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REVISION OF THE NEARCTIC SPECIES OF THE  
GENUS *AMIOTA* LOEW  
(DIPTERA: DROSOPHILIDAE)

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LANCE E. JONES AND DAVID A. GRIMALDI



BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 458, 177 pp., 97 figures, 1 table

Issued September 15, 2022

## CONTENTS

Abstract.....	3
Introduction.....	3
Early history .....	3
Diversity of <i>Amiota</i> .....	4
Natural history .....	6
Species concepts, classification, and sequence data .....	8
Morphology .....	9
Materials and methods.....	12
Abbreviations .....	12
Field collections .....	12
Specimen preparation .....	14
Terminalia dissections.....	14
External micrographs and measurements .....	15
Genitalic images and illustrations.....	15
Phylogenetic analysis.....	16
Rationale .....	16
Character selection.....	16
Parsimony analysis .....	16
Species concept definition.....	17
Systematics .....	17
Phylogenetic analysis.....	17
Genus <i>Amiota</i> Loew .....	20
The <i>hsui</i> species group.....	20
The <i>alboguttata</i> species group.....	23
The <i>mariae</i> species group .....	34
The <i>cervites</i> species group .....	50
The <i>avipes</i> species group .....	66
The <i>rufescens</i> species group.....	80
The <i>subtusradiata</i> species group.....	91
The <i>nebojsa</i> species group .....	98
The <i>nigrescens</i> species group.....	108
The <i>nagatai</i> species group .....	122
Ungrouped species .....	125
Discussion .....	139
Conclusions .....	145
Acknowledgments.....	172
References.....	173

## ABSTRACT

Thorough biotic inventories are still needed even in families with paradigm organisms like *Drosophilidae*, including well-studied areas such as North America. This work presents a taxonomic revision of the species of the genus *Amiota* Loew in North America and the Nearctic portion of Mexico. *Amiota steganoptera* Malloch is currently excluded from the Nearctic and *Amiota setigera* Malloch is synonymized under *Amiota humeralis* Loew. Specimens of *Amiota subtusradiata* Duda were not encountered during this study along with its synonym *Amiota quadrata* Takada and Toda; however, based on previous descriptions we include *A. subtusradiata* in the Nearctic fauna. All other previously described species from the Nearctic are redescribed. Thirty-six species are described as new: *Amiota amputata*, *A. antitormentum*, *A. avipes*, *A. biacuminis*, *A. brayi*, *A. byersi*, *A. cervites*, *A. cruciatum*, *A. didens*, *A. durangoensis*, *A. elsaltoensis*, *A. floridiensis*, *A. forceps*, *A. fulvitibia*, *A. hyalou*, *A. imperator*, *A. incurva*, *A. laevifurca*, *A. latilabrum*, *A. mcalpinei*, *A. multiplex*, *A. nanonigrescens*, *A. occidentalis*, *A. onyx*, *A. oviraptor*, *A. pseudominor*, *A. raripennis*, *A. sinaloensis*, *A. subnebojsa*, *A. tessae*, *A. texas*, *A. tibialis*, *A. tormentum*, *A. uniacuminis*, *A. wheeleri*, and *A. zaliskoi*. This increases the total species known in the Nearctic from 13 to 49. All species in the Nearctic are illustrated, adult diagnostic features are discussed, and distributions are provided.

A cladogram based on parsimony analysis of 46 morphological characters established species groups in the genus. Most of the Nearctic species were accommodated into 10 species groups. Three species groups were previously erected for species in China and Europe. Seven species groups are newly established: the *avipes*, *cervites*, *hsui*, *mariae*, *nebojsa*, *nigrescens*, and *subtusradiata* groups.

Diversity in *Amiota* appears to be partially dependent on elevation and latitude in the Nearctic, with high diversity found in southern Ontario, the Appalachians, the Ozarks, mountain forests of Arizona and New Mexico, and the Sierra Madre of central Mexico. The taxonomic history of the Nearctic species is reviewed, and various aspects of their biology is presented. Males of species in the *A. mariae* species group are polymorphic for mirror-image, asymmetric genitalia, called chiral variants. Besides morphology, larval saproxyly, adult lachryphagy, and biogeography are reviewed. Challenges to the study of *Amiota* and future prospects are discussed.

## INTRODUCTION

### EARLY HISTORY

*Amiota* Loew was described during what could be thought of as the beginning of North American dipterology (Loew, 1862a). The previous era, marked by a scattered and disorganized literature, would see the first systematic surveys of the *Diptera* fauna in the young American republic. This was in part attributable to the founding of the Smithsonian Museum of Natural History in 1846 (Thompson, 2009). Leveraging the new museum's resources was a Russian diplomat, Carl Robert von Osten Sacken (1828–1906). Osten Sacken published the first checklist of fly species in North America (1858), a monograph (1869), and eventually a synoptic catalog (1878). Most notable was his effort that orga-

nized some of the first field surveys in the country. Probably understanding that he alone could not study the large amount of material, he arranged to have it studied by the preeminent Prussian dipterist, Hermann Loew (1807–1879) (Alexander, 1969). Loew's contributions to the North American fauna comprised three large works (1862b, 1864, 1873), which in turn were translated into English for American specialists by Osten Sacken (Alexander, 1969).

Loew erected *Amiota* to accommodate two specimens collected by Osten Sacken in Washington D.C. and Pennsylvania (1862a; figs. 43, 71). He noted the brilliant white spots found on the face, postpronotal (“humeral”) lobe and wing base as uniting the American species, along with a European species he transferred from *Drosophila* Fallén: *Amiota alboguttata* (Wahlberg). In the

Nearctic, *Amiota* grew over the next 150 years to include 15 species—roughly one species per decade. The genus has never been formerly revised in the Nearctic but has gradually expanded by periodic descriptions of new taxa.

Before the Nearctic catalog of Drosophilidae by Marshall R. Wheeler (1965), several authors described species, including: Hermann Loew (1862a), John R. Malloch (1921, 1924, 1926), Charles W. Johnson (1921), and Wheeler (1952). The interval following the publication of the Nearctic catalog is interesting in one respect. It is defined by 50 years of species descriptions of the North American fauna by workers from Europe and Asia. These include descriptions by Haruo Takada and Masanori Toda (1981), Jan Mác (2003), and Hong-Wei Chen et al. (2004).

Perhaps the closest a revision came for Nearctic *Amiota* was from George C. Steyskal (1909–1996). Steyskal was a machinist by trade and polymath by nature who later worked in the Systematic Entomology Laboratory of the USDA, housed at the Smithsonian, from 1962 to 1979 (Sabrosky, 1997). His research primarily focused on Sciomyzidae, Otitidae, Platystomatidae (Sabrosky, 1997), but he harbored a keen interest in *Amiota* (D.A.G., personal commun.). His notes on the genus are held in the AMNH and include 70 sketches with accompanying notes, a dichotomous key, SEM micrographs, and correspondence with drosophilid experts (fig. 1). In the newsletter of the Michigan Entomological Society (1961, vol. 5, no. 1), Steyskal proclaimed his desire to revise the genus in North America, although this never came to pass.

#### DIVERSITY OF *AMIOTA*

The genus consists of 154 species found worldwide (Bächli, 2020; Wang et al., 2020), but the greatest number is found primarily in the northern temperate areas of the world comprising the Nearctic and Palearctic Region. Southwestern China, especially the Hengduan Mountains, is home to an exceptionally rich fauna (Chen et al., 2005; Zhang and Chen, 2006;

Cao et al., 2008). With a large number of species waiting to be described from Nearctic, four times the number previously known from the region, this area is now another center of species diversity for this genus.

Diversity of *Amiota* seems much lower outside of the temperate zones. They appear to be relatively absent from low tropical islands like those of the Caribbean, where just one species is known to us (an undescribed one from Jamaica in the collections of the AMNH). In their treatment of the drosophilids of Micronesia, Wheeler and Takada recorded no species of *Amiota* (1964). Few species have been described from the Paleotropics, and only one has been described from the mainland Neotropics, *A. steganoptera* Malloch, although many undescribed species do occur there based on museum collections (L.E.J., personal obs.).

Prior authors have attempted to delineate lineages within the genus and as the genus became more narrowly defined. At times, *Amiota* has contained nearly six subgenera, including: *Amiota* s.str., *Phortica* Schiner, *Erima* Kertész, *Apsiphortica* Okada, *Paraphortica* Duda, and *Sinophthalmus* Coquillett (Mác, 2003). Of all the subgenera, only *Amiota* s.str. seems to be worldwide, and only three of the subgenera are known from the Nearctic: *Amiota*, *Phortica*, and *Sinophthalmus* (Marshall, 1965), the last of which is now considered a synonym of *Phortica*. According to Mác (2003), *Amiota* now contains no subgenera; these subgenera were reinstated at the genus level or transferred to other genera.

Although the study of this worldwide genus may have begun with a study of American species, during the last 70 years most descriptive work has been conducted on the Palearctic species. Some important works include Okada (1956, 1960, 1971). These works primarily centered on the Japanese fauna but are notable in their foresight of including descriptions and figures of the male genitalia, which has aided in the understanding of Nearctic species. The European fauna was initially revised by Duda



(1934) and later by Máca (1980). A third revision, including the East Asian species, was conducted by Chen and Toda (2001). Bächli et al. (2004) provided a key, descriptions, and illustrations of most known species in western Palearctic. Most descriptive work in the genus, however, has been in South and southwestern China, especially the Hengduan Mountains, by Chen and colleagues (Chen et al. 2005; Zhang and Chen, 2006; Cao et al. 2008; Wang et al., 2020; and others). The region of high diversity has been hypothesized to be the center of origin for the genus (Chen et al., 2005; Wang et al., 2020), but this has never been tested with a global phylogenetic analysis.

Compared with well-known animals such as birds, insects are vastly understudied. Unlike birds, where features such as geographic ranges, diets, plumage variation, female morphology, calls, nesting preferences, and behavior is well documented for most species, essentially nothing is known about the biology of most invertebrate species. In fact, many insect species are known only from their holotype or from a small number of specimens (Bickel, 2009; Deng et al., 2019). The difficulty of studying insects is probably due to many factors, including the immense number of invertebrate taxa, the low number of working specialists relative to species richness, lack of collection effort for certain taxa, high rates of endemism, diverse life histories that make collection difficult or require specialized protocols, and a lack of literature for identification in most groups.

For these reasons and others, the study of *Amiota* is still at an exploratory stage. This stage is essentially defined by taxonomic descriptions and the gradual fleshing out of regions of diversity with every new record acquired. Scant is known of how they live. What little is known about their biology is scattered and anecdotal in the literature, primarily concerning the Palearctic fauna. Indeed, as Steyskal found, *Amiota* has been ripe for revision for decades.

## NATURAL HISTORY

One of the more underexplored parts of *Amiota* biology is their saproxylic life history, or association with dead and dying wood. Saproxylic organisms can be defined as “species of invertebrates that are dependent, during some part of their life cycle, upon dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics” (Speight, 1989). Some authors also include organisms dwelling on the outer surface of logs such as mosses, the dead hollows of living trees, and species that spend their lifecycle in or under the bark layer (Stokland et al., 2012). *Amiota* can likely be defined as saproxylic based on its use of sap runs, larval development beneath the bark of trees, and possible associations with fungi. Female *Amiota* are commonly intercepted by quickly sweeping a long insect net up and down tree trunks and under large, overhanging branches, particularly trees that are injured or in incipient stages of dying.

Reports in the literature indicate an affiliation of *Amiota* with sap flows and other tree wounds (Malloch, 1924; Storå, 1957; Ferrar, 1987). This is a well-known environment for finding drosophilids in general; the animal feeds on microorganisms present in sap and other resins. Species in this study known to visit tree wounds and sap fluxes include *Amiota hyalou*, sp. nov., a specimen series collected by the second author (AMNH), *A. hsui* Máca (INHS), *A. humeralis* Loew (INHS), and *A. mariae* Máca, a series that was caught on tree wounds (DEBU).

The larvae of Palearctic species such as *A. albilabris* (Roth) were found under the bark of dying aspen trees (Krivoshchina, 2008). Máca (1980) reported that *Amiota* were found in emergence traps containing beech logs. Numerous specimens in the collection of the University of Guelph (DEBU), emerged from tree stumps including *Amiota steyskali* Máca, *A. fulvitibia*, sp. nov., and *A. nigrescens* Wheeler. Neotropical species are saproxylic as well. Jones et al. (2021)

recorded one unidentified species of *Amiota*, likely an undescribed species, reared from the wood of *Tachigali tessmannii* Harms (Fabaceae) in Costa Rica.

What role are the larvae likely performing in these dead-wood ecosystems? It seems possible that the larvae may be saprophagous on fungi. The Palaearctic species, *Amiota alboguttata* (Wahlberg), was reared from the ascomycete, *Daldinia concentrica* (Bolton) Ces. and De Not. (Buxton, 1960; Hingley, 1971). This same species has also been found under the bark of dying aspen trees, concentrated on areas damaged by flask fungi, *Nectria* spp. (Krivosheina, 2008).

Several studies suggest these flies may spend most of their time high in the tree canopies. Eric B. Basden conducted some of the few ecological studies involving *Amiota* (Basden, 1954; Basden and Harnden, 1956). After placing traps baited with fermenting apples in 177 locations around Scotland to study drosophilids, Basden found *Amiota alboguttata* in traps positioned from 27 to 52 feet (~8–15 m) in the tree canopy, while they were absent from baits at or near the ground (1954). During a university expedition to Norway, he and colleagues discovered something similar. This time, traps at different elevations from sea level to 2000 feet (~600 m) above sea level were used to find elevational trends of Drosophilidae. Not only were *Amiota alboguttata* consistently trapped high in the tree canopy, it was also occupying a large gradient of elevation in the landscape, the second greatest in the study, where it was found from sea level to 500 feet (~150 m) above sea level (1956). Other stratification studies in Japan have found the same canopy preference (Toda, 1977; Tanabe, 2002).

Why would species spend so much time high in the tree canopy? Diet and microhabitat preferences could play a role (Tanabe, 2002). Toda (1977) suggests that canopy dwelling is associated with adult sap feeding. While the life histories of *Amiota* are mostly unknown, sap feeding was the known preference of the other canopy dwellers in that study. Regardless, given that the studies were conducted on different continents

and with different, distantly related species, it is reasonable to hypothesize that these behaviors and life histories are probably also found in the Nearctic species.

The most interesting and bizarre aspect of *Amiota* biology is probably lachryphagy, the consumption of tears and eye secretions (Máca and Otranto, 2014). This behavior is widely documented in the genera *Amiota* and *Phortica* but has been known to occur in other Steganine genera including *Apenthesia* Tsacas, *Gitona* Meigen, and *Paraleucophenga* Hendel (Máca and Otranto, 2014). Many may be familiar with the sight of lachryphagy by its more charismatic practitioners: certain nymphalid butterflies, erebid moths, and halictid bees. Malloch (1921) first remarked on this when describing *Amiota minor* and its attraction to perspiration and persistence in trying to land on his hands and face. The phenomenon is now well known among members of the genus throughout the world (Okada, 1968; Máca, 1980; Zhang and Chen, 2006; Chen et al., 2007). Nearly half of the Nearctic species of *Amiota* are known to engage in this behavior (L.E.J., personal obs.), based on specimens collected for this study and collection data for other specimens consulted. It is likely that most species in the region are lachryphagous.

This behavior does have consequences for humans. In their quest for tears, species of the closely related *Phortica variegata* (Fallén) have been known to infect humans and other animals with larvae of the nematode *Thelazia callipaeda* Railliet and Henry (Spirurida: Thelaziidae) in the Palaearctic (Otranto et al., 2006). Immature stages of the nematode reside within the fly, where they are deposited onto the eye during feeding (Máca and Otranto, 2014). In the past, speculation surrounded *Amiota nagatai* Okada and its possibility as a vector, but currently this is not supported (Nagata, 1959; 1960). Thelaziasis infection is primarily of veterinary concern, but human cases are rising (Otranto and Dutto, 2008), a scenario that will likely become more pervasive as the vector species, *P. variegata*, spreads (Palfreyman et al., 2018).

In Lepidoptera it seems that sodium is the key attractant of tears, due to low levels found in plant tissues, and that sodium is passed on from males, which usually sequester the nutrient while puddling, to females during mating (Plotkin and Goddard, 2013). In *Amiota* it is less clear what resource is needed, although it is likely sodium. The behavior is usually displayed by males, which are the majority of individuals caught around the head of mammals (Máca and Otranto, 2014; L.E.J., D.A.G., personal obs.), although females can also be found around the head (L.E.J., personal obs.). This is in direct contrast to other familiar strategies of flies, like blood feeding in certain groups—usually females (Harrington et al., 2001) for which a blood meal supplies abundant sodium for egg production.

One obvious question would be the ratio of males to females in a population given that males are usually collected while tear feeding. It could be that males are just more prevalent and therefore more likely to be captured during lachryphagy. This is probably not the case. Basden (1954) in his tree canopy sampling found a nearly equal number of males and females in his Scottish survey of *Amiota alboguttata* (Wahlberg). Toda (1977), in his study of vertical distributions of drosophilid species in Japan, often collected more females than males in his study using traps baited with fermenting banana. It is likely that this is true across most species. Females may spend more of their time high in the canopy where they are breeding (Toda, 1977).

