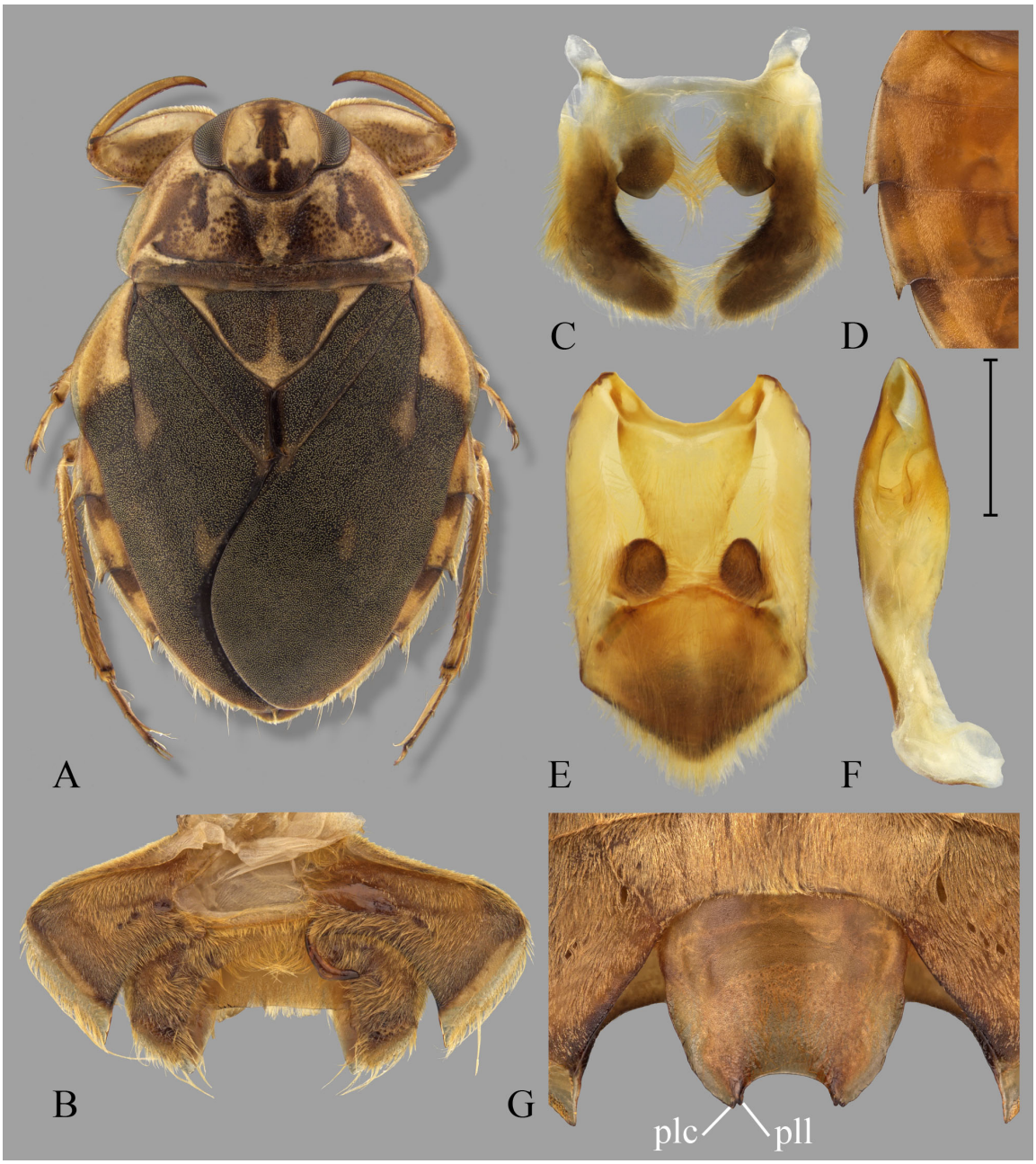

Figure 16. Structures of *Ambrysus mormon*. (A) dorsal habitus of female, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed). plc = posterolateral corner, pll = posterolateral lobe.

Type Locality. United States: Utah: Washington Co., St. Georges.

Repository. Montandon (1909) reported that specimens were deposited in his collection and that of M. Schouteden. La Rivers (1951) indicated that the type was in the BMNH; however, M. Webb (pers. com.) recently informed us that the type is not there. Thus, the repository of the type specimen is unknown.

Distribution. In the United States, the species is widely distributed in all the states (except Washington) west of the Great Plains geophysical province. In Mexico, La Rivers (1958) reported this species from the states of Chiapas, Guerrero, and Jalisco. At the CAS, we examined specimens of *A. mormon* from these three states and consider it likely that those are the same specimens on which La Rivers (1958) based the records of the species from central and southern Mexico. Based on our extensive collecting throughout Mexico and all the material examined from different museum collections, this species is distributed in Mexico only in two northwestern states in the Mexican Plateau (Chihuahua) and the Sierra Madre Occidental (Durango) biogeographical provinces (Fig. 2). Davis (1986) reported this species from the state of Sonora (northernmost limit of the Mexican Pacific Coast biogeographic province); although we did not examine the specimen on which he based this record, it is possible that *A. mormon* occurs in that area. The disjunct southern distribution based on specimens from Chiapas, Guerrero, and Jalisco is problematic because *A. mormon* apparently does not occur in that area at the present time. Either the species was originally widely distributed in western areas of Mexico and the United States and later the range contracted to the distribution we see today, or those specimens from central and southern Mexico were collected further north and mislabeled. Data from these specimens housed at the CAS are given in the Material

Examined section, although the localities are not represented in Figure 2 because we consider the records from Chiapas, Guerrero, and Jalisco to be dubious. La Rivers did not include those records in the original description, although he labeled the specimens as paratypes, but later included the specimen data in a paper reporting new records from Mexico (La Rivers 1958).

Published Records. Mexico: Chiapas, Chihuahua, Guerrero, Jalisco, Sonora (La Rivers 1953, 1958, 1971; Davis 1986; Polhemus & Polhemus 1988). United States: Arizona, California, Colorado, Idaho, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oregon, South Dakota, Utah, Wyoming (Montandon 1909; La Rivers 1951a, 1971; Davis 1986; Polhemus & Polhemus 1988; Tinerella & DeLorme 2005; Clark 2014).

Type Material Examined. Type material of *A. m. mormon* was not available for examination. HOLOTYPE ♂: **MÉXICO: CHIHUAHUA:** Rio San Pedro between Chihuahua & Naica, Mex., 6-22-34, Smith and Dunkle / *Ambrysus mormon australis* La Rivers HOLOTYPE / 1948 *Ambrysus mormon australis* La Rivers determined by Ira La Rivers (SEMC). PARATYPES: Rio San Pedro between Chihuahua & Naica, Mex. 6-22-34, Smith and Dunkle / *Ambrysus mormon australis* La Rivers PARATYPE / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♀ CAS); same but / *Ambrysus mormon australis* La Rivers determined by Ira La Rivers '50 (1♂ CAS). HOLOTYPE ♀: **UNITED STATES: WYOMING:** [Yellowstone] Natl. Park, geyser basin, Wy. / *Ambrysus Heidemanni* (sic) Montandon Type 1909 / Museum Paris 1910 A. L. Montandon 1909 (MNHN). HOLOTYPE ♀: **UNITED STATES: IDAHO:** Hot Creek Falls, Bruneau Canyon, Owyhee Co., Idaho, 22Jul52, W. F. Barr / *Ambrysus*

m. minor La Rivers HOLOTYPE / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 / California Academy of Sciences Type No. 13403 (CAS). **Material Examined. MÉXICO: CHIAPAS:** Escuintla, Chiopas [Chiapas], Mex. VIII.18.1926, J.J. White / 30 / *Ambrysus mormon australis* La Rivers PARATYPE / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 / an unpublished Paratype Det. 1978 by Vincent F. Lee (1♀ CAS). **CHIHUAHUA:** Camargo, Río Conchos, 17 August 1952, John D. Lattin Cal.Acad.Sci.Coll. / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (4♂, 2♀ CAS); Casas Grandes, 15-VII-85, H. Brailovsky (2♂, 2♀ CNIN); Mpio. Satevo, Satevo, Río Satevo, 30 December 2013, L-1706 / 1377 m, 27° 57' 44.7" N, 106° 07' 35.6" W, DRV & PRH colls. (1♂ UMC); same but 31 December 2013, L-1707 (2♂, 1♀ UMC); Mpio. Valle de Zaragoza, Valle de Zaragoza, Río Conchos, L-1705, 30 December 2013 / 1342 m, 27° 27' 35.8" N, 105° 49' 21.4" W, DRV & PRH colls. (11♂, 7♀ UMC); Rio Bahuerachic 18 km W of La Junta on new Hwy to Basaseachic [Basaseachi], June 17, 1978, R. R. & F. H. Miller (1♂ UMMZ); Río Conchos, M78-8, 23 Mayo 1978, Miller, Marsh & Smith (2♀ UMMZ); Rio Conchos at Valle de Nargoya [Zaragoza ?], 23 May 1978, Miller, Marsh & Smith, M78-8 (1♂ UMMZ); Río Papigochi, VI-19-1978, R. R. Miller et al. (1♀ UMMZ); Rio Papigochic 5 mi W of Miñera, on rd. Pachera-Creel, 19 June 1964, R. R. Miller (2♀ UMMZ); Rio San Pedro at San Lucas, Chihuahua, Mex., May 21, 1937 / Seth Benson collector (1♀ EMEC); Río San Pedro just above Satevó, M78-9, 23–24 Mayo 1978, Miller, Smith & Marsh (2♂, 1♀ UMMZ). **DURANGO:** Mpio. Guanaceví, El Cuervito, Pte. Morelos, 02 January 2014, L-1715 / 1963 m, 25° 45' 14.3" N, 105° 47' 30.6" W, DRV & PRH colls. (1♀ UMC); Mpio. Guanaceví, El Potrero