#### SPECIES CONCEPTS, CLASSIFICATION, AND SEQUENCE DATA

In spite of the conceptual controversy surrounding them, species are still the basic and comparable units of biodiversity (Wilson, 1992). While a family of fish cannot be compared to a family of ascomycete fungi, which cannot be compared to a family of flowering plants, we make explicit assumptions that species of these entities are comparable, even though shaped by

different histories, different biology, and formed by different processes.

Prior to the work by Máca (2003) in North America, all species descriptions of Nearctic *Amiota* relied on external characters, especially color, for delimitation. While useful for a few taxa, the reliance on external characters is complicated by the fact that: (1) many species of *Amiota* look remarkably similar externally and (2) individuals of a species vary in color. Both features lead to confusion on the identity of species. Citing a specimen series that “shows graded color variations completely connecting the two extremes,” Sturtevant synonymized one of Loew’s original species and moved them to another genus in his treatise of North American drosophilids (1921). Wheeler similarly described the first two western North American species of *Amiota* from a few series in Arizona and New Mexico (1952): the paratype series of one (*A. buccata* Wheeler) consisted of two externally similar species with radically different male genitalia, *A. buccata* Wheeler and *A. nebojsa* Máca (see Comments below).

The taxonomic use of the internal male genitalia could have prevented some of the current issues. Current taxonomists probably take for granted the use of these structures in defining species, but the primacy of genitalia in delimiting insect species in many taxa is rather recent (Snodgrass, 1957). The first documentation of male genitalia within *Amiota* was by Malloch and McAtee (1924). The authors provided figures of the “male hypopygium” of most of the then known North American species. This was far ahead of its time for the Nearctic fauna. It should be noted that *Amiota* was the only genus in that publication with the genitalia figured, perhaps a realization by the authors that they were elaborate and highly varied among species and might be useful for identification. Later works by Marshall Wheeler and Haruo Takada (1963, 1966, 1971) surveyed genital morphology in the Nearctic fauna, although these efforts were primarily centered on the Drosophilinae.

Higher-level relationships in the Drosophilidae are well resolved in some parts, such as within and among some of the subgenera and species groups of *Drosophila* (O'Grady and DeSalle, 2018). With few exceptions, classifications of the Drosophilidae have included two subfamilies, the Drosophilinae and Steganinae, since the publication of the latter by Duda (1926). Steganinae, the subfamily containing *Amiota* in most classifications, has been conceptualized by authors as containing the more "primitive" genera of the family (Throckmorton, 1975), certainly retaining more of the plesiomorphic features common to Ephydroidea in general. Steganinae would seem critical in understanding morphological evolution and other biological trends in the family, but have been included in very few studies (Otranto et al., 2008; O'Grady and DeSalle, 2018).

The next attempt at updating the classification since Sturtvevant (1921) was the phenetic-based classification of Okada (1989), using 14 characters. This was the first attempt at a tribal classification, placing *Amiota* in the new tribe Steganini Okada. Only a year later and with a much larger dataset, Grimaldi (1990) used cladistic methods to propose a new generic classification for the Drosophilidae based on 217 morphological characters of 120 species. The phylogeny and resulting classification was quite different from the one obtained by Okada, especially concerning *Amiota*. In this classification, *Amiota* was put into a new tribe, Gitonini Grimaldi, and the revised Steganini was dramatically reduced in size. A departure from these large-scale analyses was the study of Chen and Toda (2001), focused on East Asian taxa, which was the first morphology-based cladistic study on species relationships within *Amiota*.

Few studies utilizing sequence data have been performed on the genus. Perhaps one reason for this is the difficulty in collecting, rearing, and identifying Steganinae (Otranto et al., 2008). There is certainly less interest in studying flies with a relatively distant relationship to *Drosophila*. Molecular studies within the genus have

focused on particular species groups within the Palaearctic fauna and were usually based on one gene region (Otranto et al., 2008; He et al., 2009; Zhao et al., 2013; Shao et al., 2014; Wang et al., 2020). Otranto et al. (2008) was notable as the first molecular study with wide sampling within the subfamily, albeit with just COI regions. A widely sampled phylogeny including *Amiota* and many other members of the Steganinae, with multiple genes, is still needed.

## MORPHOLOGY

Species of *Amiota* are readily identifiable even in the field by the striking milky-white patches found on the face, postpronotal lobe, and on an area immediately ventral to the wing base (Wheeler, 1952; Chen and Toda, 2001; Máca, 2003). The function of these spots is unknown, but they may serve as visual cues. Werner et al. (2018) demonstrated that these spots fluoresce under UV light, wavelengths commonly visible to insects (Briscoe and Chittka, 2001). The spots are uniform in location, size, and brightness among species, so their signaling value may be generalized. Interestingly, the white patches on the face and postpronotal lobe are on cuticle; the subalar spot is membranous. It is likely that all the spots are due to accumulations of uric acid (Timmermann and Berenbaum, 1999).

Other characters of *Amiota* include the presence of a basal-medial wing cell (Grimaldi, 1990; Sidorenko, 2002), and the broad, dorsally flattened aedeagal apodeme in the male genitalia (Máca, 1980; Grimaldi, 1990; Sidorenko, 2002; Chen et al., 2004).

**MALE TERMINALIA:** *Amiota* are known for the uniformity of their external morphology, with few characters separating many of the Nearctic species (Wheeler, 1952). The male genitalia, though, vary radically among most species and are the main way to distinguish species. According to Grimaldi (1990), if the number, shape, and size of various genital components, and their elaboration, were taken into consideration, *Amiota* could be considered to have some of the most complex genitalia

in the Drosophilidae. Unfortunately, questions remain about the homology of some genital elements (Máca, 1980; Grimaldi, 1990). Except for studies by Okada (1971) and Grimaldi (1990), little attention has been given to the genitalia of this genus.

Overall, the male genitalia in *Amiota*, and the closely related genus *Phortica*, are quite complex and highly divergent among species, making them ideal for separating and identifying species. Some structures are typical for drosophilids and easily recognizable, such as the epandrium and surstyli; the remainder are highly modified and unusual for the family (e.g., paraphyses [postgonites], aedeagal apodeme, subepandrial sclerite, hypandrium). The paraphyses and extensions of the subepandrial sclerite are dominant features: sclerotized, large, elaborate and often spiny. The aedeagus in *Amiota* s.str. is lacking or may persist as a vestigial, membranous sac. Most structures of the male terminalia are bilaterally symmetrical, the paraphyses commonly being the exception.

**Epandrium:** This structure is always well developed, and basic; almost always with microtrichia covering most of the surface; macrosetae variously developed from long to short, most arrayed along the posteromesal margin and on the ventral lobe. The most distinctive feature is the dorsal bridge, which is often incomplete as a narrow to wide gap. The membrane between the cerci and dorsal bridge has minute microtrichia. Besides presence/absence of a dorsal bridge, shapes of the epandrium differ moderately among some species.

**Cerci:** These are always fully covered with microtrichia and some setae; never connected laterally to epandrium, but in some species the cerci grade dorsally into membrane and appear dorsally attached to the epandrium. Cerci are usually flattened and recessed into the epandrium, barely protruding, but projecting in a few species. In some species cerci are connected at a low level, with their ventral margins extended below that of the epandrium.

**Subepandrial Sclerite:** In *Amiota* this varies from a simple sclerite lying within the epan-

drium and behind the surstyli, to one possessing a large, curved appendage (the dorsal arch: Bächli et al., 2004). The posterolateral corners of the subepandrial sclerite articulate with the posterolateral arms of the hypandrium (sometimes this connection is membranous); posteromedially it articulates with the surstyli. The dorsal arch is derived from the posteroventral margin of the subepandrial sclerite, formed into an upcurved shelf. Most commonly this shelf forms a short, broad, roughly heart-shaped lobe just below the surstyli. In its most extreme form the dorsal arch is a heavily sclerotized appendage that is apically complex (e.g., spp. *A. byersi*, sp. nov., *A. leucostoma* Loew, *A. tibialis*, sp. nov.), resembling an aedeagus. This structure has been called the gonite by Chen and Toda (2001) and Máca (2003). The term "gonite" is sometimes used synonymously with "gonocoxite," "postgonite" or "pregonite" to refer to a paired periphallitic structure in insects, so its use here is inappropriate. The dorsal arch is not always developed in *Amiota*.

**Sternite 6:** In male *Amiota*, sternite 6 is modified into a saclike structure, with the open end facing the genitalia, which are deflexed and face somewhat forward. Sternite 7 is poorly developed or lost. Sternite 6, moreover, is partially sclerotized and has a faintly cobbled surface, sometimes with microtrichia as well. The structure presumably functions as a reservoir or for storage.

**Aedeagus:** In schizophoran flies, the aedeagus (phallus) is a central, unpaired, tubular structure whose base lies between the two arms of the aedeagal apodeme. Chen and Toda (2001) and Máca (2003) refer to the inner paraphyses as the aedeagus and basiphallus, respectively. This is unlikely, given the distinctively paired nature of the inner paraphyses. However, most striking may be the likely loss of the aedeagus, observed by Grimaldi (1990), with apparently no conspicuous membranous remnant remaining (an exception possibly being *A. imperator*, sp. nov.). But, if there is no aedeagus, how do male *Amiota* inseminate females? It is possible that the distinctive aedeagal apodeme and dorsal arch

TABLE 1

Summary of Terminology Applied to Paraphyses.

For this work we adopt the terms used by Bächli et al. (2004), for the sake of consistency and homology. Grimaldi (1990) did not distinguish between inner and outer pairs of paraphyses.

Bächli et al., 2004	Grimaldi, 1990	Chen and Toda, 2001	Máca, 2003	Cumming and Wood, 2009
inner paraphysis	paraphysis	aedeagus	basiphallus	pregonite
outer paraphysis	paraphysis	paramere	paramere	postgonite
dorsal arch	–	gonite	gonite	–

coordinate to jettison and channel sperm, the latter also grasping/retracting during copulation. Indeed, a tradeoff in development of structures implies some functions: when the paraphyses are elaborate and spiny the dorsal arch is undeveloped; conversely, in species with simple paraphyses a dorsal arch is well developed.

*Surstyli*: Very recognizable, paired lobes that, in *Amiota*, are tucked under the cerci and between the epandrial lobes. These always have a comblike row of sclerotized prensisetae, which are usually rounded at the apex (pointed in a few species); lengths and numbers of prensisetae vary. Proportions of the length and width of the surstylus can vary among species, ones with slender surstyli usually have the fewest prensisetae. Most species have a small lobe just distal to the prensisetal comb.

*Hypandrium*: This is always a thin, U-shaped sclerite in *Amiota*, tips of the arms articulating with the lateral corners of the subepandrial sclerite. It is never a platelike sclerite as is found in most other Drosophilidae. A middle section of the hypandrium is sometimes unsclerotized or even membranous; in some species there is a pair or two of small flanges laterally. Usually there is a lobe on the posterior margin of each hypandrial arm, which Bächli et al. (2004) identify as a gonopod.

*Aedeagal apodeme*: In most drosophilids, the aedeagal apodeme is a slender Y-shaped structure with a laterally flattened stem. In *Amiota* the apodeme is broad, scoop shaped, and even strongly bent (greater than 90°). The curvature and shape often varies among species, but the apodeme is usually well sclerotized; very rarely is it poorly developed. This broad and flat structure

is anchored on either side by a lateral arm that connects with the paraphyses and probably serves to jettison sperm through the action of muscles (Grimaldi, 1990).

*Paraphyses*: These are paired, paramedian, sclerotized lobes in *Amiota*, varying wildly from simple lobes to intricate structures with many spines. There are commonly (but not always) two pairs: the outer [more distal] paraphyses, which are generally larger, close together, and almost always have one or more sensilla trichodea on each lateral surface (these are very useful as landmarks to distinguish even the most modified outer paraphyses). The inner paraphyses are generally smaller, their bases articulating with the base of the outer paraphyses, they lack sensilla, and are usually simpler (e.g., lacking spines). Grimaldi (1990) hypothesized that the paraphyses might actually serve as a replacement for the apparently missing aedeagus in *Amiota*, with the spines and hooks potentially holding the female oviprovector for mating.

Various terms have been applied to paraphyses and the dorsal arch in *Amiota*, which are summarized in table 1. We are adopting the terms used by Bächli et al. (2004), for the sake of consistency and homology. Grimaldi (1990) did not distinguish between inner and outer pairs of paraphyses.

In a few species (e.g., *A. cruciatum*, *A. brayi*) where the asymmetrical inner paraphyses are spined, like a gardening claw, individuals from the same locality have the paraphyses reversed, a feature we are calling *chiral variants*. We could find no differences between chiral specimens in these species in any feature

except the direction of spines. The reversal is always a mirror image, so it is impossible that these appendages are simply twisted or flipped. It seems very unlikely that we are dealing with multiple species (exceptions being *A. tormentum*, sp. nov., *A. antitortum*, sp. nov., and possibly *A. mariae* Máca), but COI barcoding may help resolve this. Alternatively, this could be a developmental phenomenon, where perhaps the genital anlage for this structure becomes flipped in the embryo.

Asymmetry in the genitalia of insects is not uncommon and is known to occur throughout Diptera (Huber et al., 2007). In some taxa, including Cyclorrhapha flies (except for Ephydroidea + Calyptrata), asymmetry is the ground plan, but in many it seems to recur independently. Huber et al. (2007) suggests two main reasons for these asymmetrical arrangements. One is likely due to mating position. While there may not be an advantage to asymmetrical genitalia, the possibility of different mating positions may confer one, including the ability to twist the abdomen for these purposes. Another possibility is a compartmentalization of function between the left and right sides of the genital complex, assigning different roles in courtship and mating, with a direct benefit to asymmetry. The asymmetry of *Amiota* paraphyses is unique: involving mirror-image or chiral variants of the pair, rather than the differences in size and development of paired appendages that occurs in other Cyclorrhapha.

## MATERIALS AND METHODS

### ABBREVIATIONS

This study used specimens derived from museum collections and from fieldwork conducted in much of the United States. In total, 1596 specimens were amassed for the study. Of those, 754 specimens for this revision were borrowed from eight institutions to supplement 331 specimens at the American Museum of Natural

History (fig. 2A). We were unable to examine the holdings in the United States National Museum, Smithsonian Institution (USNM), due to restrictions from the COVID pandemic. We hope to rectify this with a future supplement on Nearctic *Amiota*. All specimens caught or donated during this study reside in the collections of the AMNH. Insect collection acronyms throughout follow Evenhuis (2009):

American Museum of Natural History, Division of Invertebrate Zoology (AMNH), New York  
California Academy of Sciences, Department of Entomology (CAS), San Francisco  
Canadian National Collection, Division of Insects, Arachnids, and Nematodes (CNC), Ottawa, Canada  
Illinois Natural History Survey, Division of Entomology (INHS), Champaign, IL  
Los Angeles County Museum of Natural History (LACM), Department of Entomology, Los Angeles  
University of Guelph, Department of Environmental Biology (DEBU), Guelph, Ontario, Canada  
University of Kansas, Snow Entomological Museum (SEMC), Lawrence, KS  
Utah State University, Department of Biology (EMUS), Logan, UT  
Washington State University, Department of Entomology (WSU), Pullman, WA

### FIELD COLLECTIONS

Field collections were conducted during four summers of 2017–2020 (fig. 2B). These consisted of two extended trips in the eastern United States, one in the western United States, and numerous smaller trips. Twenty-four states were visited, from New Hampshire to California. Lands of the United States Forest Service were primarily targeted, especially areas with mature broadleaf trees and nearby water sources. Mountainous regions in the western United States were targeted due to the lower temperatures and higher precipitation