Viejo, Río Sextín, 02 January 2014, L-1713 / 1931 m, 25° 56' 28.7" N, 105° 49' 43.0" W, DRV & PRH colls. (2♂, 1♀ UMC); Mpio. San Bernardo, San Bernardo, Río Sextín (Río Nazas), 01 January 2014, L-1711 / 1607 m, 26° 00' 05.0" N, 105° 30' 17.6" W, DRV & PRH colls. (1♂, 3♀ UMC). **JALISCO:** Chapala, Mex. July 15, 1951, Drake & Hottes / *Ambrysus mormon australis* La Rivers PARATYPE / an unpublished Paratype Det. 1978 by Vincent F. Lee (1♂ CAS); Cojumatlan, Jalisco [Michoacán], Mex. 9-9-38, H. D. Thomas / 180 / Ira La Rivers collection bequeathed to the California Academy of Sciences - 1978 (1♀ CAS). **UNITED STATES: ARIZONA:** Gila Co., Tonto Creek above Gisela, 2,950 ft. elev., pool, 13 April 1992 (1♂ UMC); Mojave Co., Beaver Dam Wash, 15-IX-1974 (1♂, 1♀ BYUC); Mojave Co., Beaver Dam Wash, in Littlefield, 27-Sep-1984, M.F. Whiting (1♂ BYUC). **CALIFORNIA:** Bear Cr., Lake Co., Cal., IV-13-1968 / A. J. Gilbert (3♀ CSCA); Butte Co., Chico, Bidwell Park, Big Chico Creek, 6 April 1982, coll: R. W. Sites (10♂, 16♀ UMC); Colusa Co., Mendocino Natl. Forest, Mill Creek at Mill Creek Cmpgrd, 20 April 2015, C. Barr & W. D. Shepard / 495 m, 39º21.33'N, 112º39.32'W (48♂, 66♀ UMC); Colusa Co., Mendocino Nat. For., Mill Creek Cmpgrd, 20/IV/2015, 495 m, 39º21.33'N, 112º39.32'W, WDS-A-1981B, C. Barr & W. D. Shepard (19♂, 19♀ UMC); Colusa Co., Mendocino Natl. Forest, Red Bridge, Middle Fork Stoney Creek, 449 m, 20 April 2015 / 39º22.64'N, 112º39.14'W, W. D. Shepard leg., WDS-A-1982 (35♂, 30♀ UMC); Colusa Co., Mill Creek Cpg., IV-30-1980, Fred G. Andrews, sweeping *Quercus* sp. (1♀ CSCA); Deer Ck. Vina, Calif. Tehema Co., 6 April 1982 / R. W. Sites Collector (1♀ UMC); Del Norte Co., Klamath River, Hwy. 169, Klamath Glen, 41º 30' N, 123º 60' W, 8-VI-2005, R.W. Baumann (3♂, 2♀ BYUC); Del Puerto Canyon, Stanislaus Co., Cal., 4-20-1965 (2♀ BYUC); Del Puerto

Cyn., Stani. Co., Ca., 9-1-1988, G. Hackwell (1♂ BYUC); Denair, Calif., Stan. Co., 11-7-71, M. Ridgeway (1♀ BYUC); Kearn Co., Kern River, Bakersfield, 22-XII-1999, T.D. Waite (1♀ BYUC); Humbolt Co., Eel River, 6 mi NNE of Garberville, US 101, 6 July 1955, B55-2, coll: R. M. Bailey (3♂, 3♀ UMC); Inyo Co., Amargosa River at Tecopa, 18 May 2014, coll: G. L. Challet (7♂, ♀7 UMC); same but Armagosa [Amargosa] (1♂, 1♀ UMC); Inyo Co., pond westside Hwy 127 W of Tecopa, 30 April 2014 / 35.8872 - 116.3574, Alt. 2046, coll: G. Challet (1♀ UMC); Kern Co., I-12-1971 / ex: irrig. canal / Collector E. A. Kane (1♀); same but / Naucoridae *Ambrysus* sp. poss. *signoreti* Stal Det. E. A. Kane 71 (1♀ CSCA); Lake Co., 8 mi E Clearlake Oaks, Cache Crk., VII-3-1975, Fred G. Andrews (9♂, 4♀ CSCA); Mendocino Co., Navarro River at Hendy Woods St. Pk., 21-June-1985 / R.W. Baumann, C.R. Nelson, M.F.Whiting (5♂, 5♀ BYUC); Mendocino Co., Navarro River @ Hendy Woods St. Park, May 17 2012, G. Challet / *Ambrysus mormon* det. R. W. Sites (1♂, 2♀ UMC); Napa Co., Capelle Creek, Hwy. 128, Capelle Cross Road, 210 m, 38º28'02"N, 122º12'50"W, 17-V-1998, C.R. Nelson (1♀ BYUC); Placer Co., Doty Ravine, 2 mi. N. Lincoln, 3 mi. E. Hwy 65, 3-XI-2003, C. Batchelor (1♀ BYUC); Pope Valley, Napa Co., Cal., May 3 1969 / J. F. Ward Collector / Russell C. Biggam Collection University of Idaho Acc. Dec. 1987 (1♂, 1♀ UIEC); Preston, Cal., Sonoma Co., X-6-1968 / J. F. Ward Collector / Russell C. Biggam Collection University of Idaho Acc. Dec. 1987 (1♂, 2♀ UIEC); Richardson's Grove St. Pk., California / 7-20-57, Joe Keefe / edge of Eel River (1♀ CSCA); Riverbank, Cal., Stanislaus Co., 2-29-1963 (1♀ BYUC); Russian River, Mendocino Co., Cal., 5 mi. N. Cioverdale, Oct. 6, 1968 / A. J. Gilbert Collector (1♂, 3♀ CSCA); Santa Clara Co., Santa Clara, 21-III-1953 (8♂, 12♀ BYUC); Santa Lucia River, Arroyo Seco Camp, Monterrey

Co., Calif., V-2-64 / R. R. Pinger Jr. Acc. No. 240 (4♂, 1♀ CSCA); Shasta Co., Rt 44, Bear Crk., ca. 8 mi E of Palo Cedro, 28 Aug 1991, R. S. Zack & M. A. Valenti (4♂, 5♀ UMC); Shasta Co., Rt 44, Cow Crk. nr. Palo Cedro, 28 Aug 1991, R. S. Zack & M. A. Valenti collrs. / *Ambrysus mormon* Montandon det. R. S. Zack 1992 (20♂, 17♀ UMC); Siskiyou Co., jct of Beaver Creek and Klamath River, 41º52'09"N, 122º49'03"W, 22-VIII-2011, M. Friedman (1♀ BYUC); Stanislaus Co., Hughson / 5 Nov. 1969, C. Noriega (1♂ BYUC); Turlock, California, Stanislaus Co., 10-24-1969 / collector M.R. Pittman (1♂ BYUC); Yolo Co., Guinda, IX-17-1972, Fred G. Andrews (2♀ CSCA).

COLORADO: Archuleta Co. Lower Piedra R. Campgrd, 7 July 1979, CL13, Coll: C. N. McKinnon / *Ambrysus mormon* Montandon Det. C. N. McKinnon 79 (7♂, 1♀ UMC); Moffat Co., Yampa River, Hwy 318, near Maybell, 9-V-1997, R.W. Baumann (1♀ BYUC); Routt Co., Trout Creek, Trout Creek Ranch, near Steamboat Springs, 8-VII-2004, J. Liley (2♀ BYUC). **IDAHO:** Bruneau Hot Falls, Owyhee Co., El. 2500', Idaho, USA / June 10 1967, Wm. H. Clark Collector / Russell C. Biggam Collection University of Idaho Acc. Dec. 1987 / *Ambrysus mormon minor* La Rivers Det. William H. Clark 1969 (1♂ UIEC); Hot Cr. Falls, Ida., Owyhee Co., VI-27-1953 / W. F. Barr Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (9♂, 2♀ UIEC); Hot Cr. Falls, Owyhee Co., Ida., VI-16-1961 / W. F. Barr Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (7♂ UIEC); Hot Cr. Falls, Owyhee Co., Ida., IX-9-1965 / Collector R. L. Penrose / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (2♂, 1♀ UIEC); Hot Cr. Falls, Owyhee Co., Ida., IX-9-1965 / E. J. Allen Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (1♂, 1♀ UIEC); Hot Cr. Falls, Owyhee Co., Ida., V-12-1966 / L. S. Hawkins Jr. Collector / *Ambrysus mormon minor* La Rivers

Det. R. C. Biggam '78 (2♂, 1♀ UIEC); Hot Cr. Falls, Owyhee Co., Ida., VII-2-1967 / R. L. Westcott, J. A. Westcott Collectors / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (1♀ UIEC); Hot Cr, Falls, Owyhee Co., Ida., IX-9-1965 / E. J. Allen Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (1♀ UMC); Hot Cr, Falls, Owyhee Co., Ida., V-12-1966 / L.S. Hawkins Jr. Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (1♂ UMC); Hot Springs, Owyhee Co., Ida., III-21-1976 / T75R6ES27 G. A. Shook Collector / Russell C. Biggam Collection University of Idaho Acc. Dec. 1987 / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (3♂, 3♀ UIEC); Indian Bathtubs, Owyhee Co., Ida., T8S R6E S3, IV-17-1967 / R. C. Biggam, D. M. Benhower Collectors / Russell C. Biggam Collection University of Idaho Acc. Dec. 1987 / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (9♂, 6♀ UIEC); Indian Bathtubs, Owyhee Co., Ida., III-28-1971 / G. Chapin Collector / Russell C. Biggam Collection University of Idaho Acc. Dec. 1987 / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (2♂ UIEC); Indian Bathtubs, Owyhee Co., Ida., T8S R6E S3, May 13 1976 / R. C. Biggam Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (6♂, 3♀ UIEC); Owyhee Co. Bruneau Riv. ca 7 mi SSE Bruneau, T7S R6E Sec. 26, 22 Sept 1988, R. S. Zack collr. / *A. mormon* Montandon det. R. S. Zack (7♂, 13♀ UMC); Owyhee Co., Bruneau River, 7.6 mi SE Bruneau, 8 July 1992, R. S. Zack collr. (19♂, 20♀ UMC); Owyhee Co., Owyhee River, VI-28-2001, (177-5) (3♂, 3♀ UIEC); 5 mi S. E. Bruneau, Owyhee Co., Ida., V-23-1983 / Indian Bathtubs / J. B. Johnson Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '83 (1♂ UIEC); Portneuf River 10 mi S Pocatello, Bannock Co., Ida., VII-15-1964 / E. Fitcher Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (1♂, 1♀ UIEC); 5

mi S. E. Bruneau, Owyhee Co., Ida., V-23-1983 / Indian Bathtubs / J. B. Johnson Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '83 (1♂ UIEC). **MONTANA:** Carter Co., Boxelder Cr. 8 mi N. Mill Iron, 20May1994, K. B. Miller colr. / *A. mormon mormon* Montandon det. K. B. Miller 1995 (3♂, 3♀ UMC); Madison Co. W. Fk. Swimming Hole Warm Spr., 29 Jul 1994, K.B. Miller colr. / *Ambrysus mormon heidemanni* Montandon det K.B. Miller 1995 (7♂, 3♀ UMC); Nimrod Warm Spring, Granite Co., MT., 1133 m, N 46º42'17.9", W 113º27'19.8", II-26-2002, A. L. Sheldon, B. Reid / *Ambrysus mormon* det. R. W. Sites (37♂, 23♀ UMC). **NEBRASKA:** Dawes Co., Squaw Creek, rd 707, SW of Crawford, 8 July 1997, R.W. Baumann (1♀ BYUC); Dawes Co., White River, Hwy. 20, west of Crawford, 4 February 1995, Huntsman & Kondratieff (2♂, 1♀ BYUC); Dawes Co., White River, W. of Crawford, 3-VI-1995, Baumann & Huntsman (1♀ BYUC). **NEVADA:** Clark Co., Moapa, Warm Springs Rd., Palm Creek RV Park, 20 December 1995, coll: Nichols & Floyd, Upper Muddy River / *Ambrysus mormon* (11♂, 8♀ UMC); Clark Co., Moapa Valley W. D. pond, 7 November 1971, coll: J. F. Leser (2♂, 1♀); Clark Co., Moapa Warm Springs, 8 November 1998, colls: A. Vitheepradit and N. Whitemann (2♂, 1♀ UMC); Clark Co. Moapa Warm Spring, 8 November 1998, coll: R. W. Sites (22♂, 24♀ UMC); same but gravel streambed nr spg / *Ambrysus mormon* det. R. W. Sites (3♂, 3♀ UMC); Clark Co., Moapa Warm Springs on L.D.S. Rec. Ar., 8 November 1998, Whiteman & Vitheepradit / *Ambrysus mormon* Montandon Det. N. Whiteman 1999 (9♂, 1♀ UMC); Clark Co., Moapa Warm Springs, Outflow on LDS, 8 Nov 1998, Coll: Whitemann & Vitheepradit (2♂, 2♀ UMC); Clark Co., Moapa Warm Springs, Outflow on LDS property, 8 November 1998, Coll: Whitemann, Vitheepradit and Sites (4♂, 7♀ UMC); Clark Co., Muddy River, Warm

Springs, 36º44'N, 114º42'W, 18-XII-1995, Baumann & Huntsman (12♂, 9♀ BYUC); Clark Co. Upper Muddy River, ca 6 mi WNW of Moapa, N36º42.629', W114º41.656', 10 November 1998, R. S. Zack and C. N. Looney collectors (2♂, 4♀ UMC); Clark Co., Warm Springs, 11-IX-1987, D. Beazer (2♂, 2♀ BYUC); Clark Co., Warm Springs, 27 August 1989, coll: J. A. Back / *A. mormon* Montandon det. R. W. Sites 1991 (17♂, 19♀ UMC); Lincoln Co., Ash Warm Springs, 3750 ft. elev., 36ºC, 21 July 1992, CL 2711, J.T. and D.A. Polhemus / *Ambrysus mormon* det. RWS (3♂, 7♀ UMC); same but Ash Warm Springs Nevada ♀♀ opened for eggs (4♀ UMC); Nye Co., Hot Creek, Walter Kirch Wildlife Area [Wayne E. Kirch Wildlife Management Area], 1-VIII-1996, R.W. Baumann (1♂, 1♀ BYU; 1♂, 1♀ UMC); Nye Co., Hot Creek Spring, N. of Sunnyside, 15-V-1985, Whiting & Baumann (4♂, 1♀ BYUC); Panaca, Nevada, IV-8-51, Panaca, Nevada / Leonard D. Moore collector (1♂, 1♀ BYUC). **NEW MEXICO:** Catron Co., San Francisco River at Frisco Hot Springs, 2.5 mi. S Pleasanton, 4 May 1950, coll; R. R. Miller, M50-76 (1♂, 1♀ UMC); Colfax Co., Vermejo River, 23-IV-1986, Baumann & Wells (1♂ BYUC); Lincoln Co. Rio Hondo nr. Hondo, 26 May 1989 coll: R. W. Sites, veg. nr. margin, reared in laboratory for 2–3 wks. (1♀ UMC); Lincoln Co. Rio Hondo 2 mi E Hondo, 23 September 1988, coll: R. W. Sites, veg. in flow at margin (25♂, 24♀ UMC); Lincoln Co. Rio Hondo 2 mi E Hondo, 26 May 1989, coll: R. W. Sites, vegetation at margin (9♂, 5♀ UMC); Lincoln Co. Rio Hondo 2 mi E Hondo, 6 July 1992, coll: Brian (8♂, 2♀ UMC); Lincoln Co., Rio Honel on Hwy 360, 5.0 mi. NE Hondo, 31 May 1991, coll: D. P. Herrmann (23♂, 12♀ UMC); Pecos River at Dilia, 16 Aug 1988, R. W. Sites (1♀ UMC). **OREGON:** Crooked Cr. 7 mi E of Burns Jct. Hwy 95, Malheur County, October 1, 1962, Kenneth Goeden / Aquatic plants bordering creek, Temp. 67º F.

(1♀ UMC); 3-Forks, 40 miles S of Jordan Valley, Sept. 30, 1962, Kenneth Goeden / Runoff stream of warm springs, Temp. 90º F / *Ambrysus mormon* Montandon 1909 (Ira La Rivers) 63 (2♀ UMC); 6 mi S of Burns Jct, Hwy 95, Malheur County, Sept. 29, 1962, Crooked Creek, Kenneth Goeden (3♂ UMC). **SOUTH DAKOTA:** Fall River Co., Cascade Falls, Cascade Cr., Hwy 71, S of Hot Springs, 5 Feb. 1995, Baumann & Kondratieff (3♂, 7♀ BYUC); Fall River Co., Cascade Springs, J.H. Keith picnic area, 43º20'N, 103º32'W, 20 Aug 1996, R.W. Baumann (1♂, 2♀ BYUC); Fall River Co., Cascade Springs, Hwy 71, J.H. Keith Park, 5 Feb. 1995, Baumann & Kondratieff (6♂, 5♀ BYUC); Fall River Co., Cascade Springs, Hwy 71, J.H. Keith Park, 3 June 1995, R.W. Baumann (4♂, 6♀ BYUC); Fall River Co., Cheyenne River, Edgemont, 42º18'N, 103º49'W, 20 Aug. 1996, R.W. Baumann and B. Huntsman (3♂, 6♀ BYUC); Fall River Co., Cheyenne River, Hwy 71, 10 mi. south of Hot Springs, 3-VI-1995, Baumann & Huntsman (8♂, 10♀ BYUC); Fall River Co., Cheyenne River, Hwy. 385, below Angostura Reservoir, 18 Apr. 1996, R.W. Baumann (2♀ BYUC); Harding Co., Little Missouri River, Hwy 20, Camp Crook, 45º32'N, 103º58'W, 14 July 1997, R.W. Baumann (1♀ BYUC); Harding Co., South Grand River, Hwy 79, N of Reva, 45º38'N, 102º59'W, 15 July 1997, R.W. Baumann (2♂ BYUC); Hot Springs, S. Dak. June 22, 1940, 2 mi. NW Hot water, H. C. Severin, Coll. (5♂, 5♀ UMC); Meade Co., Elk Creek, Hwy. 26, below jct. Meadow Creek, 22 April 1996, Huntsman & Baumann (1♀ BYUC). **UTAH:** Duachesne Co., Dry Gulch Cr. at US 40 nr Roosevelt, M 60-12, 12 August 1960, colls: R.R. Miller family (1♂, 1♀ UMC); Duchesne Co., Duchesne River, below Uintah River, 28-X-77, R.N. Winget (2♀ BYUC); Duchesne Co., Uintah River at Ft. Duchesne (1♂, 1♀ BYUC); Emery Co., Christiansen Wash, S. of Emery, above Quitchupah Creek, 18-