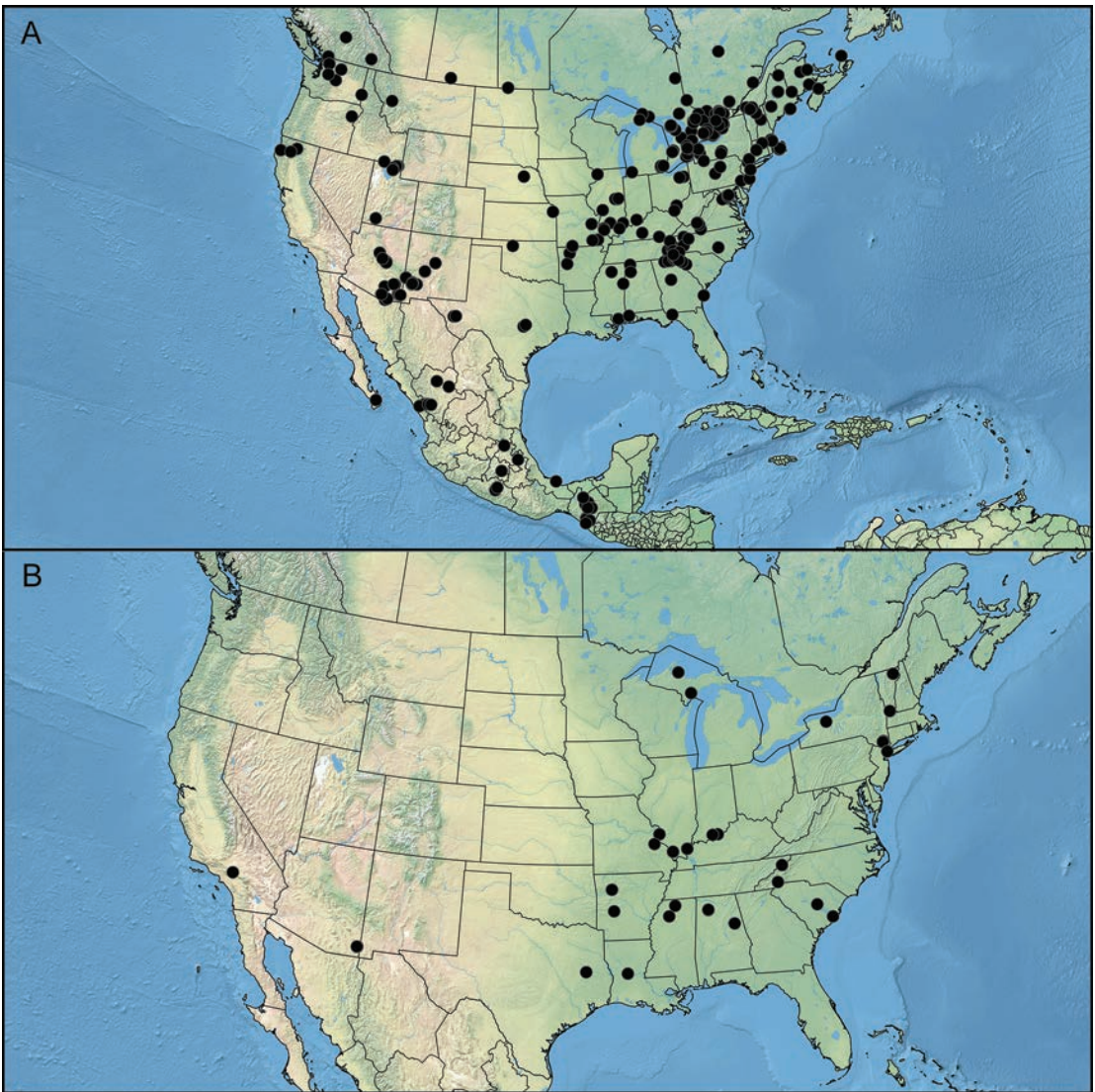


FIG. 2. Collections points of all specimens in this study. Each point represents one or more specimens. **A.** Collection localities of all loans and AMNH material. **B.** Collection localities of all specimens collected by the authors or donated.

compared with lowland areas. In all, 361 specimens were collected by the first author for this study. An additional 150 specimens were donated by collaborators (see Acknowledgments). All newly collected specimens from the first author and donated specimens are in the American Museum of Natural History, Division of Invertebrate Zoology (AMNH).

Flies attracted to eyes or perspiration were caught using a small 10 inch net with no handle attachment (Bioquip 7110DA). The apex of the net is modified to fit the size of a Falcon™ tube. The captured flies were collected directly into alcohol (EtOH, 95%). Various bait media are reported in the literature and on collection labels including bananas, apples, beer, wine, tomatoes,

mushrooms, dead mice, and dry ice (Basden, 1954; Buxton, 1961; Toda, 1977; Máca, 1980; Chen et al., 2005; Werner, 2017; Werner et al., 2018). Traps baited with fermented fruit were tried several times unsuccessfully over several years during this study. This included traps hung from tree limbs in California (summer of 2017), as well as ground level traps in Arizona and Illinois (2018). *Amiota* can be captured by the use of Malaise, emergence, and pan traps, but rarely in significant numbers. Emergence traps containing dead wood have been useful for documenting the saproxylic nature of this species on several continents (Máca, 1980; Jones et al., 2021). See lists of examined specimens and comments for information on individual species.

#### SPECIMEN PREPARATION

Prior to dissection, all specimens were given a unique number: Am. 1, 2, etc. These numbers served as specimen identification for the duration of the study. Specimen data was entered into an Excel database using the unique numbers. This database tracked identifications and loaned specimens and was used to list examined specimens and their associated locality data for species distribution maps. In examined-specimen lists, the relevant specimen number(s) are cited after collection data ("Am 10," etc.). An asterisk ("\*") following a number or series indicates that the specimen(s) has been dissected. All localities were georeferenced using Google Maps. Specimen data were mapped using Simplemapp (Shorthouse, 2010). All indicators on resulting maps may refer to one or more specimens at each locality for a given species. At the conclusion of the study, all specimens caught or donated were affixed with collection labels.

A key is not provided in this work. *Amiota* are known for the relative uniformity in their external appearance. While some Nearctic species can be easily identified on the basis of characters such as combs on the legs or a silvery frons, most species do not have features like this useful for identification. The problem becomes more acute within

species groups, where identification is most reliable through dissection. Most recent keys have necessarily relied on the importance of the male genitalia (Chen and Toda, 2001; and others). The use of such a key necessitates detailed dissection. In this case, it may be more useful to compare dissected specimens to illustrations within and consult descriptions when necessary.

#### TERMINALIA DISSECTIONS

Male individuals were selected for dissection. This initially consisted of dissecting half of any collection series, singletons, and unique localities, but eventually led to dissecting males of varying color and size. Pinned/point-mounted specimens were rehydrated in a chamber consisting of a sealed glass jar filled with vinegar-soaked paper towels to create a humid setting. The specimens remained in the chamber for 1.5 hours or until soft. Afterward, the posterior half of the abdomen was separated using Roboz™ vanna scissors (RS-5620) with a 3 mm cutting edge. Dissected abdomens were macerated in 1.5 mL Eppendorf tubes containing 0.5 mL of 10% potassium hydroxide solution (KOH). Maceration dissolves extraneous tissue facilitating characterization of hard sclerotized structures. The tubes were soaked in a water bath warmed on a small mug warmer or hotplate for 1.5 hours at a hot, but not boiling temperature. Macerated abdomens were rinsed for 10 seconds each with 5% acetic acid, followed by 70% EtOH, and then placed in glycerin. The dissections then rested in ceramic well-plates with one drop of glycerin, where the genitalic structures could be separated from the remaining abdomen and disarticulated for study. A total of 700 dissections were made for this study. Due to time constraints female terminalia were not dissected or studied, which we intend for future work. Currently, morphologically based species concepts in Drosophilidae, other Diptera and many other insects, are based on males, in which the male terminalia provide a rich source of characters.

Freshly caught material bypassed the rehydration chamber and the male abdomens were

put directly into the 10% KOH solution. After dissection, the body was preserved using hexamethyldisilazane (HMDS). Useful as an alternative to critical point drying, HMDS can preserve external structures by preventing collapse and retaining color (Brown, 1993). Specimens treated with HMDS were glued to paper points and specimen labels affixed. Male genitalia were put into glycerin-filled microvials and pinned with the specimen. Following disarticulation, all dissections were sorted into morphotypes.

#### EXTERNAL MICROGRAPHS AND MEASUREMENTS

Morphotype groups defined by male genitalia guided the examination of external characters for defining species. These characters came in two forms: from qualitative features of external cuticle and from quantitative features, e.g., measurements and proportions. Standard morphometric indices are based on Bächli et al. (2004) and Grimaldi (2018). Visual examination of external micrographs provided the basis for characters thought to be diagnostic among species. Dried and pinned specimens were measured using a Nikon SMZ 1500 stereoscope with an attached Nikon Digital Sight DS-R1i camera and accompanying NIS Elements<sup>®</sup> software.

Proportions of the head include: the width of the face between the eyes just above the ptilinal suture (FW), distance between the midpoint of the ptilinal suture and the ventral margin of the ocellar triangle (FL), distance between the proclinate orbital setae and the first reclinate orbital setae (PR), distance between the first and second reclinate orbital setae (RR), the depth of the facial marking (FML), the width of the facial marking (FMW), the length of the eye at the longest point (EL) measured laterally, the width of the eye at the widest point at a right angle to the eye length (EW), and the width of the cheek at the lowest margin (CW). As a proxy for body length, the thorax was measured from the anterior edge of the scutum to the posterior tip of the scutellum in dorsal view (ThL).

All lengths were converted to ratios with the exception of thorax length. Standard indices (Bächli et al., 2004) included: frontal index, the frontal length/frontal width above ptilinal suture (FL/FW); eye index, eye length/eye width (EL/EW); and the cheek index, eye length/cheek width (EL/CW). Two ratios created for this study include the orbital setae distance ratio, the distance between the proclinate orbital setae and first reclinate orbital seta/distance between both orbital reclinate setae (PR/RR), as well as the facial marking ratio, the length of the facial marking/width of the facial marking (FML/FMW).

Distance between orbital setae, lateral length, lateral eye width, and cheek width were measured on the fly's left side, unless unavailable due to preparation. Scutum and scutellum were sometimes measured separately due to trouble of fitting both onscreen. Thorax length was used as a proxy for body size because abdomens had been dissected to verify species identity. For each species, the value reported after each ratio abbreviation is the mean, followed by the range in parentheses. For species where no range is reported, either the species is represented by a single specimen, or the measurement did not vary among specimens. Measurements of orbital and dorsocentral seta lengths were not made, nor were wing veins, since these appeared barely variant among species based on visual comparisons.

#### GENITALIC IMAGES AND ILLUSTRATIONS

With male genitalic structures as complex as those in *Amiota*, it is hardly surprising that this morphology is critically important diagnostically for species. Indeed, genitalic images are sine qua non; verbal descriptions merely point out the most salient features. This complexity, however, also compromises digital light photomicrography, especially of the heavily sclerotized and melanized lobes, through which light barely passes, and the overlapping lobes interfere with the ability of z-stacking programs to accurately distinguish margins. Confocal laser microscopy also has several problems, one being the strong

background signal from the mountant, another being weak color fidelity (e.g., sclerotization of lobes). Scanning electron microscopy likewise doesn't distinguish colors or membrane from cuticle and requires extensive preparation.

As a result, male terminalia for this study were illustrated. It requires more time but has the advantage that various views of structures are easily shown, including their degree of sclerotization and minute features like sensilla and membranes that are poorly resolved in photomicrographs. Here, macerated male terminalia were mounted in glycerin jelly on microscope slides and repositioned several times for various views of certain structures. A Wild compound microscope with a drawing tube was used for sketching the outlines of major structures at 100–40 $\times$ ; 3-dimensionality and overlap of structures was checked with several stereoscopes at 100–175 $\times$ . Pen and ink were used for outlines and Adobe Illustrator® for final rendering (see Acknowledgments). The epandrium was usually not shaded. All illustrations were produced by the second author.

#### PHYLOGENETIC ANALYSIS

**RATIONALE:** Phylogenetic analysis does not need to precede nor even cooccur with species descriptions. However, there are advantages of putting a great many new species into a phylogenetic context: it presents a phylogenetic hypothesis where none existed and provides a framework for organizing species. In this case, a phylogenetic hypothesis was generated for the purposes of creating species groups. The rank of informal species groups, not recognized by the ICZN (1999), is a convenient way for organizing species and the information about them.

**CHARACTER SELECTION:** While most characters chosen were from the character-rich male genitalia, an effort was made to select as many external characters as possible. Forty-six characters were ultimately chosen for phylogenetic reconstruction. Of these, 25 characters were derived from the male genitalia. In total, 37 char-

acters were binary and one was multistate, while five were continuous and three were defined as meristic. All unknown states were entered as “?”. Characters were scored from observing specimens, illustrations, and micrographs. All character-state scored were initially recorded in Excel.

Nine outgroup species were chosen. These were derived from eastern and western Palaearctic distributions of *Amiota*, targeting as many lineages as possible according to Chen and Toda (2001). Characters were scored preferentially from Bächli et al. (2004) due to the completeness of the descriptions. Other characters were taken from Chen and Toda (2001) and Máca and Lin (1993). At least one species was chosen for almost all species groups erected by Chen and Toda (2001): *alboguttata* species group, *A. albilaris* (Roth), *A. alboguttata* (Wahlberg); *apodemata* species group, *A. planata* Chen and Toda; *basdeni* species group, *A. basdeni* d'Assis-Fonseca; *nagatai* species group, *A. kimurai* Chen and Toda; *rufescens* species group, *A. magniflava* Chen and Toda, *A. rufescens* (Oldenberg); *taurusata* species group, *A. sacculipes* Máca and Lin; ungrouped, *A. flavoprunitosa* Duda.

**PARSIMONY ANALYSIS:** The Excel matrix was transferred into Mesquite (Maddison and Maddison, 2021). Mesquite has capabilities for coding different character types that can easily be exported into various file formats. Two matrices were built in Mesquite, one storing binary and multistate characters, with the other containing continuous and meristic data. Two files were exported from Mesquite (categorical and continuous data options) in the TNT file format. These separate data partitions were concatenated in Notepad for analysis.

Parsimony analysis was conducted with TNT (Goloboff et al., 2008). The program TNT has two advantages: capabilities for analyzing morphological datasets, as well as handling meristic and continuous data. Under ‘settings,’ the maximum number of trees (those retained in memory) was increased from the default of 100 to 1000. General RAM was set to the maximum (1000). Under ‘settings,’ the collapsing rules were

set to 'none,' Under 'analyze,' New Technology Search was selected. The default search options were kept (Sect. Search and Tree Fusing), and Ratchet and Drift options were also selected. The option for 'init. addseqs' was increased from 5 to 100. The search was then performed. The resulting tree was displayed (with and without synapomorphies) and exported.

#### SPECIES CONCEPT DEFINITION

With many definitions proposed, it has been recommended that works describing new species state explicitly the criterion used (Luckow, 1995). This study uses the phylogenetic species concept sensu Q.D. Wheeler and Platnick (2000), defined as "the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states." Although reproductive isolation—the *process*—is not an explicit criterion of a phylogenetic species concept, as is the Biological Species Concept of Mayr (1942), it is implied by unique characters and combinations thereof (Nixon and Q.D. Wheeler, 1990). Indeed, the two normally overlap; genetically discrete groups of individuals can usually be separated morphologically, behaviorally, or ecologically. In the case of insects, where morphological characters are rarely limited, most species (including those newly described in this study), have primarily been defined on the basis of morphology. All new species in this work are authored by L.E.J. and D.A.G.

#### SYSTEMATICS

##### PHYLOGENETIC ANALYSIS

The characters used in the parsimony analysis are as follows:

Number of dorsal branches on the arista.

1. Average thorax length (ThL) in mm.
2. Arisal ratio [continuous character]
3. Number of prensisetae per surstylus.
4. Number of ventral branches on the arista.
5. Average length of eye to cheek depth ratio (EL/CW).

6. Average of facial marking length to facial marking width (FML/FMW).
7. Ratio of ejaculatory apodeme size to epandrium.
8. Frons with silvery microtomentum (1 present, 0 absent).
9. White facial marking (1 present, 0 absent).
10. Milky white area on gena (1 present, 0 absent).
11. Body color (1 yellowish, 0 dark).
12. Palp coloration (1 black, brown, brownish black; 0 yellowish to fuscous, sometimes dark tip).
13. Katepisternum lighter than rest of pleuron (1 present, 0 absent).
14. Section of C between  $R_{2+3}$  and  $R_{4+5}$  with small spinules (1 present, 0 absent).
15. Median gap on dorsal bridge of epandrium (1 present, 0 absent).
16. Distal-lateral lobe on surstylus (1 present, 0 absent).
17. Outer paraphysis laterally flattened, with rounded apex and small, sclerotized, preapical dorsal hook (1 present, 0 absent).
18. Sternite 6 formed into partially sclerotized sac with faint surface cobbling: (1 present, 0 absent).
19. Subepandrial sclerite with greatly developed, protruding subepandrial appendage (1 present, 0 absent).
20. Distal margins of subepandrial appendage with irregular serrations and spines (1 present, 0 absent).
21. Apex of subepandrial appendage bulbous, roughly heart-shaped (1 present, 0 absent).
22. Finely striate, membranous sac surrounding subepandrial appendage and outer paraphyses (1 present, 0 absent).
23. Outer paraphyses long, slender, linear (1 present, 0 absent).
24. Distal margins of inner paraphyses serrate (1 present, 0 absent).
25. Inner paraphyses strongly asymmetrical, with large spines, scissoring, articulating into opposite sides across each other (1 present, 0 absent).