VI-2003, R.W. Baumann & S.M. Clark (2♀ BYUC); Enterprise, Ut. / Leonard D. Moore collector (1♀ BYUC); Enterprise, Ut. / Vasco M. Tanner collector (1♀ BYUC); Garfield Co., Escalante River, Hwy 12, near jct. Calf Creek, 37º47'N, 111º25'W, 30-VII-2003, R.W. Baumann (3♂, 6♀ BYUC); Garfield Co., Grand Starircase- Escalante Natl. Mon., Calf Creek, beaver pond below Calf Creek Campground / 37º47'N, 111º25'W, 10 July 2002, S.M. Clark and J.S. Robertson (1♀); Garfield Co., Grand Starircase- Escalante Natl. Mon., Escalante River at Calf Creek, Hwy 12, 1 Aug. 2002, S.E. Morrison (23♂, 8♀ BYUC); Garfield Co., Grand Staircase-Escalante Natl. Mon., Escalante River at Calf Creek, Hwy 12, 1 Aug. 2002, S.E. Morrison (3♂, 6♀ BYUC); Garfield Co., Grand Starircase- Escalante Natl. Mon., Calf Creek, Cmpgd, lower falls trail, 37º47'37"N, 111º21'18"W / 9 May 2001, D.J. Cavan, K.F. Kuehni #24 (2♂ BYUC); Garfield Co., Grand Starircase- Escalante Natl. Mon., Deer Creek, Cmpgd., jct Burr Trail, 37º51'20"N, 111º21'18"W / 21 May 2001, D.J. Cavan, K.F. Kuehni #46 (1♀); same but 7-May-2001 (1♂ BYUC); Garfield Co., Grand Starircase- Escalante Natl. Mon., Harris Wash, off Hole-in-the-rock Road / 12 July 2001, K. Clarke & E. Green, #220 (3♂, 2♀ BYUC); Garfield Co., Grand Starircase- Escalante Natl. Mon., North Creek Rd. jct Hwy 12, 3.5 miles W Escalante / 37º46'23"N, 111º41'16"W, 10 May 2001, D.J. Cavan, K.F. Kuehni #26 (1♀ BYUC); Garfield Co., Grand Starircase- Escalante Natl. Mon., Steep Creek downstream from jct Burr Trail / 37º51'21"N, 111º10'36"W, 7 May 2001, D.J. Cavan, K.F. Kuehni #14 (12♂, 3♀ BYUC); Utah, Garfield Co., Grand Starircase- Escalante Natl. Mon., Rt. 100, Steep Creek, The Gulch / 37º51'N, 111º19'W, 11 July 2002, S.M. Clark and J.S. Robertson (1♂, 2♀ BYUC); Garfield Co., GSENM, Calf Creek Cmpg., Calf Creek, 23-VIII-2000, R. W. Baumann, K.F. Kuehnl & D.J. Cavan (1♂ BYUC); Garfield

Co., GSENM, Escalante River, Hwy. 12, 24-VIII-2000, R. W. Baumann and K.F. Kuehnl (2♂, 4♀ BYUC); Garfield Co., GSENM, Steep Creek, Burr Trail, The Gulch, 37º51'N, 111º19'W, 20-VI-2002, R.W. Baumann & S.M. Clark (1♀ BYUC); Garflield Co., Smiths Fork Canyon, 132 mi. N. Less Ferry, 10-VII-1958, Smith (1♂ BYUC); Garfield Co., Ticaboo Canyon, 148.5 mi. N. Less Ferry, 6-VII-1958, G.R. Smith & G.G. Musser (3♂, 1♀ BYUC); Garfield Co., Warm Springs Creek, 136.5 mi. N. Lees Ferry, 9-VII-1958, Smith (2♂, 2♀ BYUC); Garfield Co., 5 mi. from mouth of Ticaboo Canyon, 6-VII-1958, Smith (1♂ BYUC); Genola Spr. Utah, Mar.4.1961 / R.L. Richart collector (1♀ BYUC); Goshen, Utah, 1 May 1905, C.S. Herrin / Aquatic (1♂, 4♀ BYUC); Goshen, Utah, Apr. 30 1962 / G.L. Jensen collector (3♂, 1♀ BYUC); Goshen, Utah, 2 May 1962 / D.E. Peterson collector (1♂, 1♀ BYUC); Goshen, Ut., Utah Co., 4-17-69 / D.M. McKell (1♀ BYUC); Goshen, Ut., Utah Co., 4-17-69 / G.A. McKell (1♀ BYUC); Goshen, Ut., 10-3-64 / Pamela G. Jones collector (2♂, 1♀ BYUC); Goshen Cyn. Ut. Co. 4-17-69 / G.A. McKell (1♂ BYUC); Goshen Pond, Utah Co, Utah, 14 Feb 1967 / J.G. Brooks water (1♂ BYUC); Goshen Pond, Utah Co, Utah, 14 Feb 1967 / K.M. Duke Collector (2♀ BYUC); Goshen Pond, Utah Co, Utah, Apr. 13 1968 / George W. Lee (2♂ BYUC); Goshen Springs, Utah Co., UT., 11 May 1960 (1♂ BYUC); Goshen, Utah, 1 May 1965 / aquatic (1♀ BYUC); Goshen Springs, Utah Co., Ut., 11 May 1960 (1♂, 2♀ BYUC); Kane Co., Coyote Gulch, 14-VII-1995, H.S. Jacob (2♂ BYUC); Kane Co., East Fork Virgin River, 1 mi. E. Mineral Gulch, 28-V-2003, S.M. Clark (2♂, 1♀ BYUC); Kane Co., GSENM, Rt. 100, Steep Creek, The Gulch, 37º51'N, 111º19'W, 15-X-2002, S.M. Clark (2♀ BYUC); Leeds Environs, Wash. Co., Ut., Apr. 17 1970 / M.W. Hastriter (1♀ BYUC); Magatsu, Ut. / Leonard D. Moore collector (1♂ BYUC); Provo, Utah, June 1959, C.

Kitchens (1♂ BYUC); Provo, Utah, 1961 (1♂ BYUC); Rich Co., Birch Crk. Res., 12-IX-1996, C. Keegan (2♂ BYUC); San Juan Co., Kane Creek, 5-Feb-1984, Whiting & Wells (1♂ BYUC); San Juan Co., small canyon, 51.5 mi. N. Lees Ferry, 29-VII-1958, Smith (1♂ BYUC); Sevier Co., Salina Creek, Hwy I-70, exit 61, 6 mi. E Salina, Gooseberry Road, 13-V-1998, C.R. Nelson / 38º54'54"N, 111º44'26"W, elev. 1950 m (1♀ BYUC); Salt Lake Co., Jordan River, road S. of state prison, 28-XI-1959, B. Francy (7♂, 12♀ BYUC); Sevier River, Sevier Co., Ut., Aug. 2, 196 / D. Sarrett collector (1♂ BYUC); Springs E. of Goshen, Ut. Co., Utah, 20 Mar. 1959 (3♂, 2♀ BYUC); St. George, Ut., St. George, Ut., Leonard D. Moore collector (1♂ BYUC); Tooele Co., Deseret Livestock Company, Skull Valley, spring, 30-IV-1960, D.W. Argyle (6♂, 4♀ BYUC); Tooele Co., Horseshoe Springs, Skull Valley, 40º37'N, 112º42'W, 23-VIII-2005, R.W. Baumann (14♂, 21♀ BYUC); Tooele Co., pond, Deseret Livestock Company, 17-X-1959 (7♂, 15♀ BYUC); Uintah Co., Uintah R., na Roosevelt, May 13, 1989, S. Wells (2♂, 2♀ BYUC); Uintah Co., Vernal, May 14, 1953, T. Blaine Moore (2♂, 7♀ BYUC); Utah Co., Athery Reservoir, Hwy 36 @ Faust, 29-IX-2000, J.A. Robertson (1♀ BYUC); Utah Co., creek, Goshen, June 10, 1989, S.A. Wells (1♀ BYUC); Utah Co., Currant Creek, Goshen Canyon, 18-VII-2002, A.A. Gordon (1♀ BYUC); Utah Co., Currant Creek, Goshen Canyon, 18-VII-2002, L.C. Price (1♂ BYUC); Utah Co., Goshen, 16-X-1961, G.L. Jensen (67♂, 57♀ BYUC); same but 16 Oct 1961 (5♂, 5♀ BYUC); Utah Co., Goshen Canyon, 21-IX-1995, M.M. Stone (1♂ BYUC); Utah Co., Goshen Canyon, Current Creek, 18-VII-2002, B.R. Jensen (1♀ BYUC); Utah Co., Goshen Cyn, Current Creek, 18,VII,2002, E.T. Krimme (1♀ BYUC); Utah Co., Goshen Cyn. Current Crk., 18-VII-2002, P.A. Fungal (2♂ BYUC); Utah Co., Goshen pond, 6-IV-69 (3♂, 1♀ BYUC); Utah

Co., Goshen Ponds, 17-IX-1996, J.G. Ritz (1♀ BYUC); Utah Co., Goshen ponds, 20-IX-1996, J.G. Ritz (1♂, 1♀ BYUC); Utah County, Goshen P[ond]d., 23 IX 96, A. Furstenau (1♂ BYUC); Utah Co., Goshen ponds, 22-IX-1999, S. Bellnap (1♂ BYUC); Utah Co., Goshen Ponds, 22-IX-1999, S.R. Anderson (1♀ BYUC); Utah Co., Utah Co., Goshen Ponds, 27-Mar 2000, B.D. Jessop (1♂ BYUC); Goshen pond, 30-VII-2001, G.S. Streeter (1♀ BYUC); Utah Co., Goshen pond, 30-VII-2001, J. Huish (2♂, 1♀ BYUC); Utah Co., Goshen Ponds, 13-VII-2006, A. Thomson (1♂, 2♀ BYUC); Utah Co., Goshen, Goshen Ponds, 13-VII-2006, M. Hunt (2♀ BYUC); Utah Co., pond, Goshen Ponds, E of Goshen, 22-IX-2000, J. McDonald (2♂ BYUC); Utah Co., Goshen Ponds, E of Goshen, 22-IX-2000, R. Lorimer (1♂, 1♀ BYUC); Utah Co., Goshen Ponds, E of Goshen, 20-IX-2001, K.I. Shaw (2♀ BYUC); Utah Co., Goshen pond, near Goshen, 13-VII-2006, D.B. Christenson (1♂, 5♀ BYUC); Utah Co., Goshen pond, N39.96º, W111.85º, elev. 1385 m, 22 September 2004, M.R. Nelson #005 (1♀ BYUC); Utah Co., Goshen Warm Springs, 39.95928º N, 111.85556º W, elev. 1377 m, 3-X-2006, L.C. Price (1♂ BYUC); Utah Co., Goshen Ponds, 39.95959ºN, 111.85554ºW, elev. 1385 m, 22-IX-2004, M.H. Goodman (1♀ BYUC); Utah Co., Utah Lake, 6 July 1976, B.D. Clark (1♂ BYUC); Utah Co., Salem Ponds, 9-Apr-1985, Wells & Whiting (1♂, 3♀ BYUC); Utah Co., Soldier Creek at Thistle, 39º59.7'N, 111º29.7'W, 5100 ft.,16-IX-2010, S.M. & J.M. Clark (1♂ BYUC); Utah Co., Utah Lake St. Pk., 03-VII-1991, T.R. Clawson (1♂ BYUC); Utah Co., Warm Springs Wildlife Management Area, near Goshen, 27-IX-2006, B.M. Bush (1♀ BYUC); Utah Lake, Utah Co., Utah, May 3 1964, B.W. Cornaby (1♂ BYUC); Washington Co., Beaver Dam Wash, abv. Lytle Ranch, 4-X-1996, J.G. Ritz (2♂, 1♀ BYUC); Washington Co., Beaver Dam Wash, Lytle Preserve, 22-IX-2006, B.M. Bush (1♂, 2♀ BYUC);

Washington Co., Beaver Dam Wash, Lytle Ranch, 4-X-1996, J. G. Ritz (1♀ BYUC); Washington Co., Beaver Dam Wash, Lytle Reserve, N37.14333 W114.02220, Elev. 863, 17 September 2004, L. Oswald (1♂ BYUC); Washington Co., Lytle Preserve, elev 844 m, 37º8.669'N, 114º1.438'W, 19 Oct. 2013, M.T. Porter (1♂ BYUC); Washington Co., Lytel Ranch, 6-3-88, R.H. Blassford (1♀ BYUC); Washington Co., Lytle Ranch, 19-IX-2008, N.R. Hunter (1♀ BYUC); Washington Co., Lytle Ranch, Beaver Dam Wash, 37.1419º N, 114.0254º W, 23 Sep 2011, 2764' elev. R.L. Johnson, J.A. Sharp (1♀ BYUC); Washington Co., Lytle Ranch, 36 mi. W. of St. George, near campground, 19-20 Sept. 2008, T. Lillrose (1♂, 1♀ BYUC); Washington Co., pond at Washington, 9-X-1992, J.T. Zenger (1♂ BYUC); Wash[ington] Co., Red Cliffs Rec., 25-IX-1982, M.F. Whiting (1♂ BYUC); Washington Co., Santa Clara River, abv. Gunlock Reservoir, 26-V-76, D.J. Tipton (2♀ BYUC); Wayne Co., Fremont River, near Torrey, 15-V-66, R.N. Winget (1♀ BYUC); Wayne Co., Sulphur Creek, at junction Fremont River, 16-X-1988, R.W. Baumann (1♂, 3♀ BYUC). **WYOMING:** Crook Co., Beaver Creek, above Cook Lake, Cook Lake Cmpgd., Deer Lodge Mountains, 24 Apr. 1996, R.W. Baumann (1♀ BYUC); Crook Co., Beaver Creek, Hwy 24, above Alva, 8 June 1995, R.W. Baumann (4♂, 2♀ BYUC); Crook Co., Belle Fourche River, Hwy 24, Hulett, 7 February 1995, Baumann & Kondratieff (2♂, 4♀ BYUC); Crook Co., Belle Fourche River, Hwy 24, Hulett, 24 April 1996, Huntsman & Baumann (4♂, 5♀ BYUC); Crook Co., Belle Fourche River, Hwy 24, Hulett, 44º41'N, 104º36'W, 27 Aug. 1996, R.W. Baumann (3♀ BYUC); Goshen Co., N Platte River, Hwy 85, Torrington, 18 Apr. 1996, R.W. Baumann (1♀ BYUC); Lamar River, Yellowstone N. P., 23 VIII 1964 / E. Fichter Collector / *Ambrysus mormon minor* La Rivers Det. R. C. Biggam '78 (1♀ UIEC); Natrona Co. ca

10 mi W Midwest, 10 August 1996, K. B. Miller colr. (2♂ UMC); Niobrara Co., Lower Cheyenne River, 6-IX-2011 (1♂, 1♀ BYUC); Old Faithful Yellowstone Nat. Park, Wyo., VIII 3 30 / RLUsinger Collector (1♀ UMC); Park Co., Yellowstone National Park, Crawfish Creek, 15-VIII-2007 (1♂, 2♀ BYUC); Yellowstone Nat. Park, Old Faithful, VIII 3 30 / RLUsinger Collector / Exchanged with R. L. Usinger (1♂ UMC); Yellowstone N. P., 6-10-42, Wyoming / G.F. Edmundus (4♂ BYUC).

Ambrysus noveloi **Reynoso & Sites NEW SPECIES**
(Figs. 10, 17–18)

Description. Submacropterous female. HOLOTYPE, length 8.32; maximum width 5.12. Paratypes (n = 10), length 7.92–8.80 (mean = 8.48); maximum width 4.96–5.52 (mean = 5.25). General shape elongate, parallel-sided; widest across embolia (Fig. 17A). Overall dorsal coloration of hemelytra dark brown with light brown oval and triangular marks at lateral and posterior margins of corium, respectively; pronotum and head light brown with dark brown marks; legs light brown. Dorsal surface coarsely punctate. Ventral coloration of head pale yellow, thorax light brown to medium brown, abdomen with brown pubescence.

Head. Head length 1.60; maximum width 2.40. Mostly light brown with medium brown medially and posteriorly; coarsely punctate. Eyes convergent anteriorly, synthlipsis 1.00; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 6.2% of head length; posterior margin between eyes strongly convex, extending posteriorly 31.2% of head length. Labrum width 2.1× length, evenly rounded. Labium with three visible yellowish brown segments, darkening

distally, extending 0.40 beyond labrum not including extruded stylets. Antennal proportions 3:10:15:6, length 0.66, extending to near lateral margin of eye, elongate hairs on segment 4 and distal 2/3 of 3.

Thorax. Pronotum coarsely punctate, ground color light brown, extensive darker brown markings, brown line behind eyes; transverse sulcus marking anterior border of transverse band in posterior 1/3; transverse band pale yellow anteriorly, brown posteriorly; lateral margins brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners rounded; width 2.8× length; length at midline 1.56; maximum width at posterolateral corners 4.40. Prothorax ventrally pruinose throughout, except lateral 1/7; apices of propleura meeting at midline, not appressed to prosternellum; propleuron brown, medial 2/3 of posterior margin with golden setae. Probasisternum with sharp median carina and row of setae lateral to carina. Scutellum coarsely punctate, triangular, brown, light brown coloration on anterior and posterior apices, width 2.2× length, width 2.88, length 1.30. Hemelytra densely punctate, dark brown, length 5.92 (chord measurement); corium with light brown oval and triangular marks at lateral and posterior margins, respectively. Clavus brown, length 4.0× width, length 3.36, width 0.84; claval commissure brown, length 1.14. Embolium length 2.60, greatest width 0.86; lateral margin convex, light brown in anterior 2/3, dark brown posteriorly. Hind wings extending to posterior margin of tergum V. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina, apex acute.

Legs. All legs segments light brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to five spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.02, tibia 1.58, tarsus 0.38; middle leg, femur 2.00, tibia 1.88, tarsomeres 1–3, 0.18, 0.40, 0.38; hind leg, femur 2.56, tibia 2.84, tarsomeres 1–3, 0.24, 0.76, 0.56.

Abdomen. Dorsally with connexiva of III–VI exposed, each laterotergite dark brown in anterior 1/3 and light brown posteriorly (Fig. 17A); lateral margin finely serrate, marginal row of intermixed short and long yellow setae, group of trichobothria near posterolateral corners. Posterolateral corners of II (visible ventrally) –V narrowly rounded to right angled and not spinose, VI–VII bluntly acute. Ventrally brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to

oval patches around spiracles on laterosternites II–VI. Mediosternite VII (subgenital plate) width 1.2× length; length at midline 0.95; maximum width 1.12; lateral lobe at mid-length of left margin, slightly deflexed ventrad, posterolateral corners short and pointed, notched central lobe nearly parallel-sided and produced further posteriorly than posterolateral corners (Fig. 17G).

Submacropterous male. Paratypes (n = 10), length 7.52–8.24 (mean = 7.94); maximum width 4.72–5.20 (mean = 4.98). Coloration, setation, pronotum proportions, posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for holotype. Otherwise hind wings extending to middle of tergum V. Accessory genitalic process of tergum VI evenly curved to right, not expanded distally (Fig. 17B). Medial lobes of tergum VIII (pseudoparameres) narrow, symmetrical, posteromesal corners narrowly rounded, posterolateral corners broadly rounded (Fig. 17C). Phallosoma elongate, linear, constricted basally; left ventral lobe lateroflexed at mid-length, right ventral lobe lateroflexed in proximal half (Fig. 17F). Parameres symmetrical, almost as long as wide, mesal margin slightly convex, setae emanating from distal 1/3 of dorsal surface. Proctiger slightly longer than width at base. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 17E).

Variation. Females sometimes present the central lobe of the SGP with lateral margins curved. Males can present the AGP slightly angled to the right at mid-length.