26. Apices of prensisetae pointed (1 present, 0 absent).
27. Aedeagal apodeme strongly arched in lateral view (1 present, 0 absent).
28. Aedeagal apodeme significantly longer than broad (1 present, 0 absent).
29. Distal margin of aedeagal apodeme entire (1 present, 0 absent).
30. Comb on hind femur (1 present, 0 absent).
31. Comb on hind tibia (1 present, 0 absent).
32. Comb on middle femur (1 present, 0 absent).
33. Comb on middle tibia (1 present, 0 absent).
34. Light coloration on T1 and sometimes T2 (0 absent; 1 present, but faint and small; 2 well developed, occurring on T1 and T2).
35. Femora brown or nearly black (1 present, 0 absent).
36. Tibia brown or nearly black (1 present, 0 absent).
37. Surstylus armlike with few prensisetae (1 present, 0 absent).
38. Strong lateral wing on hypandrium (1 present, 0 absent).
39. Cerci fused dorsally to surrounding membrane (1 present, 0 absent).
40. Sensilla on outer paraphysis (1 present, 0 absent).
41. Inner paraphysis (1 present, 0 absent).
42. Prominent lateral lobe on epandrium (1 present, 0 absent).
43. Hypandrium "tooth" near apex (1 present, 0 absent).
44. Gap at hypandrium apex (1 present, 0 absent).
45. Hypandrium with strong mucronate "notch" at apex (1 present, 0 absent).

The phylogenetic analysis conducted in this work is the first to address the Nearctic fauna of *Amiota* (fig. 3). The analysis searched ~310,000,000 arrangements yielding one best score and retaining one tree. Nine species groups were defined using the cladogram. While many of the smaller groups were monophyletic and based on genitalic characters, the cladogram was disregarded in some cases for the creation of spe-

cies groups. This was the case when we felt strongly that a species was more closely related to another group or when strong characters could not be found for presumably related species. Examples include the inclusion of *Amiota hsui* Máca and *A. hyalou* into a separate grouping (the *hsui* species group), as well as the inclusion of *A. minor* (Malloch), *A. pseudominor*, sp. nov., and *A. biacuminis*, sp. nov., into the *avipes* species group.

One complication is the outsize impact that nonbinary data can have on phylogenetic construction. While only eight of the characters were of continuous or meristic data, these characters disproportionately define higher-level clades composed of species groups, rather than species groups themselves. The problems of continuous characters and ratios in constructing phylogenies is well known (Bardin et al., 2013; Koch et al., 2015). It is likely that a robust and well-supported phylogeny of *Amiota* will require a multigene molecular phylogeny in order to test morphological and biogeographical hypotheses.

The species groups and the species contained derived from the cladogram are as follows:

The *hsui* species group:

*A. hsui* Máca

*A. hyalou*, sp. nov.

The *alboguttata* species group:

*A. communis* Chen and Steyskal

*A. durangoensis*, sp. nov.

*A. lineiventris* Máca

*A. steyskali* Máca

The *mariae* species group:

*A. antitortum*, sp. nov.

*A. brayi*, sp. nov.

*A. cruciatum*, sp. nov.

*A. incurva*, sp. nov.

*A. mariae* Máca

*A. texas*, sp. nov.

*A. tormentum*, sp. nov.

*A. wheeleri*, sp. nov.

*A. zaliskoi*, sp. nov.

The *cervites* species group:

*A. cervites*, sp. nov.

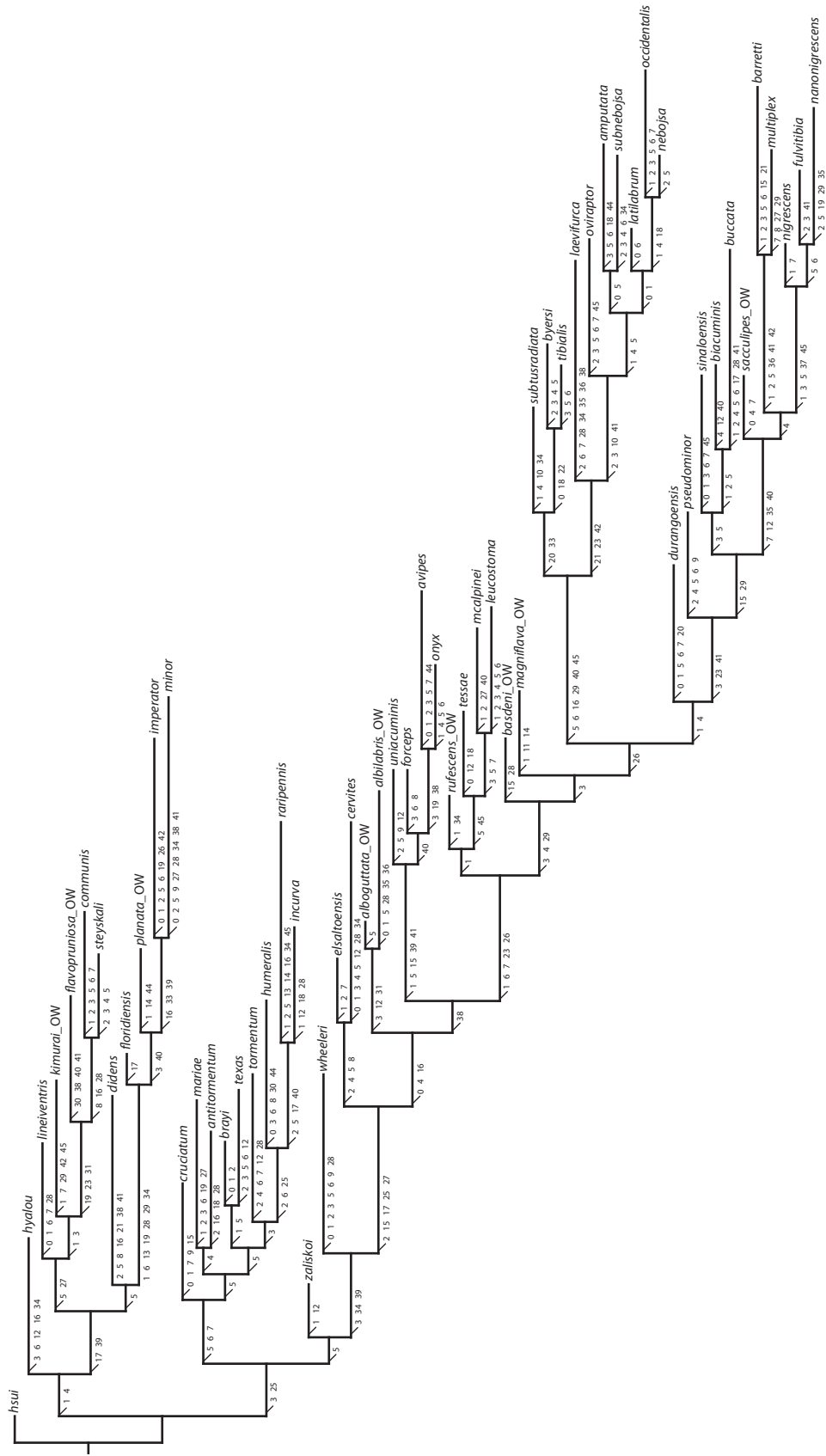


FIG. 3. Parsimony cladogram of Nearctic *Amiota* and nine outgroups based on morphology. Numbers represent synapomorphies. Species names denoted with “\_OW” are Old World taxa.

*A. elsaltoensis*, sp. nov.

*A. multiplex*, sp. nov.

The *avipes* species group:

*A. avipes*, sp. nov.

*A. biacuminis*, sp. nov.

*A. forceps*, sp. nov.

*A. minor* (Malloch)

*A. onyx*, sp. nov.

*A. pseudominor*, sp. nov.

*A. uniacuminis*, sp. nov.

The *rufescens* species group:

*A. leucostoma* Loew

*A. mcalpinei*, sp. nov.

*A. tessae*, sp. nov.

The *subtusradiata* species group:

*A. byersi*, sp. nov.

*A. subtusradiata* Duda

*A. tibialis*, sp. nov.

The *nebojsa* species group:

*A. amputata*, sp. nov.

*A. latilabrum*, sp. nov.

*A. nebojsa* Máca

*A. occidentalis*, sp. nov.

*A. oviraptor*, sp. nov.

*A. subnebojsa*, sp. nov.

The *nigrescens* species group:

*A. fulvitibia*, sp. nov.

*A. nanonigrescens*, sp. nov.

*A. nigrescens* Wheeler

The *nagatai* species group:

*A. raripennis*, sp. nov.

Ungrouped Species:

*A. barretti* (Johnson)

*A. buccata* Wheeler

*A. didens*, sp. nov.

*A. floridiensis*, sp. nov.

*A. humeralis* Loew

*A. imperator*, sp. nov.

*A. laevifurca*, sp. nov.

*A. sinaloensis*, sp. nov.

Wheeler, 1952 (key to Nearctic species);

Wheeler, 1965 (*Drosophilidae* catalog, north of Mexico); Máca, 1980 (revision of European species); Chen and Toda, 2001 (revision of European and East Asian species); Bächli et al., 2004 (key to west Palaearctic species); Brake and Bächli, 2008 (worldwide catalog of *Drosophilidae*).

DIAGNOSIS: Small to large drosophilids (ThL 0.90–2.09 mm), most black or dark brown, to light honey-golden color; oral margin, postpronotal lobe, and area immediately ventral to wing base with characteristic milky-white patches (except in *A. minor*); arista short to long, plumose, some species with branches pointing mediad; postocellar setae very small; anterior reclinate orbital seta well developed, usually half or more the length of proclinate; face flat or with upper portion slightly carinate; pair of prescutellar setae present; hind femur and/or tibia sometimes with comb of long, fine bristles; aedeagal apodeme broad, dorsoventrally flattened; paraphyses modified in most species to large, heavily sclerotized, swordlike or broad structures with apical hooks and commonly with asymmetrical spines.

TYPE SPECIES: *Amiota leucostoma* Loew, established by Coquillett (1910).

COMMENTS: This genus consists of about 154 species found worldwide, but with most diversity centered in the north temperate forests of the world. Larvae are saproxylic, developing under bark and/or in decaying wood. Most species are known to be lachryphagous and attracted to the eyes and face of humans and other mammals.

#### THE *HSUI* SPECIES GROUP (NEW GROUP)

DIAGNOSIS: Small to medium-sized flies; dark brown to black-brown, with typical white markings of genus; arisal branches long to short; frons dark, almost entirely dull. Male genitalia: Inner paraphysis simple, with apex finely serrate; outer paraphysis simple, lacking large dorsal spines, having only small preapical dorsal hook.

#### GENUS *AMIOTA* LOEW

*Amiota* Loew, 1862a: 229 (original description);

Duda, 1934 (revision of European species);

NEARCTIC SPECIES: *Amiota hsui* Máca and *A. hyalou*.

COMMENTS: The two species in this group, *A. hsui* Máca and *A. hyalou* have very large distributions across North America, among the largest known in the Nearctic fauna.

*Amiota hsui* Máca, 2003

Figures 4A–B, 5A, 6, 81A

*Amiota hsui* Máca, 2003: 265 (original description); Malloch and McAtee, 1924: 41, plate VIII, figs. 2–5 (figure of male genitalia, referred to as *A. humeralis*); Brake and Bächli, 2008: 252 (world catalog).

DIAGNOSIS: Medium-sized fly (ThL 1.20–1.28 mm), dark brown to almost black; frons slightly pollinose; outer paraphysis long, laterally flattened, in lateral view bent at nearly 90°, with apical hook; inner paraphysis heavily sclerotized, projecting laterally, the apex serrated; similar to *Amiota hyalou*, but *A. hsui* differing by larger male genital complex; aedeagal apodeme of *A. hsui* well developed, widely flared distally, heavily sclerotized, with pair of rounded anterolateral projections on either side.

DESCRIPTION: Medium-sized fly (ThL 1.20–1.28 mm), dark brown to almost black, legs dark yellow. Frons slightly pollinose, upper half of frons dark, almost black, fading to light brown just above ptilinal suture. Eyes nearly globose anteriorly. Palp yellow. Arista: Long plumose; longest branch D2; A.R. 0.52; 4 long dorsal, 2 ventral branches; none pointed mediad/laterad; arista trunk with short microtrichia along most of length. Male genitalia: Epandrium not dorsally split, covered with 10–12 ventrolateral setae and 3–4 sparse setae in row along cercus margin to dorsal apex. Cercus grading dorsally into surrounding membrane. Surstylus with row of 9 prensisetae, apices blunt; 10–12 setulae sparsely arranged; small thumblike lobe adjacent to lateralmost prensisetae. Subepandrial sclerite Y-shaped, behind surstyli, with thickened outer

arms. Outer paraphysis laterally flattened, with small cluster of 4–6 sensilla on lateral portion near distal end; prominent preapical claw present, with small, proximal tooth, relatively sclerotized and fading toward ventral portion. Inner paraphysis heavily sclerotized, distal end serrated, at nearly 90° relative to outer paraphysis. Aedeagal apodeme width and length nearly equal, distal end flared, the margin slightly concave, with lateral projection on either side. Hypandrium U-shaped, simple. Ejaculatory apodeme relatively long, approximately 0.6× length of epandrial lobe. Head and thorax measurements: (n = 5; Am 68, 355, 405, 421, 712): FL/FW 0.81 (0.77–0.92), EL/EW 1.3 (1.15–1.38), EL/CW 15.89 (12.2–22), FML/FMW 0.3 (0.28–0.33), PR/RR 0.52 (0.45–0.60), ThL 1.23 (1.20–1.28 mm).

TYPE MATERIAL: **Holotype:** Description from Máca (2003): “♂: USA, Arizona: Cochise Co., Huachuca Mts, Ash Cyn., 5100 ft., 9.8.1991, leg. Y.F. Hsu” [not examined]. Coll. Jan Máca, to be deposited in National Museum of Prague, Czech Republic (NMPC). **Paratypes:** “Same data,” 4♂ (Coll. Jan Máca, intended for NMPC).

OTHER MATERIAL EXAMINED: **Canada:** **Ontario:** Lambton Co., Port Franks, Watson Property nr L-lake, 1996-07-12 through 1996-07-15, leg. J. Skevington, pans, 1♂ (Am 631\*, DEBU); Picton, 1970-07-07, leg. J.F. McAlpine, 2♂ (Am 1557\*, 1560\*, CNC); Sandbanks Pk, nr Picton, 1970-07-01, leg. J.F. McAlpine, 2♂ (Am 1561\*, 1567\*, CNC); Smith’s Bay, nr. Picton, 1970-07-01, leg. J.F. McAlpine, 1♂ (Am 1185\*, CNC); Windsor, Ojibway Prairie Reservation, 1983-08-18, leg. K.N. Barber, 1♂ (Am 624\*, DEBU). **Quebec:** Lac Phillippe, 45 37 N, 76 W, 1955-07-30, leg. J.R. Vockeroth, “Paratype” [never published], 1♂ (Am 1347\*, CNC). **USA:** **Alabama:** Clay Co., Talladega Nat. For., 33.443496, -85.839339, 2018-08-15, leg. L.E. Jones, swept around head, 1♂ (Am 657\*, AMNH). **Arizona:** Catalina Highway near Tucson, along creek in pine forest, 1725 m, 2007-08-07, leg. J. Skevington, CNC Diptera #9933, 1♂ (Am 1304\*, CNC). Chiricahua Mts., 1940-07-04, leg. D.E. Hardy, 1♂ (Am 439\*, SEMC); Cochise Co., campground nr. SWRS, 31.872506, -109.233923, 2019-07-19, leg. L.E. Jones and J.L. Hughes, swept around head, 1♂ (Am 712\*, AMNH); Cochise Co.,

Vicinity of SWRS, 31.882018, -109.206636, 2019-07-18, leg. L.E. Jones and J.L. Hughes, swept around head, 4♂ (Am 714\*, 717-719\*, AMNH); 2019-07-19, leg. J.L. Hughes and L.E. Jones, swept around head, 2♂ (Am 709\*, 711\*, AMNH). **Arkansas:** Logan Co., Magazine Mt. 2750 ft, 1992-07-06, leg. D. Grimaldi, 11♂ (Am 323\*, 326, 331, 339, 340, 347, 353, 355\*, 356, 358, 361\*, AMNH). **California:** 5 mi W. Willow Creek, 1951-07, leg. M. Wasserman and W.B. Heed, 2182.7, 1♂ (Am 68\*, AMNH); Los Angeles Co., Angeles National Forest, vicinity of BYA Harmony Pines Camp, 2017-06-05 through 2017-06-17, leg. D. Grimaldi, flying about head, 1♂ (Am 525\*, AMNH). **Georgia:** Towns-White Cos., Unicoi Pk., 1954-10-02, leg. H.R. Dodge, net, 3♂ (Am 410\*, 412, 415, WSU). **Illinois:** Carlinville, 1954-08-23, [collector unknown], 1♂ (Am 65\*, AMNH); Hardin Co., Shawnee Nat. For., 37.594631, -88.382478, 2018-08-08, leg. L.E. Jones and J.L. Hughes, 1♂ (Am 649\*, AMNH); 2018-08-08, leg. J.L. Hughes and L.E. Jones, 1♂ (Am 735\*, AMNH); Savoy, 1916-05-23, [leg. J.R. Malloch], on sap, 1♂ (Am 1587, INHS); Henderson Co., 3.0 mi E Oquawka, 1989-08-30, leg. E.A. Lisowski, malaise trap, 1♂ (Am 1596\*, INHS); Vermilion Co., Forest Glen Forest Pres., 5 mi. SE Westville, 1977-08-08, leg. D.W. Webb, 1♂ (Am 1598\*, INHS); White Heath, 1915-08-08, [leg. J.R. Malloch], 1♂ (Am 1588, INHS). **Missouri:** Carter Co., Ridge Road at Road C, 4.5 mi SW of Van Buren, 1967-08-04, leg. H.B. Leech, 1♂ (Am 381\*, CAS); Taney Co., Mincy Conservation Area, ex. Bear Mtn., 36 32 55.74 N, 4 33.60 W, 350 m, leg. B.J. Sinclair, CNC1450106, 1♂ (Am 1297\*, CNC). **New Mexico:** Gila National Forest, Cherry Creek campground, 32.914167 S, 108.22500 W, 2103 m, 2007-08-14, leg. S. Kelso, Dip-tera #58837, 1♂ (Am 1288\*, CNC); 12 mi N Silver City, 1950-08, leg. M.R. Wheeler, 2051, 1♂ (Am 58\*, AMNH). **New York:** Jeff Co., Wellesley Is., 1963-08-22, leg. L.L. Pechuman, 1♂ (Am 37\*, AMNH); Sta. Study Insects, Tuxedo, 1928-06-25, leg. C.H. Curran, 1♂ (Am 43\*, AMNH); Tompkins Co., Texas Hollow, 1983-07-26, leg. D. Grimaldi and L.L. Pechuman, flying about head, 2♂ (Am 24\*, 35\*, AMNH); Orange Co., Cornwall, Black Rock Forest, 2014-09-06 through 2014-09-07, leg. D. Grimaldi, 1♂ (Am 421\*, AMNH). **North Carolina:** Cumberland Co., Fort Bragg, 1967-05-14, leg. J.D. Birchim, 1♂ (Am 405\*, AMNH); 1967-05-15, leg. J.D. Birchim, 1♂ (Am 403\*, AMNH); 28 v-3, 1967-06, leg. J.D.