Discussion. *Ambrysus noveloi* is a small species comparable in size to *A. itsipatsari* **n. sp.** Although both species have a similar size, the features of the female SGP, male pseudoparameres, and the overall color pattern easily distinguish these two species. The

characteristic shape of the SGP in this species is general similar to that of *A. bowlesi* **n. sp.**, *A. contrerasi* **n. sp.**, and *A. guttatipennis*, although the central lobe on the posterior margin is produced further posteriorly than the posterolateral corners.

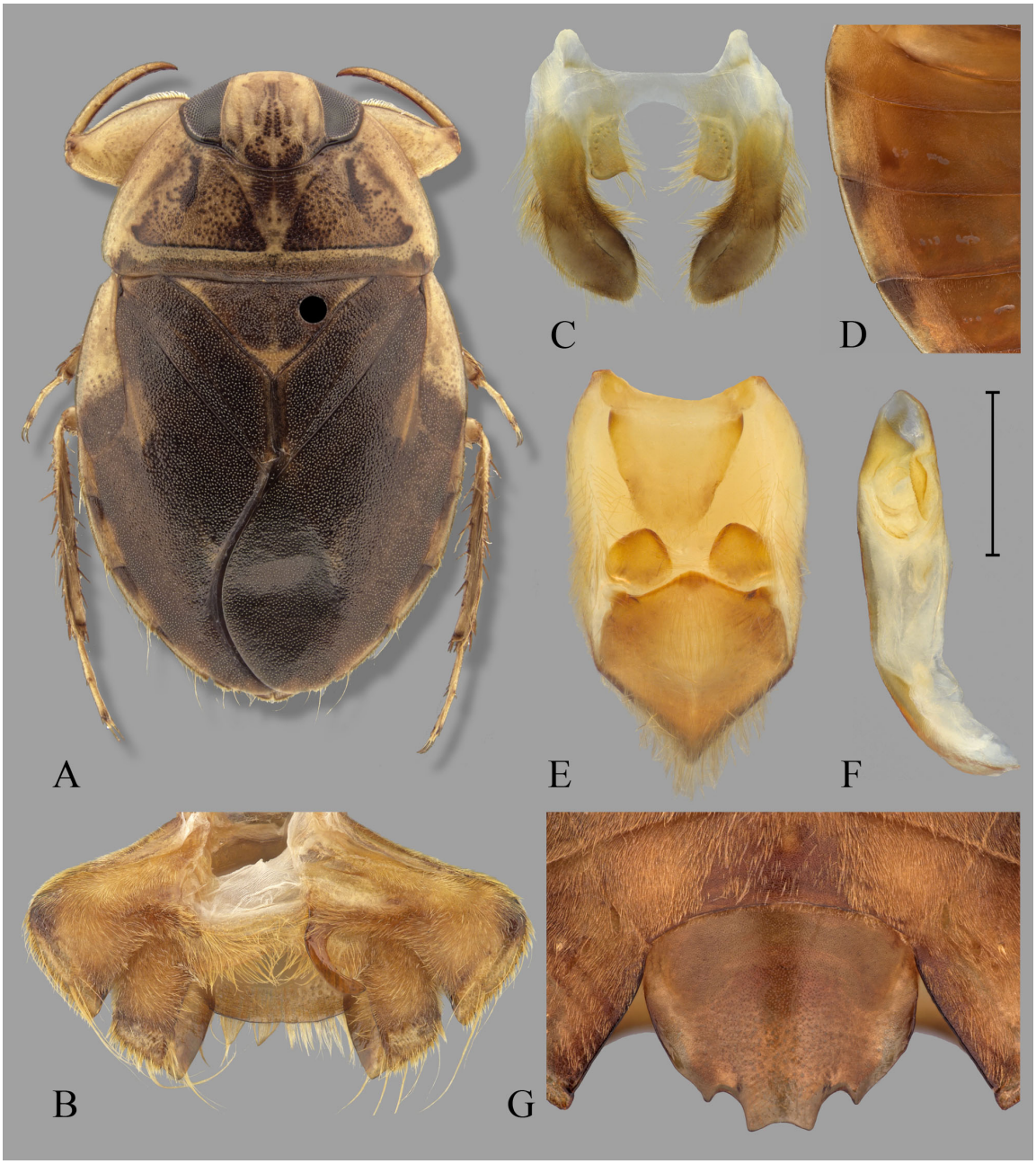

Figure 17. Structures of *Ambrysus noveloi* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed).

Diagnosis. This is a small size species at 7.52–8.80 mm in length that can be distinguished from the rest of species in this complex by the posterolateral corners of connexiva not produced (Figs. 17A, D). Females present the posterior margin of the SGP with the central lobe straight-sided, notched, and produced further posteriorly than the posterolateral corners (Fig. 17G). Males present the AGP evenly curved to right (Fig. 17B). The narrow pseudoparameres present the posteromesal corner narrowly rounded (Fig. 17 C).

Habitat Description. The Sierra Paraíso is in the western area of the state of Jalisco. La Ciénega is a first order stream (Fig. 18) running through a semi-deciduous forest where the endemic species *Pinus jaliscana* Pérez de La Rosa is present. The stream is heavily shaded, shallow (10–30 cm), and varies in width (1–5 m). The predominant substratum is sand and gravel and leaf packs are common on the margins of the stream (Novelo-Gutiérrez, per. com.).

Figure 18. Type locality of *Ambrysus noveloi* **n. sp.** at Arroyo La Ciénega (Jalisco, México).

Distribution. This species is known only from three localities in the municipality of Cabo Corrientes (Jalisco), in the tropical lowlands of the Mexican Pacific Coast

biogeographic province (Fig. 10).

Etymology. This species is dedicated to our colleague and friend Rodolfo Novelo-Gutiérrez, to whom I am particularly grateful for support during my doctoral studies, his help in the field, and his kind donation of saucer bugs for my project. The specimens collected and donated by Rodolfo, including this species, have been extremely helpful in developing an understanding of the taxonomy of *Ambrysus* in Mexico.

Repository. The holotype and some paratypes will be deposited in the Colección Nacional de Insectos (Mexico City); additional paratypes will be deposited in the California Academy of Sciences (San Francisco), Colección Entomológica del Instituto de Ecología A.C. (Xalapa), Enns Entomology Museum (University of Missouri), and the United States National Museum of Natural History (Washington D.C.).

Type Material Examined. HOLOTYPE ♀. **MÉXICO: JALISCO:** Mpio. Cabo Corrientes, Sierra Paraíso, Arroyo La Ciénega, 2-Sep-2015 / 635 m, 20º 22.840' N, 105º 19.664' W, R. Novelo col. PARATYPES: same data as holotype (16♂, 10♀ UMC); Mpio. Cabo Corrientes, Sierra Paraíso, Arroyo La Ciénega, 18 Marzo 2014 / 635 m, 20º 22.840' N, 105º 19.664' W, R. Novelo, S. Smith, & J. A. Gómez cols. (11♂, 4♀ UMC); same locality information but 7 September 2014, J. A. Gómez, S. Smith, & R. Novelo cols. (2♂, 2♀ CAS; 5♂, 5♀ CNIN; 5♂, 5♀ IEXA; 8♂, 13♀ UMC; 5♂, 5♀ USNM); Mpio. Cabo Corrientes, Puente Las Cañadas, 564 m, 20º 24.990 N, 105º 18.837' W, 18 Marzo 2014, R. Novelo, J. A. Gomez, & S. Smith cols. (2♂, 1♀ UMC); same but 7 September 2014 (2♂ UMC); 6 km al E del camino al Coale, 4 km al N del Tuito, 25-XI-90, E. González, G. Ortega, C. Mayorga, S. Rodríguez (2♂, 1♀ UMC).

Ambrysus veracruzanus Reynoso & Sites NEW SPECIES
(Figs. 10, 19–20)

Description. Submacropterous female. HOLOTYPE, length 10.88; maximum width 7.04. Paratypes (n = 10), length 10.16–10.88 (mean = 10.46); maximum width 6.40–7.04 (mean = 6.64). General shape elongate, parallel-sided; widest across embolia (Fig. 19A). Overall dorsal coloration of hemelytra dark brown with light brown oval marks at lateral and posterior margins of corium; pronotum and head light brown with dark brown marks; legs light brown. Dorsal surface coarsely punctate. Ventral coloration of head pale yellow, thorax light brown to dark brown, abdomen with brown pubescence.

Head. Head length 1.92; maximum width 3.14. Mostly light brown with brown medially, posteriorly, and laterally; coarsely punctate. Eyes convergent anteriorly, synthlipsis 1.36; thin band of cuticle along posterolateral margin of eye; eyes not raised above level of vertex or pronotum. Anterior margin between eyes slightly convex, extending anteriorly in front of eyes 6.2% of head length; posterior margin between eyes strongly convex, extending posteriorly 26% of head length. Labrum width 1.8× length, evenly rounded. Labium with three visible yellowish brown segments, darkening distally, extending 0.52 beyond labrum not including extruded stylets. Antennal proportions 3:13:16:6, length 0.72, extending to near lateral margin of eye, elongate hairs on segment 4 and distal half of 3.

Thorax. Pronotum coarsely punctate, ground color light brown, extensive brown marking, brown line behind eyes; transverse sulcus marking anterior border of transverse band in posterior 1/3; transverse band light brown; lateral margins brown, convergent, evenly convex, explanate; posterior margin straight; anterior margin deeply concave between eyes to embrace convex posterior margin of head; posterolateral corners

rounded; width 3.1× length; length at midline 1.92; maximum width at posterolateral corners 6.00. Prothorax ventrally pruinose throughout, except lateral 1/7; apices of propleura meeting at midline, not appressed to prosternellum; propleuron dark brown, medial 2/3 of posterior margin with golden setae. Probasisternum with sharp median carina and row of setae lateral to carina. Scutellum coarsely punctate, triangular, brown, light brown coloration along middle and on anterior and posterior apices, width 2.3× length, width 4.40, length 1.92. Hemelytra densely punctate, dark brown, length 8.16 (chord measurement); corium with light brown oval marks at lateral and posterior margins. Clavus dark brown, length 4.7× width, length 4.56, width 0.96; claval commissure black, length 1.30. Embolium length 3.44, greatest width 1.18; lateral margin convex, light brown in anterior 2/3, dark brown posteriorly. Hind wings extending to middle of tergum VI. Mesobasisternum midventral tumescence negligible, with sulcus on midline continuing through triangular mesosternellum. Metasternellum (= metaxyphus) transverse, subtriangular, with median carina expanded distally, apex rounded.

Legs. All legs segments light brown. Profemur posterior margin with row of tightly arranged setae in basal 2/3, row of short brown spines along middle third; anterior margin with dense pad of setae without associated spines. Protibia and tarsus with occlusal inner surface flattened and with spatulate setae; tarsus immovable, one-segmented; pretarsal claw single, minute, triangular. Procoxa with cluster of stout, brown anteromedial spines. Meso- and metacoxae partially recessed into thorax. Meso- and metafemora with row of short, brown spines on anterior margin; spines restricted to basal half on mesofemur, nearly full length of metafemur. Mesotibia with ventrolateral and

dorsolateral rows of stout reddish-brown spines; mesolateral rows intermixed with combs of two to five spines. Metatibia with ventrolateral and dorsolateral rows of stout reddish-brown spines. Meso- and metatibiae with semi-circlet of spines at apex of dorsal and mesal margins; two comb rows of stout spines near apex of ventral margin. Meso- and metatibiae and metatarsus with long, yellow swimming hairs; hairs profuse on metatibia and -tarsus. Meso- and metapretarsi with paired claws slender, gently curved, with small basal tooth. Leg measurements as follows: foreleg, femur 2.60, tibia 1.94, tarsus 0.50; middle leg, femur 2.64, tibia 2.24, tarsomeres 1–3, 0.20, 0.50, 0.46; hind leg, femur 3.40, tibia 3.84, tarsomeres 1–3, 0.28, 0.90, 0.68.

Abdomen. Dorsally with connexiva of III–VI exposed, each laterotergite dark brown in anterior 1/3 and light brown posteriorly giving checkered appearance (Fig. 19A); lateral margin finely serrate, marginal row of short yellow setae, group of trichobothria near posterolateral corners. Posterolateral corner of II (visible ventrally) narrowly rounded to right angled, III–V acute and spinose, VI–VII bluntly acute. Ventrally brown, with dense pile of fine hairs. Lateral margin with thin, glabrous band. Glabrous rounded to oval patches around spiracles on laterosternites II–VII. Mediosternite VII (subgenital plate) width 1.2× length; length at midline 1.30; maximum width 1.56; lateral lobe at mid-length of left margin, slightly deflexed ventrad; posterolateral corners short and pointed; wide, notched central lobe giving appearance of two rounded lobes, slightly produced further posteriorly than posterolateral corners (Fig. 19G).

Submacropterous male. Paratypes (n = 10), length 8.80–10.00 (mean = 9.53); maximum width 5.88–6.40 (mean = 6.14). Coloration, setation, pronotum proportions,

posterolateral corners of pronotum, scutellum proportions, embolium length generally same as for holotype. Otherwise hind wings extending to posterior margin of tergum V. Accessory genitalic process of tergum VI evenly curved to right in basal 2/3, distal 1/3 angled to right to continue almost perpendicular to the body axis, slightly expanded at angle (Fig. 19B). Medial lobes of tergum VIII (pseudoparameres) narrow, symmetrical, posteromesal and posterolateral corners broadly rounded (Fig. 19C). Phallosoma elongate, linear, constricted basally; left ventral lobe lateroflexed at mid-length, right ventral lobe lateroflexed in proximal half (Fig. 19F). Parameres symmetrical, slightly longer than wide, mesal margin straight, setae emanating from distal 1/3 of dorsal surface and along the posterior margin in the distal half. Proctiger almost as long as width at base. Pygophore with elongate setae sparsely distributed over most of surface, with thick brush on posterior margin (Fig. 19E).

Variation. Some specimens present a lighter brown coloration of the hemelytra. The light brown mark on the posterior margin of the corium can be larger and triangular, similar to that present in most of the species in this complex. Females can exhibit the SGP with posterolateral corners rounded and some have the posterolateral corners and central lobe particularly low (barely visible). Males can have the AGP continuously curved from base to the apex without an angle.

Discussion. This species presents similar diagnostic features to those of *A. mexicanus.* However, the overall darker coloration, more rounded shape, and particularly features of the SGP support the concept of *A. veracruzanus* as a distinct species. The SGP presents a lateral lobe at mid-length on the left margin, whereas *A. mexicanus* has an expanded flap-like left margin. Also, the posterolateral corners and the central lobe in *A. veracruzanus*

are shorter than those of *A. mexicanus* and the notched central lobe of *A. veracruzanus* gives the impression of two lobes. In two of the localities (L-1559 & L-1557) where this species was collected we also found specimens of two species of *Ambrysus* (*Syncollus* La Rivers) that have been recently described (see Chapter III). In this area of east-central Mexico, on the border of the Transmexican Volcanic Belt and the Sierra Madre Oriental biogeographic provinces, seem to inhabit species of *Ambrysus* that have been isolated from other closely related species.

Diagnosis. This is a medium size species at 8.80–10.88 mm in length that can be distinguished from the other species in this complex with slightly produced posterolateral corners of the connexiva (Figs. 19A, D) by the left margin of the SGP convex apically and the lateral lobe at mid-length (Fig. 19G). Males present the AGP evenly curved to right in basal 2/3 and angle to right and almost perpendicular to the body axis in distal 1/3 (Fig. 19B). The pseudoparameres have the posteromesal corners and the posterolateral corners broadly rounded (Fig. 19C).

Habitat Description. Río Tizapam is a small stream that originates on the eastern slope of the Sierra Madre Oriental (Veracruz). The river is part of the Río La Antigua Basin that drains to the Gulf of Mexico. At the type locality, the river is small (approximately 5 meters wide) with boulders and cobble (Fig. 20). Most of the collecting was conducted from submerged vegetation (attached to boulders) and the roots of riparian vegetation.

Distribution. This species was collected in Veracruz from three mountain streams above 1300 meters elevation in the Río La Antigua Basin in the central part of the state, in the Sierra Madre Oriental biogeographic province (Fig. 10).

Etymology. The specific epithet is a noun in apposition and refers to the state of

Veracruz, where the specimens were collected.

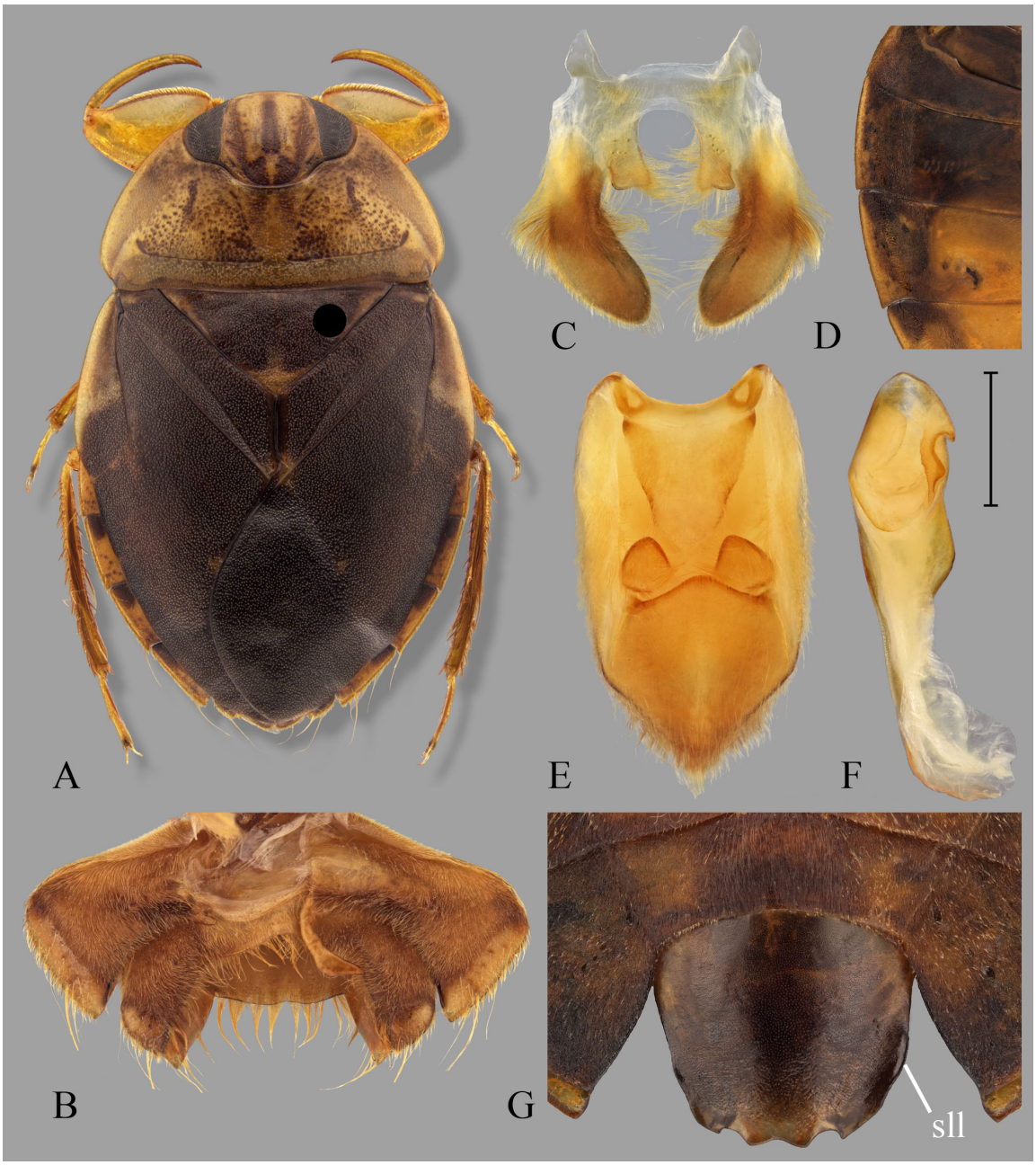

Figure 19. Structures of *Ambrysus veracruzanus* **n. sp.** (A) dorsal habitus of holotype, (B) 6th and 7th abdominal terga of male, (C) 8th abdominal tergum of male, (D) Abdominal terga II–IV (wings removed), (E) genital capsule of male (phallosoma removed), (F) ventral side of phallosoma, (G) sternum VI and subgenital plate of female (terminal abdominal segments removed). sll = sublateral lobe.