Birchim, 1♂ (Am 404\*, AMNH). **Ohio:** Sand Run Pk., 1938-09-10, leg. G.E. Shewell, "Paratype - No. 8018 Paratype" [not published], 1♂ (Am 1348\*, CNC); Vinton, 1900-06-05 through 1900-06-12, [collector unknown], 1♂ (Am 466\*, SEMC). **Oklahoma:** Woods Co., 3 mi W. Waynoka, old road to Herman, 1967-08-12, leg. H.B. Leech, 1♂ (Am 378\*, CAS). **Virginia:** Giles Co., #98 Mt. Lake Biol. Sta., 1973-07-27, leg. G.W. Byers, 1♂ (Am 437\*, SEMC) Prince William Co., 0.5 km NE Thorofare Gap, vic. Haymarket, 1966-06-25, leg. P.H. Arnaud Jr., 1♂ (Am 402\*, CAS).

**DISTRIBUTION:** *Amiota hsui* is very widespread, inhabiting most of Eastern North America, with populations as far west as Arizona and California. Populations in southern as well as northern California suggest this species may possibly be more extensively distributed in western United States than current collections show.

**COMMENTS:** It is likely that most male flies referred to as *A. humeralis* in older literature are of the then undescribed *A. hsui*, likely the identity of "*Amiota* species A" in Wheeler (1952). *Amiota setigera* Malloch is now known to be the male of *A. humeralis*. In their treatment of Drosophilidae in the D.C. area, Malloch and McAtee (1924) figured the male genitalia of *A. hsui* (erroneously referred to in the text as *A. humeralis*). This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

### *Amiota hyalou*, sp. nov.

Figures 4C–D, 5B, 7, 8, 81B

**DIAGNOSIS:** Small to medium-sized fly (ThL 0.92–1.31 mm), dark brown to black; genital complex lightly sclerotized, except inner paraphysis, which is serrate at apex and along one margin; hypandrium narrow in middle; aedeagal apodeme small, roughly square, distal end faint; similar to *Amiota hsui* Máca, but male genital complex of *A. hyalou* smaller, translucent, and aedeagal apodeme without anterolateral projections on either side.

**DESCRIPTION:** Small to medium-sized fly (ThL 0.92–1.31 mm), dark brown to black (fad-

ing to rusty red or light brown in older specimens), legs yellow. Setation on body varying black to golden. Frons black, fading to brown above ptilinal suture. Cheek variable, wide for body size (EL/CW 12.50–19.33), milky posteriorly. Palp yellow. Tergite 1 lightly colored. Arista: Medium plumose; longest branch D3; A.R. 0.42; 4 dorsal, 3 shorter ventral branches, none pointed mediad/laterad; arista trunk with short microtrichia along much of length. Male genitalia small, translucent, lightly sclerotized: Epandrium not split medially, ventral lobe with a point. Cercus grading into membrane and dorsal bridge of epandrium; cercus long, exposed, not recessed into epandrium. Surstylus bowl or socket shaped with reticulating margin dorsally; 7 prensisetae, apices blunt; ca. 10 setulae, scattered, long. Subepandrial sclerite simple, slightly upturned posteriorly with short apex between surstyli. Outer paraphysis laterally flattened, bent nearly 90° near middle, lightly sclerotized; several clustered sensilla in lateral view near middle portion; distal end rounded with a prominent preapical claw present, small tooth proximal to preapical claw. Inner paraphysis heavily sclerotized, at 90° angle from attachment to outer paraphysis, serrated on distal end and dorsal margin. Aedeagal apodeme square shaped, nearly equal in length and width; distal end small, slightly concave, reduced to margin, flared slightly wider than width of base. Hypandrium simple, anterior margin narrow in middle, tapering to rounded distal edge anteriorly; lateral arms with posteriorly directed gonopod. Ejaculatory apodeme not studied. Head and thorax measurements: (n = 5; Am 62, 452, 455, 526, 648): FL/FW 0.87 (0.75–0.95), EL/EW 1.42 (1.34–1.66), EL/CW 15.92 (12.50–19.33), FML/FMW 0.27 (0.25–0.29), PR/RR 0.57 (0.50–0.70), ThL 1.17 (0.92–1.31 mm).

**TYPE MATERIAL:** **Holotype:** male: 12 mi. N. Silver City, N.M. [New Mexico], [33.019248, -108.263582], MR Wheeler, Aug 1950, “2051,” Am 54, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratype:** 12 mi. N.

Silver City, N.M., MR Wheeler, Aug 1950, “2051,” Am 62, 1 ♂ (Am 62\*, AMNH).

**OTHER MATERIAL EXAMINED:** **Canada:** **Ontario:** Marmora, 1952-06-07, leg. J.R. Vockeroth, 1 ♂ (Am 1434\*, CNC). **USA:** **Arizona:** Chiricahua Mts, 1950-07-21, leg. P.P. Cook, 1 ♂ (Am 441\*, SEMC); Cochise Co., Vicinity of SWRS, 31.882018, -109.206636, leg. L.E. Jones and J.L. Hughes, 2019-07-19, swept around head, 1 ♂ (Am 715\*, AMNH); Oak Creek Canyon, 1941-07-09, leg. R.H. Beamer, 4 ♂ (Am 452-455\*, SEMC); Tonto Creek Camp, 1951-06, leg. M.R. Wheeler and W.B. Heed, 2168.3, 1 ♂ (Am 72\*, AMNH). **California:** Los Angeles Co., Angeles Nat. For., 34.389176, -117.716479, 2017-06-05 through 2017-06-17, leg. L.E. Jones, swept around head, 1 ♂ (Am 526\*, AMNH). **Illinois:** Hardin Co., Shawnee Nat. For., 37.594631, -88.382478, 2018-08-08, leg. L.E. Jones and J.L. Hughes, swept around head, 1 ♂ (Am 648\*, AMNH).

**ETYMOLOGY:** From *hyalos*, Greek for “glass,” in reference to the translucent, fragile, nonsclerotized nature of the male genitalia.

**DISTRIBUTION:** This species is widespread, a band stretching from southwestern New Mexico, through central Arizona, and into southern California. Single specimens have also been identified from southern Illinois and Ontario.

**COMMENTS:** *Amiota hyalou*, as treated here, may be a species complex (fig. 8), though a lack of large series makes this difficult to assess. The various specimens differ in respect to the broadness of the distal end of the aedeagal apodeme as well as the size and positioning of the apical hook on the outer paraphysis. It is likely that the single specimen from Illinois represents a new species, but more collections and sequence data would make this easier to judge. Western populations of *A. hyalou* as well as the individual from Illinois exhibit the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

#### THE *ALBOGUTTATA* SPECIES GROUP

**DIAGNOSIS:** Small to medium-sized flies; dark brown to black-brown, with typical white markings; arisal branches with short to long branches;

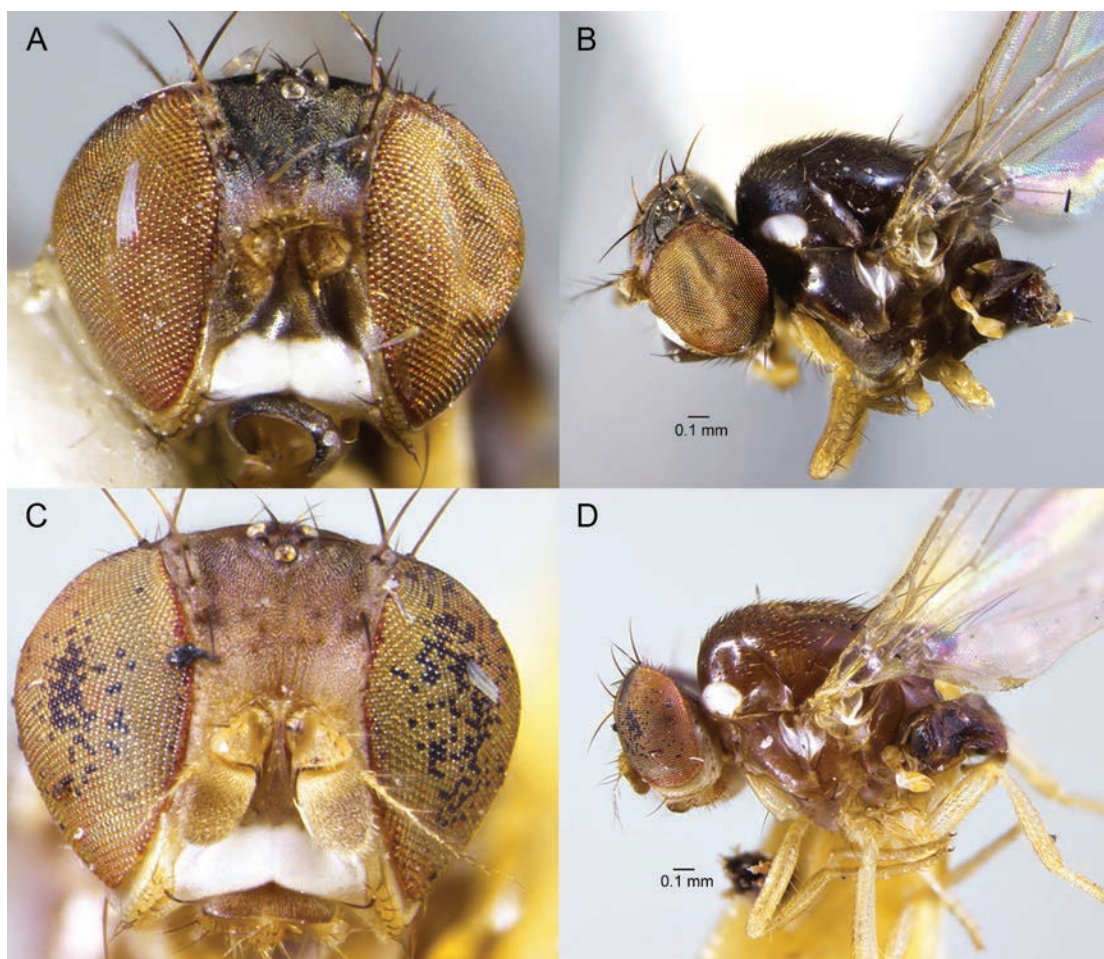


FIG. 4. Heads and lateral views, A. *hsui* species group. A–B. *A. hsui* Máca (Am 381). C–D. *A. hyalou*, sp. nov. (Am 62, paratype, lateral image flipped).

frons faintly pollinose to silvery reflective; some species with comb on the hind tibia (*A. communis* and *A. steyskali*). Male genitalia: Outer paraphysis linear, simple (no spines); subepandrial sclerite large and recurved.

NEARCTIC SPECIES: *Amiota communis* Chen and Steyskal, *A. durangoensis*, sp. nov., *A. lineiventris* Máca, and *A. steyskali* Máca.

COMMENTS: This is a large species group established by Chen and Toda (2001), for what are now 48 Palearctic and Asian species. The group was defined morphologically, based on the male hind legs: tibia with a ventral row of

long setae; tarsomeres 2–5 broadened, shorter than 1.5× the width. We have found that the short tarsomeres is a continuous character that is not well defined in Nearctic species. We are also proposing in the diagnosis above several male genitalic features that group the Nearctic and at least some of the Palearctic species. Wang et al. (2020) analyzed COI and ND2 sequences of the group; they did not include *A. communis*, *A. steyskali*, or *A. subtusradiata* Duda. *Amiota subtusradiata* we classify into a separate group with two Nearctic species based on the distinctive genitalia.

*Amiota communis* Chen and Steyskal, 2004

Figures 9A–B, 11A, 12, 81C

*Amiota communis* Chen and Steyskal, 2004;

Chen et al. 2004: 65 (original description); Malloch and McAtee, 1924: 41, plate VIII, figs. 12, 13 (figure of male genitalia, as *A. alboguttata*); Brake and Bächli, 2008: 251 (world catalog).

**DIAGNOSIS:** Medium-sized fly (ThL 1.15–1.42 mm), dark brown almost black; frons shiny; hind tibia with comb of 8–12 setae; outer paraphysis long, slender, sinuous in dorsal/ventral views, robust, apex strongly curved and clawlike, each possessing a strong medially curving seta; inner paraphysis about 1/2 length of outer paraphyses, heavily sclerotized, slender, expanded at base, acutely bent 2/3 of the length from apex.

**DESCRIPTION:** Medium-sized fly (ThL 1.15–1.42 mm), dark brown to black, legs yellowish. Frons slightly pollinose, golden; ventral half shiny, silvery. Palp yellow, the tip brown. Tergites 1 and 2 lightly colored. Hind tibia with comb composed of 8–12 setae. Arista: Very long, plumose; longest branch D1; A.R. 0.50; 5 long dorsal, 3 ventral branches; D5 pointed slightly mediad; arista trunk with medium microtrichia on basal half, apical half bare. Male genitalia: Epandrium distinct, split at middle dorsal point, but no gap, each epandrial lobe made up of 2 distinct plates or regions, microtrichia and long setae absent outside plates, each epandrial half with long ventral lobe, 9–10 long setae along the ventral margin. Cercus distinct from surrounding membrane, pyramidal membranous area above, ventral to epandrial apex. Surstylus with 6 prenisetae, apices blunt; 15–18 scattered setae, most along ventral portion. Subepandrial sclerite rounded in dorsal view, subepandrial appendage arising from subepandrial sclerite, slightly pointed, directed posteriorly. Outer paraphysis long, slender, sinuous in dorsal-ventral views, robust, tapering into a curved hook distally, a central fracturelike cleft

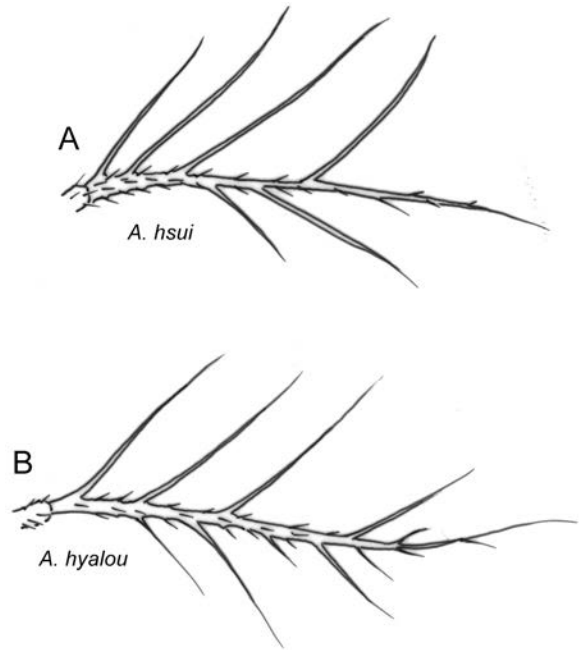


FIG. 5. Aristae, *A. hsui* species group. **A.** *A. hsui* Máca. **B.** *A. hyalou*. Not to same scale.

running the length dorsally, 6–9 sensilla on lateral surface near distal end, large setae past mid-point curving medially. Inner paraphysis heavily sclerotized, slender, base bulbous, tapering to a point, curved laterally at 2/3 the length to the apex; length ~1/2 that of outer paraphysis. Aedeagal apodeme longer than wide, strongly bent in lateral; distal end lightly flared with a small depression, inner region bell shaped. Hypandrium simple, U-shaped, lateral arms bowing outward, scalloped on end distal from apex. Ejaculatory apodeme small and stout, slightly longer than 1/3 the length of epandrium. Head and thorax measurements: (n = 5; Am 169, 320, 393, 425, 560) FL/FW 0.78 (0.67–0.92), EL/EW 1.31 (1.24–1.38), EL/CW 21.39 (19.66–23), FML/FMW 0.32 (0.30–0.38), PR/RR 0.58 (0.54–0.66), ThL 1.25 (1.15–1.42 mm).

**TYPE MATERIAL:** **Holotype:** As reported by Chen et al. (2004): “♂, USA: Wayne County, Michigan, 16.VI.1960, (G, Steyskal)” [not examined]. Deposited in National Museum of Nature

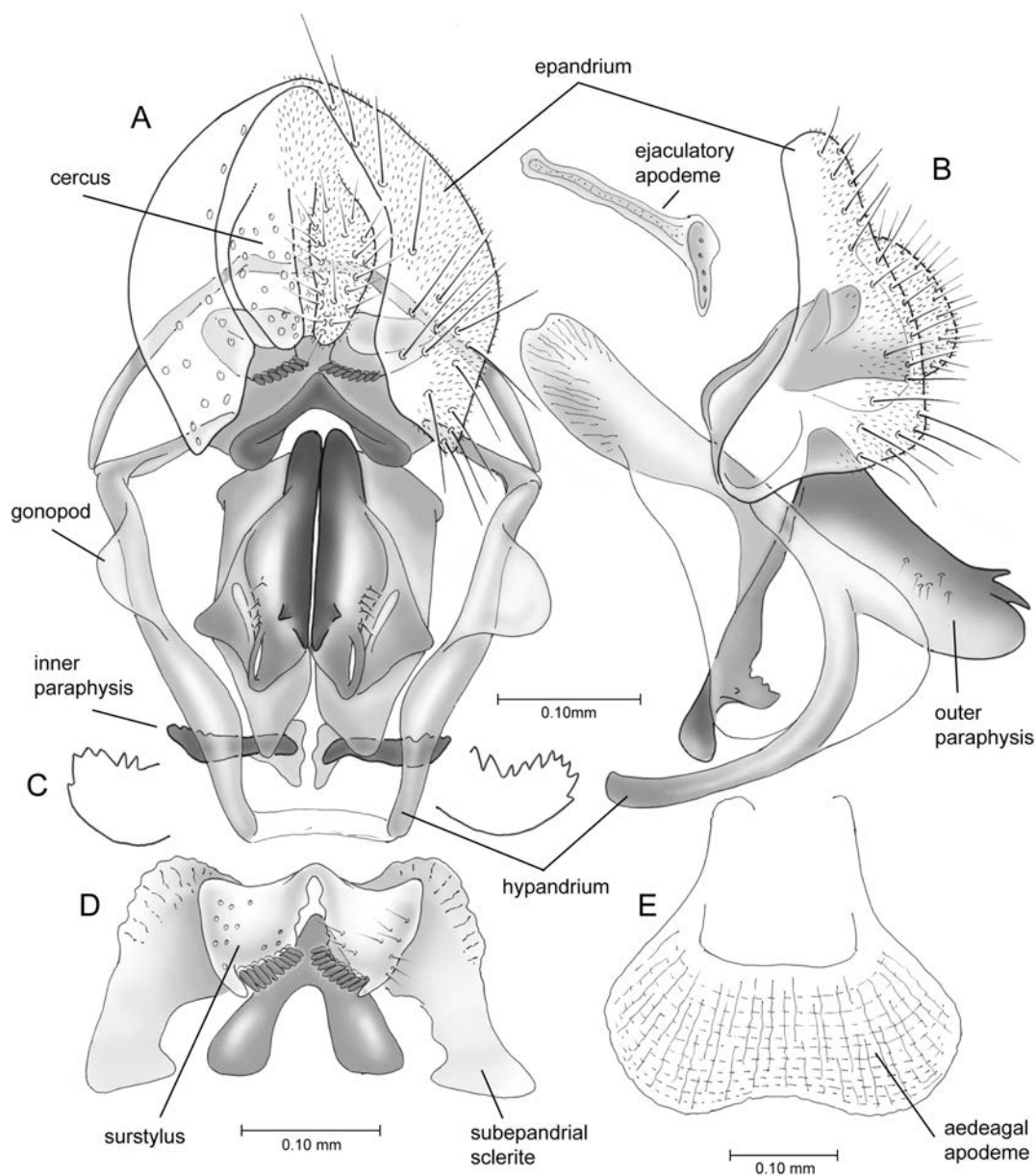


FIG. 6. Male terminalia, *A. hsui* Máca. **A.** Posterior view. **B.** Lateral view. **C.** Inner paraphysis, distal margin. **D.** Surstyli and subepandrial sclerite. **E.** Aedeagal apodeme. (Am 68).

and Science, Tokyo (NSMT). **Paratypes:** "4♂, same data as holotype" (NSMT).

**OTHER MATERIAL EXAMINED:** **Canada:** **Ontario:** Algoma District, Hilton Beach, edge of hardwood forest and field, 1992-07-05, leg. J.E. Swann, malaise, debu00282842, 1♂ (Am 563\*,

DEBU); 1992-07-05, leg. J.E. Swann, edge of hardwood forest and field, debu00282850, 1♂ (Am 564, DEBU); 1992-07-26, leg. J.E. Swann, edge of hardwood forest and field, debu00298081, 1♂ (Am 630\*, DEBU); Algonquin Province Park, Swan Lake Station, Scott Lake Survey, 1994-07-01 through 1994-

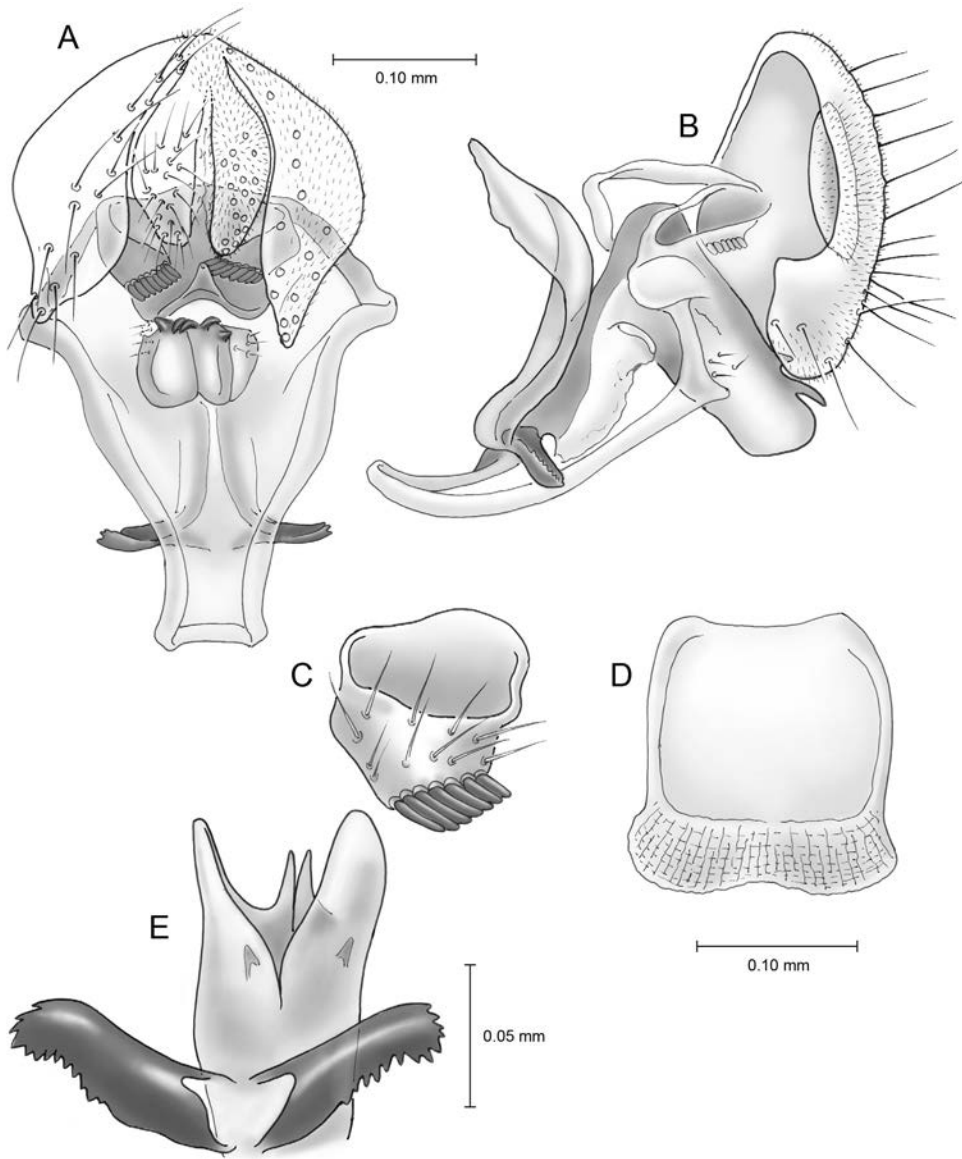


FIG. 7. Male terminalia, *A. hyalou*. A. Posterior view. B. Lateral view. C. Surstylus. D. Aedeagal apodeme. E. Inner paraphysis and outer paraphysis. (Am 54, holotype)

07-10, [collector unknown], C1 Shore malaise trap, 1♂ (Am 565, DEBU); Bruce Co., Dunks Bay, 2000-07-23 through 2000-07-27, leg. S.A. Marshall, debu00079593, 1♂ (Am 615\*, DEBU); Bruce Co., Jack Poste Side trail, 4km N Hope Bay, 44 55 25 N, 81 09 17 W, 2011-07-05, leg. J.M. Cumming, 1♂ (Am 1286, CNC); Gros Cap 20 km W S.S.Marie,

1986-08-31, leg. K.N. Barber, mixed forest, 1♂ (Am 560\*, DEBU); Hald.-Norfolk Reg., Cronmiller prop., ~6 km St. Williams, site 1, 2011-09-01 through 2011-09-20, leg. Brunke and S. Paiero, forest mals pans, debu00352726, 1♂ (Am 570\*, DEBU); Hald.-Norfolk Reg., Turkey Point Provincial Park, site 1, 2011-07-05 through 2011-08-05, leg. Brunke and S.

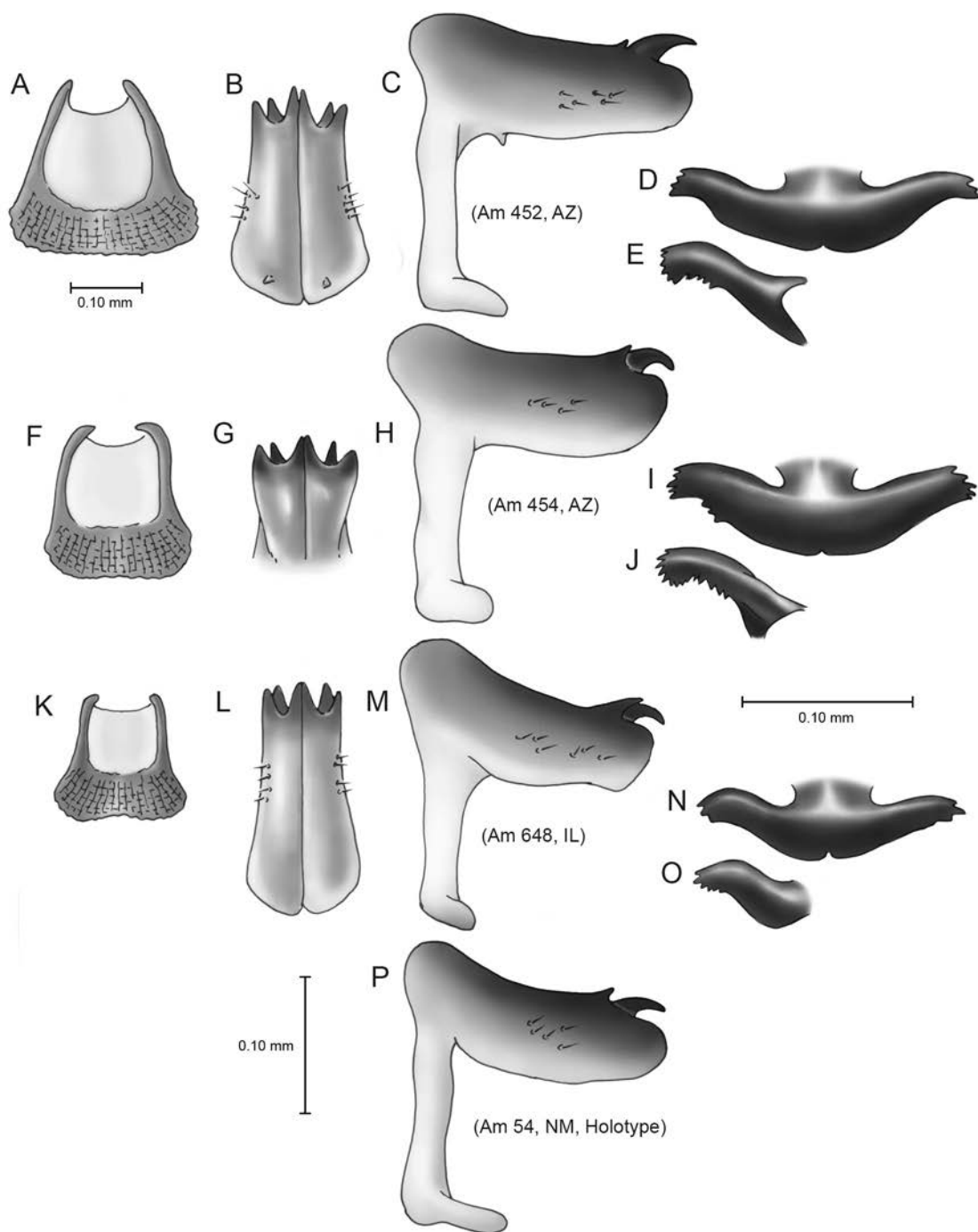


FIG. 8. Species complex, *A. hyalou*. A-E. Am 452, AZ. F-J. Am 454, AZ. K-O. Am 648, IL. P. Am 54, NM, holotype.