Repository. The holotype and some paratypes will be deposited in the Colección

Nacional de Insectos (Mexico City); additional paratypes will be deposited in the California Academy of Sciences (San Francisco), Colección Entomológica del Instituto de Ecología A.C. (Xalapa), Enns Entomology Museum (University of Missouri), and the United States National Museum of Natural History (Washington D.C.).

Figure 20. Type locality of *Ambrysus veracruzanus* **n. sp.** at Río Tizapam (Veracruz, México).

Type Material Examined. HOLOTYPE ♀. **MÉXICO: VERACRUZ:** Mpio. Xico, Río Tizapam, 1.6 km SW of Xico, 1300 m, 19º 24' 26.7" N, 97º 00' 53.05" W, 16 June 2013, L-1559 / Sites, DRV, PRH & Shepard colls., rocks, gravel, marginal vegetation., submerged vegetation in current. PARATYPES: same data as holotype (3♂, 3♀ CNIN; 3♂, 3♀ IEXA; 9♂, 5♀ UMC; 3♂, 3♀ USNM); Mpio. Xico, Arroyo Avestruces, 1401 m, 19° 23' 53.8" N, 97° 02' 29.9" W, 16 June 2013, L-1557, Sites, DRV, PRH & Shepard

colls (2♂, 2♀ CAS; 8♂, 7♀ UMC); same locality information but 29 May 2014, L-1799, DRV & PRH colls. (3♀); Xalapa, arroyo en Conecalli, 30 April 2003, R. Novelo coll. (6♂, 2♀ UMC).

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References Cited

Champion, G. C. 1901. Fam. Naucoridae, pp. 354–361. In: Godman F. D. & O. Salvino (eds.). Biologia Centrali-Americana Vol. II Rynchota. Hemiptera-Heteroptera. R. H. Porter, London, [1897–1901].

Clark, A. 2014. Northern distribution of *Ambrysus mormon* Montandon (Heteroptera: Naucoridae). Western North American Naturalist 74: 478–481.

Davis, J. R. 1986. New distributional records of Naucoridae (Hemiptera) from the United States and Mexico, with morphological and taxonomic notes. The Southwestern Naturalist 31: 535–539.

Hungerford, H. B. 1919. The biology and ecology of aquatic and semiaquatic Hemiptera. The Kansas University Science Bulletin (Entomology) 11: 3–328.

La Rivers, I. 1948. A new species of *Ambrysus* from Death Valley, with notes on the genus in the United States (Hemiptera: Naucoridae). Bulletin of the Southern California Academy of Sciences 47: 103–110.

La Rivers, I. 1951a. A revision of the genus *Ambrysus* in the United States (Hemiptera: Naucoridae). University of California Publications in Entomology 8: 277–338.

La Rivers, I. 1951b. Two new Ambrysi from South America (Hemiptera, Naucoridae). Proceedings of the Entomological Society of Washington 53: 288–293.

La Rivers, I. 1952. A new subgenus of *Ambrysus* from South America (Hemiptera: Naucoridae). Entomological News 63: 33–39.

La Rivers, I. 1953. The *Ambrysus* of Mexico (Hemiptera, Naucoridae). The University of Kansas Sciences Bulletin 35: 1279–1349.

La Rivers, I. 1957a. A new *Ambrysus* from Mexico (Hemiptera, Naucoridae). Entomological News 68: 232–237.

La Rivers, I. 1957b. Re-description of the Stockholm types of *Ambrysus signoreti* and *Ambrysus mexicanus* (Hemiptera: Naucoridae). The Wasmann Journal of Biology 15: 99–106.

La Rivers, I. 1958. New *Ambrysus* records from Mexico. Proceedings of the Entomological Society of Washington 60: 71–74.

La Rivers, I. 1963. Two new Ambrysi (Hemiptera: Naucoridae). Biological Society of Nevada Occasional Papers 1:1–7.

La Rivers, I. 1965. The subgenera of the genus *Ambrysus*. Biological Society of Nevada Occasional Papers 4: 1–7.

La Rivers, I. 1970. A new *Ambrysus* from Venezuela (Hemiptera, Naucoridae). The Great Basin Naturalist 30: 1–4.

La Rivers, I. 1971. Studies of Naucoridae (Hemiptera). Biological Society of Nevada Memoirs 2: 1–120.

La Rivers, I. & N. Nieser. 1972. The *Ambrysus* of Surinam, with the description of a new species, *A. bifidus* (Hemiptera, Naucoridae). Biological Society of Nevada Occasional Papers 29: 1–8.

Mayr, E. 1982. Of what use are subspecies? The Auk 99: 593–595.

Montandon, A. L. 1897. Hemiptera Cryptocerata. Fam. Naucoridae. Sous-fam. Cryptocricinae. Verhandlungen Zoologisch-Botanischen Gesellschaft in Wien 47: 6–23.

Montandon, A. L. 1909. Naucoridae, descriptions d'espèces nouvelles. Bulletin de la Société des Sciences de Bucarest-Roumanie 18: 43–61.

Montandon A. L. 1910. Hydrocorises de l'Amerique du Nord. Notes and descriptions d'espèces nouvelles. Bulletin de la Société des Sciences de Bucarest-Roumanie 18: 180–191.

Nieser, N., A. Pelli & A. L. de Melo. 1999. Two new Ambrysinae (Heteroptera: Naucoridae) from Minas Gerais, Brazil. Acta Societatis Zoologicae Bohemicae 63: 157–163.

Polhemus, D. A. & J. T. Polhemus. 1988. Family Naucoridae, Leach, 1815: The creeping water bugs, pp. 521-527. *In*: Henry, T. J. & R. C. Froeschner, (eds.), Catalog of Heteroptera, or True Bugs, of Canada and the Continental United States. Brill, Leiden.

Sites, R. W. & M. R. Willig. 2000. Morphometric variation among populations of Ambrysus mormon Montandon (Heteroptera: Naucoridae). Proceedings of the Entomological Society of Washington 102: 533–541.

Sites, R. W. & D. Reynoso-Velasco. 2015. Review of the *Ambrysus stali* La Rivers species complex (Heteroptera: Nepomorpha: Naucoridae) with the description of a new species from Mesoamerica. Zootaxa 4018: 279–291.

Sites, R. W., M. R., Willig & R. S. Zack. 1996. Morphology, ontogeny, and adaptation of *Ambrysus mormon* (Hemiptera: Naucoridae): Quantitative comparisons among

populations in different thermal environments. Annals of the Entomological Society of America 89: 12–19.

Stål, C. 1876. Enumeratio Hemipterorum. Bidrag till en förteckning öfver alla hittills kända. Hemiptera, jemte systematiska meddelanden. Kongliga Svanska Vetenskaps-Akademiens Handlingar 14: 141–147.

Tinerella, P. P. & A. W. DeLorme. 2005. First records of the creeping water bug, *Ambrysus mormon* Montandon (Heteroptera: Naucoridae) from North Dakota. Journal of the Kansas Entomological Society 78: 176–178.

Usinger, R. L. 1946. Notes and descriptions of *Ambrysus* Stal with an account of the life history of *Ambrysus mormon* Montd. (Hemiptera, Naucoridae). The University of Kansas Sciences Bulletin 31: 185–210.

Van Duzee, E. P. 1917. Catalogue of the Hemiptera North of Mexico: Excepting the Aphididae, Coccidae, and Aleurodidae. University of California Publications, Technical Bulletins, Entomology 2: 1–902.

Wilson, E. O. & W. L. Brown Jr. 1953. The subspecies concept and its taxonomic application. Systematic Zoology 2: 97–111.

VITA

Daniel Reynoso Velasco was born to Rosalía Velasco Villavicencio and Pedro Reynoso Hernández on October 1st, 1981 in Mexico City, Mexico. In 2002, he started his college education at the Faculty of Sciences of the National Autonomous University of Mexico (UNAM). It was during his junior year in college when he became in contact for the first time with the fascinating world of insects and from that moment onwards his research focused on this group. In 2007, he graduated with a Bachelor of Sciences in Biology. In the same year, Daniel transferred to the Institute of Biology (UNAM) to start his Master's degree program. In 2010, he graduated with a Master's degree in Biological Sciences, with emphasis in Systematics. In December 2010, his nephew Diego Antonio was born, who quickly became the most important person for Daniel. In the fall of 2011, Daniel began the Plant, Insects, and Microbial Science Ph.D. program in the entomology program area at the University of Missouri on a combined National Sciences Foundation and Division of Plant Sciences Doctoral Fellowship. In December 2015, his beautiful niece María José was born; now she and Diego are Daniel's main motivation in life. In May 2016, Daniel graduated with his Ph.D. degree. Over the course of his studies, Daniel has published his research in important journals and presented the results of his research at national and international meetings.