Paiero, forest, malaise pans, debu 00350353, 1 ♂ (Am 571, DEBU); 2011-08-05 through 2011-08-17, leg. Brunke and Paiero, forest malaise pans, debu00349960, 1 ♂ (Am 572, DEBU); Lambton Co., Port Franks, Karner Blue Sanctuary, 1996-09-10, leg. J. Skevington, debu01084394, 1 ♂ (Am 528\*, DEBU); Lanarck Co., Patterson Lake, 1979-07-21, leg. S.A. Marshall, 2 ♂ (Am 632, 635\*, DEBU); 1979-07-22, leg. S.A. Marshall, 1 ♂ (Am 633, DEBU); Marmora, 1952-07-16, leg. J.R. Vockeroth, 1 ♂ (Am 1357, CNC); Northumberland Co., Peter's Woods Provincial Nature Preserve, back woods, 2011-08-26 through 2011-09-12, leg. Brunke and Paiero, forest malaise pans, 44 7 28 N, 78 2 14 W, debu00352726, 1 ♂ (Am 568\*, DEBU); Norway Point, Lake of Bays, 1919-07-31, leg. J. McDunnough, "Paratype - No. 8016 paratype" [never published], 1 ♂ (Am 1346, CNC); Ottawa Montfort Hospital, 45 26 52 N, 75 38 27 W, 2007-07-16, leg. J.R. Vockeroth, Acer- Betula Wood, Aerial sweep at 7:30PM, 1 ♂ (Am 1224, CNC); Sandbanks Pk, nr Picton, 1970-07-01, leg. J.F. McAlpine, 1 ♂ (Am 1564, CNC); Simcoe, 1939-06-29, leg. G.E. Shewell, "Paratype No. 8016 paratype" [never published], 1 ♂ (Am 1342, CNC); Smith's Bay, Nr. Picton, 1970-01-07, leg. J.F. McAlpine, 1 ♂ (Am 1190, CNC); Thwartway Island, St. Lawrence Is. National Park, 1976-07-06, leg. A. Carter, Sweep, Ostrich fern, Code 4045-O, 1 ♂ (Am 1238, CNC); 1976-08-27, leg. A. Carter, Malaise trap, Code4529-G, 1 ♂ (Am 1239, CNC); 7 mi E. Griffith, 1989-07-08, leg. B.E. Cooper, 2 ♂ (Am 1232, 1233, CNC); [no specific locality], 1990-09-02, leg. J.E. Swann, Edge of HDWD forest and field, malaise, 1 ♂ (Am 622\*, DEBU). **Quebec:** Duncan Lake nr. Rupert, 1988-08-08, leg. J.F. McAlpine, hovering at my ear, 1 ♂ (Am 1402, CNC); Gatineau Park, King Mountain, 45 29 28 N, 75 51 31 W, 2011-08-19, leg. J.M. Cumming, 1 ♂ (Am 1284, CNC); Lac Phillippe, 1955-07-30, leg. J.R. Vockeroth, 1 ♂ (Am 1358, CNC); Old Chelsea, 1959-09-27, leg. J.R. Vockeroth, 1 ♂ (Am 1435, CNC); 1959-09-28, leg. J.R. Vockeroth, 1 ♂ (Am 1436, CNC); 1959-09-30, leg. J.R. Vockeroth, 1 ♂ (Am 1438, CNC); 1966-08-09, leg. D.D. Monroe, 1 ♂ (Am 1260, CNC); Old Chelsea, King Mt., 1961-06-16, leg. J.G. Chillcott, 1 ♂ (Am 1581, CNC); Old Chelsea, Summit King Mtn., 1965-06-20, leg. D.M. Wood, 2 ♂ (Am 1440, 1464, CNC); 1964-08-26, leg. D.M. Wood, 1 ♂ (Am 1395, CNC). **USA: Arkansas:** Logan Co., Magazine Mt., 2750 ft., 1992-07-06, leg. D. Grimaldi, 8 ♂ (Am 320\*, 321, 325, 329\*, 333, 335\*, 343, 364, AMNH). **District of Columbia:** Rock Creek Park, 1957-06-07, leg. P.H. Arnaud, Jr., 1 ♂ (Am 394\*, CAS). **Georgia:** Black Rock Mt. S.P., 1953-07-04, leg. M.R. Wheeler, 5 ♂ (Am 167, 168, 169\*, 170, 171, AMNH); Blood Mt., 1952-07-15, leg. P.W. Fattig, 1 ♂ (Am 498\*, EMUS); Lumpkin Co., 15 mi NW Dahlonega, 1973-06-15, leg. M.R. Humphrey, 1 ♂ (Am 497\*, EMUS). **Illinois:** Mason Co., Sand Ridge St. For., 4 mi NW Forest City, 1976-06-01, leg. C.T. Maier, 1 ♂ (Am 1597\*, INHS); Union Co., Trail of Tears State Forest 37.499757, -89.340117, 2018-08-08, leg. L.E. Jones and J.L. Hughes, swept around head, 1 ♂ (Am 650\*, AMNH). **Indiana:** Crawford Co., Hoosier N.E., Hemlock Cliffs, 1991-05-19, leg. B.J. Sinclair, ex. Trickling stream, 1 ♂ (Am 1302, CNC); Harrison Co., O'Bannon Woods St. Pk., 38.194962, -86.267880, 2018-08-14, leg. L.E. Jones, swept around head, 1 ♂ (Am 740\*, AMNH). **Kentucky:** Edmonson Co., Mammoth Cave National Park, 1991-06-09, leg. J.E. Swann, sweep in forest by wet sink hole, 1 ♂ (Am 750, DEBU). **Maryland:** Glen Echo, 1921-07-10, [leg. J.R. Malloch], 1 ♂ (Am 1613, INHS). **Massachusetts:** Brookline, 08-23 [no year], [collector unknown], Univ. of Kan., Lot 958, 3 ♂ (Am 460, 461\*, 462, SEMC); E. Falmouth, 1924-07-22, [collector unknown], 1 ♂ (Am 192\*, AMNH); Lexington, 1956-06-05, [collector unknown], 1 ♂ (Am 193\*, AMNH); Riverside, 08-16 [no year], [collector unknown], Univ. of Kan., Lot 958, 1 ♂ (Am 463\*, SEMC); Woods Hole, 1950-07-17, [collector unknown], 1 ♂ (Am 189\*, AMNH). **Michigan:** Berrien Co., St. Joseph, 1973-09-02, leg. D.D. Wilder, 1 ♂ (Am 387\*, CAS); Delta Co., Escanaba, 45.732003, -87.081676, 2018-06, leg. T. Werner, 1 ♂ (Am 1093, AMNH); Marquette Co., Huron Mtns., Huron Mtn. Club property vicinity, 46.874950, -87.891717, 2018-07-06 through 2018-07-12, leg. T. Werner, 1 ♂ (Am 1064, AMNH). **Missouri:** Lithium, 1962-09-05, [collector unknown], 1 ♂ (Am 186\*, AMNH). **New York:** Putnam Co., Hudson Highlands St. Pk., 41.448627, -73.966484, 2017-09-23, leg. L.E. Jones and C. Liriano, swept around head, 9 ♂ (Am 519-522\*, 728-730\*, 1012, 1014, AMNH); Jeff Co., Wellesley Is., 1963-08-22, leg. L.L. Pechuman, 1 ♂ (Am 38\*, AMNH); Orange Co., Cornwall, Black Rock Forest, 2014-09-06 through 2014-09-07, leg. D. Grimaldi, 11 ♂ (Am 417, 418, 420, 423, 424, 425\*, 426\*, 427-429, 431\*, AMNH); Sta. Study Insects, Tuxedo, 1928-07-06, leg. C.H. Curran, 1 ♂ (Am 41, AMNH); Tompkins Co., Texas Hollow, 1983-07-26,

leg. D. Grimaldi and L.L. Pechuman, flying about head, 6♂ (Am 22\*, 23\*, 26, 27, 28\*, 31\*, AMNH); Monroe Co., Rochester, Highland Pk., 43.132600, -77.602784, [no date], leg. J. Jaenike, 1♂ (Am 723\*, AMNH). **North Carolina:** Black Mts., 09-00 [year and day unknown], [collector unknown], 3♂ (Am 308, 309, 310, AMNH); 09-00 [year and day unknown], [collector unknown], "Phortica n. sp.," 1♂ (Am 317, AMNH); Graham Co., Robbinsville, 1976-06-09, leg. G.E. Bohart, 1♂ (Am 501\*, EMUS); Highlands, 3800', 1957-06-08, leg. J.R. Vockeroth, 1♂ (Am 1361, CNC); 3800', 1957-06-15, leg. J.R. Vockeroth, 1♂ (Am 1360, CNC); 1957-07-14, leg. C.J. Durden, 1♂ (Am 1379, CNC); Pisgah Forest, Looking Glass Park, 1957-07-31, leg. W.R. Richards, 1♂ (Am 1383, CNC). Wayah Bald, 1957-07-13, leg. C.J. Durden, 1♂ (Am 1211, CNC). **Ohio:** Portage Co., West Branch State Park, 1988-07-17, leg. B.A. Foote, 3♂ (Am 312, 313\*, 314, AMNH). **Pennsylvania:** Centre Co., 1972-07-04, leg. D.D. Wilder, 1♂ (Am 391\*, CAS); Lycoming Co., 1972-07-27, leg. D.D. Wilder, 2♂ (Am 392\*, 393\*, CAS). **Tennessee:** Cades Cove, GSMNP, 1953-07 through 1953-08, leg. J.M. Carpenter, 9♂ (Am 172, 175, 176\*, 177, 178\*, 179, 180, 181\*, 190, AMNH); Unicoi Co., Cherokee Nat. For., 36.137782, -82.350719, 2018-08-20, leg. L.E. Jones, swept around head, 1♂ (Am 661\*, NH). **Vermont:** Orleans Co., nr. Bald Mtn., 1650 ft., 44.793912, -71.987952, 2016-07-19 through 2016-07-21, leg. D. Grimaldi, 1♂ (Am 368\*, AMNH). **Virginia:** Blackburg, 1953-09-09, [collector unknown], "male," 1♂ (Am 166\*, AMNH); Floyd Co., #1, Mile 175.4 Blue Ridge Parkway, 1960-06-23, leg. G.W. Byers, 1♂ (Am 435, SEMC); Giles Co., Cascade Falls, 2001-05-19, leg. O. Lonsdale, 38 21 0 N, 80 36 30 W, debu01007850, 1♂ (Am 641\*, DEBU); Scott Run, 1954-07, leg. M.R. Wheeler, 1♂ (Am 194\*, AMNH). **Wisconsin:** Waupaca Co., Hartman Ck. Pk., 1974-08-13, leg. T.R. Marsh, flying around person, 2♂ (Am 1591\*, 1592\*, INHS).

**DISTRIBUTION:** *Amiota communis* is very common in the northeastern U.S. and Appalachia and as far west as the Ozarks. The distribution of *A. communis* is similar to the closely related species *A. steyskali* Máca.

**COMMENTS:** In their key to the Drosophilidae of the District of Columbia, Malloch and McAtee (1924) referred to the male genitalia of the then undescribed *A. communis* as *A.*

*alboguttata* (Wahlberg) in figures 12 and 13 at the end of the work. Although confusion has surrounded this name, *A. alboguttata* is not known to occur in the Nearctic. Chen and Steyskal described *communis* from material found in the National Science Museum of Tokyo (NSMT). The holotype, collected by George Steyskal (1909–1996) and labelled under his manuscript name as *A. communis*, was presumably sent to Toyohi Okada (1909–2000) along with other collections of *Amiota* from North America. Steyskal sent *Amiota* specimens to other institutions as well, including the National Museums Scotland (NMS), which contains specimens collected in Michigan (L.E.J., personal obs.). *Amiota communis* exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

#### *Amiota durangoensis*, sp. nov.

Figures 9C–D, 11B–C, 13, 82A

**DIAGNOSIS:** Small fly (ThL 0.99–1.13 mm), dark blackish brown; cheek deep (EL/CW 8.33–11.20), grayish white; arista with short plumosity; subepandrial sclerite with uniquely paired, grasping, subepandrial appendage: each half armlike, apices with strongly sclerotized spines and teeth, asymmetrical, curving inward medially; outer paraphysis simple, linear, sclerotized; inner paraphysis armlike, with 5–6 sclerotized, toothlike structures at distal end; ejaculatory apodeme extremely large, length greater than depth of epandrium.

**DESCRIPTION:** Small fly (ThL 0.99–1.13 mm), dark blackish brown, legs yellow. Frons very dark, dark brown to black. Cheek deep (EL/CW 8.33–11.20), grayish-white. Palp yellow. Tergite 1 lightly colored. Arista: Short, plumose, branches decumbent; longest branch D2; A.R. 0.29; 2 dorsal, 2 ventral branches; branch V1, V2 pointed medially; arista trunk with medium microtrichia, trunk zigzagged at apical third. Male genitalia: Epandrium separated at dorsal midline, but margins discrete (not grading into surrounding

membrane). Cercus semicircular, relatively small and flattened, surrounded by large membranous region. Surstylus approximately square; 10 long prensisetae, apices blunt, closely arranged, comb-like; setulae scattered over broad surface. Subepandrial sclerite very distinctive: Paired, each half armlike, large, broad in lateral view, curving medially; distal ends with heavily sclerotized spines and teeth, including large dorsal spine on each, “dentition” differs between each half; subepandrial complex covered in membrane. Outer paraphysis long, slender, linear (very slightly sinuous), distal end more heavily sclerotized, tapered to blunt point, cluster of long trichoid sensilla just proximal to midpoint. Inner paraphysis armlike, smaller than subepandrial appendage (~1/2 length of outer pair); distal end with 5–6 heavily sclerotized, irregular toothlike projections. Aedeagal apodeme slightly expanded at distal end, no concave depression; slightly longer than wide; moderately bent at posterior end, in lateral view. Hypandrium wide, of varying thickness; with 4 small, flat, wrinkled lobes on outer margin straddling the apex. Ejaculatory apodeme very large, 1.25× length of epandrium. Head and thorax measurements: (n = 5; Am 1414, 1456, 1458, 1513, 1520) FL/FW 0.79 (0.74–0.82), EL/EW 1.25 (1.15–1.33), EL/CW 9.63 (8.33–11.20), FML/FMW 0.22 (0.21–0.24), PR/RR 0.63 (0.55–0.66), ThL 1.05 (0.99–1.13 mm).

**TYPE MATERIAL:** **Holotype:** male: 14 mi. SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June “9” 1964, J.F. McAlpine, Am 1520, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC). **Paratypes:** 14 mi. SW. El Salto, Dgo. [Durango] MEX., 8000', June “9” 1964, J.F. McAlpine, attracted to man [2 specimens], 5♂ (Am 1456\*, 1458\*, 1502\*, 1513\*, 1554\*, CNC).

**OTHER MATERIAL EXAMINED:** **Mexico:** **Durango:** 14 mi. SW. El Salto, 8000', 1964-06-26, leg. J.F. McAlpine, attracted to man, 1♂ (Am 1509\*, CNC). **Sinaloa:** Portrerillos, 15 mi. W El Palmito, 5000', 1964-07-08, leg. J.F. McAlpine, 1♂ (Am 1414\*, CNC).

**ETYMOLOGY:** Derived from the state of Durango in Mexico, location of the type series.

**DISTRIBUTION:** *Amiota durangoensis* is currently known only from the states of Durango and Sinaloa in Mexico. It may be a more restricted species given no specimens have been collected in extensively sampled areas of the south for this genus.

**COMMENTS:** The remarkable paired, grasping structure of the subepandrial appendage is unique in the genus, and is an excellent example of the trade-off in *Amiota* between development of this appendage and the paraphyses. This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota lineiventris* Máca, 2003

Figures 10A–B, 11D–E, 14, 82B

*Amiota lineiventris* Máca, 2003: 267 (original description); Brake and Bächli, 2008: 253 (world catalog).

**DIAGNOSIS:** Small to medium-sized fly (ThL 1.04–1.26 mm), dark brown; male sternites 7 and 8 with Y- and I-shaped apodemes, respectively; male genitalia distinctively simple: outer paraphyses a pair of small, ovoid lobes with narrow posterodorsal extension, several stiff, preapical setulae; inner paraphyses heavily sclerotized, simple, with distal and proximal ends a pair of short lobes, fused medially.

**DESCRIPTION:** Small to medium-sized fly (ThL 1.04–1.26 mm), dark brown, legs yellow. Frons dark, slightly pollinose in ventrolateral corners and surround ocellar triangle, with several scattered hairs. Facial marking narrow (FML/FMW 0.22–0.27). Cheek depth highly variable (EL/CW 12.50–25.50), yellowish gray. Palp yellow. Male sternites 7 and 8 distinctive, with sclerotized apodemes: Y-shaped in sternite 7 (area between arms concave), roughly I-shaped in sternite 8. Arista: Medium plumose; longest branch D1; A.R. 0.46; 3 long dorsal, 2–3 shorter ventral branches; branch D4 pointed laterad; arista trunk with

short-medium microtrichia over entire length. Male genitalia: Epandrium very distinctive; split medially into distinct halves, widely separated; with row of setae ringing the circumference. Cercus large and semicircular, protruding greatly (not recessed into epandrium); occupying most of space surrounded by epandrium. Surstylus roughly square, with 9 prensisetae of equal size, apices blunt, comblike, ventral half and margin with scattered setulae. Subepandrial sclerite simple; subepandrial appendage small, ventral to epandrium (not protruding), lightly sclerotized and membranous, apex deeply notched. Outer paraphysis ovoid, with small lobelike extension on posterodorsal end; middle region laterally with ca. 9 short scattered sensilla; distally with 2–3 long setulae, 3× length of the sensilla. Inner paraphysis heavily sclerotized, with distal and proximal ends a pair of short lobes, apparently fused in middle. Aedeagal apodeme moderately sclerotized; bent nearly 45° at midpoint in lateral view, longer than wide; base and midpoint bulging, lightly sclerotized; distal end flared, deeply notched and concave, lateral arms most heavily sclerotized. Hypandrium simple, sclerotized, thickness consistent along length, apex bent inward. Ejaculatory apodeme 0.5× length of epandrium. Head and thorax measurements: (n = 5; Am 499, 592, 749, 1189, 1250) FL/FW 0.73 (0.68–0.76), EL/EW 1.21 (1.16–1.26), EL/CW 18.17 (12.50–25.50), FML/FMW 0.25 (0.22–0.27), PR/RR 0.50 (0.36–0.62), ThL 1.16 (1.04–1.26 mm).

**TYPE MATERIAL:** **Holotype:** male: As reported by Máca (2003): “♂: Canada: Ontario: Eganville, damp meadow near lake, 2.6.1991, leg. M. Barták” [not examined]. Coll. J. Máca, to be deposited in National Museum of Prague, Czech Republic (NMPC). **Paratypes:** “Same data,” 1 ♂ (Coll. J. Máca, intended for NMPC). “Canada, Quebec: Lac Roddic, 16 km S Maniwaki, 23.6.1991 1 ♂, leg. M. Barták.” (Coll. J. Máca, intended for NMPC).

**OTHER MATERIAL EXAMINED:** **Canada:** **Ontario:** Algonquin Provincial Park, Swan Lake Station, Scott Lake Survey, 1994-07-01 through 1994-07-10, [collector unknown], C1 shore malaise trap,

1 ♂ (Am 592\*, DEBU); Ottawa, 1970-06-26, leg. J.R. Vockeroth, 1 ♂ (Am 1444\*, CNC); 1990-05-27, leg. J.R. Vockeroth, Ex damp shaded ditch in Acer wood, 1 ♂ (Am 1252\*, CNC); 1992-07-26, leg. J.R. Vockeroth, Damp second-growth Acer-Betula wood, 1 ♂ (Am 1250\*, CNC); 1995-06-24, leg. J.R. Vockeroth, Damp second-growth Acer-Betula wood, 1 ♂ (Am 1244\*, CNC); Smith's Bay, Nr. Picton, 1970-07-01, leg. J.F. McAlpine, 2 ♂ (Am 1183\*, 1189\*, CNC). **Quebec:** Old Chelsea, Summit King Mtn., 1965-06-20, leg. D.M. Wood, 1 ♂ (Am 1201\*, CNC). **USA:** **North Carolina:** Graham Co., Robbinsville, 1976-06-09, leg. G.E. Bohart, 1 ♂ (Am 499\*, EMUS). **Virginia:** Giles Co., Cascade Falls, 2001-05-19, leg. O. Lonsdale, debu01007820, 1 ♂ (Am 749\*, DEBU).

**DISTRIBUTION:** The original description by Máca (2003) cited only specimens from Canada (Ontario and Quebec), but *Amiota lineiventris* is now known from one specimen each from North Carolina and Virginia, showing a much wider distribution.

**COMMENTS:** *Amiota lineiventris* is a rarely collected species, usually as an individual rather than a series. It is unknown whether this species is attracted to the eyes and face as in other *Amiota*.

*Amiota steyskali* Máca, 2003

Figures 10C–D, 15, 82C

*Amiota steyskali* Máca, 2003: 271 (original description); Brake and Bächli, 2008: 255 (world catalog).

**DIAGNOSIS:** Small to medium-sized fly (ThL 1.04–1.34 mm), dark brown to nearly black species; frons slightly shiny; hind tibia with comb of 3–7 setae [reported as tibia of midleg in Máca, 2003]; outer paraphysis long, slender, nearly straight, apex strongly curved, clawlike; inner paraphysis heavily sclerotized, short and nearly triangular; subepandrial sclerite sclerotized, large and shelflike; ejaculatory apodeme large.

**DESCRIPTION:** Small to medium-sized fly (ThL 1.04–1.34 mm), dark brown to nearly black, legs light yellow. Frons slightly shiny, with striations from ptilinal suture radiating to

midpoint of frons. Palp yellow. Tergite 1 lightly colored. Hind tibia with comb composed of 3–7 setae. Arista: Medium plumose; longest branch D2; A.R. 0.40; 5 long dorsal, 4 short ventral branches; D4–5 branches pointed laterad; arista trunk with short microtrichia. Male genitalia: Epandrium split at middle dorsal point, long ventral lobe with 13–15 long setae. Cercus distinct from surrounding membrane, crescentic, exposing large central membranous area between and dorsal to cerci. Surstylus nearly rectangular, 6 prenisetae, apices blunt. Subepandrial sclerite triangular, extending dorsally over surstyli, sclerotized, in lateral view subepandrial sclerite thickened and wedge shaped with deep clefts, dorsal appendage thickened and pointed, extending posteriorly. Outer paraphysis long, slender, nearly straight, heavily sclerotized, apex pointed and curved into a hook, dorsally with fracturelike cleft, ca. 6 sensilla present on lateral surface near distal end. Inner paraphysis short, heavily sclerotized, nearly triangular or wedge shaped, central cleft present. Aedeagal apodeme flared wider than base, distal end barely concave, flanges and inner region forming a square, bent almost 90° in lateral at midpoint. Hypandrium U-shaped, simple, consistent thickness; lateral arm thickened posteriorly. Ejaculatory apodeme thick, roughly 2/3 the length of the epandrium. Head and thorax measurements: (n = 5; Am 173, 195, 345, 644, 733) FL/FW 0.74 (0.70–0.78), EL/EW 1.30 (1.17–1.45), EL/CW 16.98 (14.75–20), FML/FMW 0.29 (0.21–0.36), PR/RR 00.47 (0.38–0.55), ThL 1.20 (1.04–1.34 mm).

**TYPE MATERIAL:** **Holotype:** As reported by Máca (2003): “♂: USA,” Maryland [erroneously reported as Maine] “Catoctin Mt. Park, Owens Creek, 15.6.1991, leg. M. Barták” [not examined]. Coll. Jan Máca, to be deposited in National Museum of Prague, Czech Republic (NMPC). **Paratypes:** “5♂, same locality; Catoctin Mt. Park, Chestnut wood, 15.6.1991 1♂ and 1♀, leg. M. Barták. Canada, Quebec: La Roddic, 16 km S

Maniwakim 23.6.1991 1♂, leg. M. Barták” (Coll. Jan Máca, intended for NMPC).

**OTHER MATERIAL EXAMINED:** **Canada: New Brunswick:** 6 mi S.E. Sussex, 1971-07-10, leg. B.V. Peterson, 1♂ (Am 1279\*, CNC). **Ontario:** Algonquin Provincial Park, Swan Lake Station, Scott Lake Survey, 1995-05-29 through 1995-06-16, leg. S.A. Marshall, fresh stump emergence, 1♂ (Am 575, DEBU); 1995-06-16 through 1995-07-04, leg. S.A. Marshall, A transect bracket. Pans on dead maple, 1m, 1♂ (Am 574\*, DEBU); 1993-06-17 through 1993-06-18, leg. Larson/Marshall/Barr, 1♂ (Am 532, DEBU); 1993-07-12 through 1993-07-16, leg. Larson/Marshall/Barr, 1♂ (Am 533, DEBU); 1994-07-18 through 1994-07-31, [collector unknown], C1 Shore malaise trap, 1♂ (Am 567, DEBU); Algonquin Provincial Park, W.R.S., 1994-06-25, leg. R. Bonduriansky, 2♂ (Am 608, 609, DEBU); 1994-06-29, leg. R. Bonduriansky, 1♂ (Am 607\*, DEBU); 1994-07-15, [collector unknown], on moose antler, AM W2S, 1♂ (Am 604, DEBU); Dwight, 1964-07-09, leg. D.H. Pengelly, Pan A3, hemlock/clubmoss, 1♂ (Am 546\*, DEBU); Franktown, 1965-09-06, leg. D.M. Wood, 1♂ (Am 1206, CNC); Mer Bleue Trail, 2014-06-15, leg. O. Lonsdale, 1♂ (Am 1292, CNC); Norway Point, Lake of Bays, 1919-08-04, leg. J. McDunnough, “Paratype - No. 8016 paratype” [never published], 1♂ (Am 1345, CNC); Orillia, 1927-07-13, leg. C.H. Curran, 1♂ (Am 1356\*, CNC); Orleans, Chapel Hill, 2000-06-20, leg. J.R. Vockeroth, 1♂ (Am 1245, CNC); Ottawa, Beechwood Cemet., 1999-07-12, leg. J.R. Vockeroth, shaded damp earth ditch, 1♂ (Am 1270, CNC); Wentworth Co., Sheffield, 1960-06-18, leg. Taylor and Wood, 1♂ (Am 1396\*, CNC). **Quebec:** Abbotsford, 1936-08-20, leg. G.E. Shewell, “Paratype - No. 8016 paratype” [never published], 1♂ (Am 1344, CNC); 1937-06-14, leg. G.E. Shewell, “Paratype No. 8016 paratype” [never published], 1♂ (Am 1378, CNC); Mont Tremblant, 3000', 1959-07-15, leg. B.V. Peterson, 2♂ (Am 1362, 1377, CNC); Mt. Orford, 1936-07-14, leg. G.E. Shewell, “Paratype - No. 8016 paratype” [never published], 1♂ (Am 1343, CNC); Old Chelsea, Summit King Mtn., 1965-06-20, leg. D.M. Wood, 8♂ (Am 1466, 1468–1470, 1474, 1476, 1480, 1539, CNC). **USA: Arkansas:** Logan Co., Magazine Mt. 2750 ft., 1992-07-06, leg. D. Grimaldi, 3♂ (Am 342\*, 345\*, 348, AMNH). **New York:** Bronx Co., New York Bot. Garden, 40.864029, -73.875571, 2018-08, leg. L.E. Jones and

L. Li, swept around head, 1 ♂ (Am 733\*, AMNH); Orange Co., Cornwall, Black Rock Forest, 2014-09-06 through 2014-09-07, leg. D. Grimaldi, 1 ♂ (Am 416\*, AMNH); Tompkins Co., Texas Hollow, 1983-07-26, leg. D. Grimaldi and L.L. Pechuman, flying about head, 3 ♂ (Am 25\*, 34\*, 36\*, AMNH); Monroe Co., Rochester, Highland Pk., 43.132600, -77.602784, 2018-07-26, leg. J. Jaenike, 2 ♂ (Am 724\*, 725\*, AMNH); 2018-09-14, leg. J., Jaenike, 1 ♂ (Am 1169\*, AMNH); [no date], leg. J. Jaenike, 1 ♂ (Am 726\*, AMNH). **North Carolina:** Graham Co., Robbinsville, 1976-06-09, leg. G.E. Bohart, 4 ♂ (Am 500\*, 502\*, 503\*, 518\*, EMUS); Highlands, 3800', 1957-06-15, leg. J.R. Vockeroth, 1 ♂ (Am 1359, CNC). **Tennessee:** Cades Cove, GSMNP, 1953-07 through 1953-08, leg. J.M. Carpenter, 1 ♂ (Am 173\*, AMNH); Carter Co., Holston Mtn., 1965-06-02, leg. J.S. Chillcott, 1 ♂ (Am 1300, CNC). **Vermont:** Bennington Co., Green Mountain Nat. For., 42.889507, -72.976097, 2018-08-05, leg. L.E. Jones and R.D. Mannion, swept around head, 2 ♂ (Am 643\*, 644\*, AMNH); Orleans Co., Westmore, nr. Bald Mountain, 2018-08-16, D. Grimaldi, 1 ♂ (Am 664\*, AMNH). **Virginia:** Fairfax, 1954-07, leg. M.R. Wheeler, 1 ♂ (Am 195\*, AMNH).

**DISTRIBUTION:** *Amiota steyskali* is relatively common in the Northeast but is also found in Appalachia and as far west as the Ozarks. This species has a similar distribution to the closely related species *A. communis* Chen and Steyskal.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

#### THE MARIAE SPECIES GROUP (NEW GROUP)

**DIAGNOSIS:** Small to medium-sized flies (*A. incurva* and *A. mariae* large); dark brown to black-brown, with typical white markings; frons dark, sometimes with faint pollinosity, dull, never silvery; arisal branches with medium to long branches. Male genitalia: Inner paraphyses asymmetrical (except *A. incurva*), heavily spined, spines often interdigitating, fused to outer paraphysis.

**NEARCTIC SPECIES:** *Amiota antitortementum*, *A. brayi*, sp. nov., *A. cruciatum*, sp. nov., *A. incurva*, sp. nov., *A. mariae* Máca, *A. texas*, sp. nov., *A. tormentum*, sp. nov., *A. wheeleri*, sp. nov., and *A. zaliskoi*, sp. nov.

**COMMENTS:** This species group is distinctive for the asymmetrical spines of the male genitalia. Specimens with mirrored paraphyses, or chiral variants, were found in all of the species in this group. In most cases this did not represent variation at the species level, with the chirality of the asymmetrical spines being the only difference between specimens. In one case was it felt necessary to warrant recognition at the species level (*A. antitortementum* and *A. tormentum*).

#### *Amiota antitortementum*, sp. nov.

Figures 16A–B, 19A, 20, 83A

**DIAGNOSIS:** Medium-sized fly (ThL 1.15–1.29 mm), black; similar to *Amiota tormentum*, but differing externally as follows: deeper cheek, subalar spot fainter, lower frons slightly broader (i.e., inner margins of eye not as convex); genitalia of *A. antitortementum* with stouter epandrium (not as tall), ventral lobe with margin oblique; subepandrial sclerite more quadrate; outer paraphysis with slightly smaller preapical dorsal claw; inner paraphysis with asymmetrical spines in mirror image of *A. tormentum*, anteriormost spines forming forked structure, spines close and nearly parallel, oriented to the right side.

**DESCRIPTION:** Medium-sized fly (ThL 1.15–1.29 mm), black, legs yellow. Frons nearly black dorsally, brown ventrally. Facial marking small, depth 0.3× width. Subalar spot somewhat faint. Palp brown. Arista: Long plumose; longest branch D2; A.R. 0.38; 4 long dorsal, 3 shorter ventral branches, none pointed mediad/laterad; arista trunk with medium microtrichia for entire length. Male genitalia: Epandrium fused at midline, margins distinct, not grading into surrounding membrane. Cerci large, crescentic, distinct from surrounding membrane; occupying much of space surrounded by epandrium. Surstylus nearly wedge shaped; proximal half with several dozen small scales, circular; several large scales more distally, long, oval shaped; 11 prensisetae, apices blunt, closely arranged; setulae

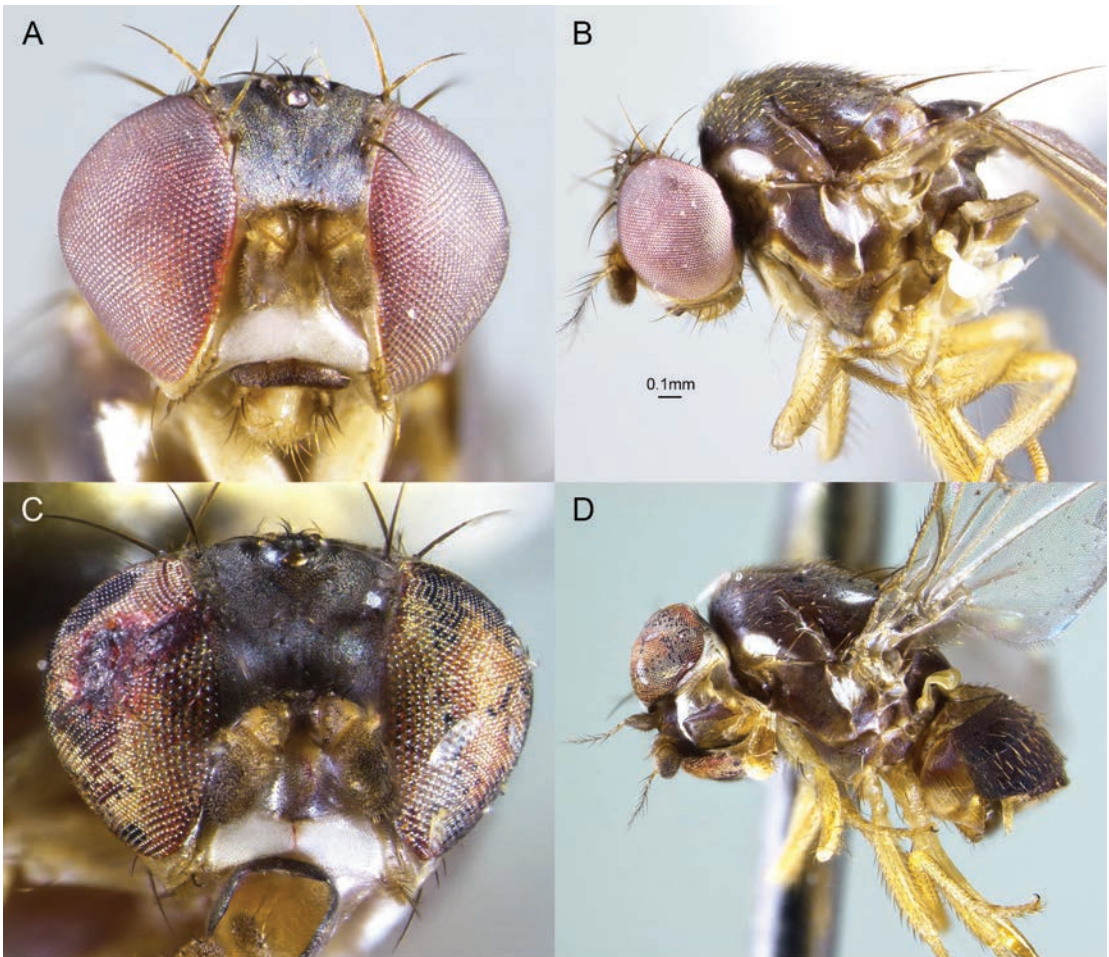


FIG. 9. Heads and lateral views, *A. alboguttata* species group. **A–B.** *A. communis* Chen and Steyskal (Am 426). **C–D.** *A. durangoensis*, sp. nov. (Am 1509).

scattered about between prensisetae and large oval scales, without lateral fingerlike lobe. Subpandrial sclerite quadrate, broad; posterior margin upturned into small rim. Outer paraphysis laterally flattened, symmetrical; distal end rounded, with small heavily sclerotized preapical dorsal claw, arising internally; large spine proximal to distal end, perpendicular to paraphysis, curving slightly medially. Inner paraphyses consisting of 2 lobes; anterior lobe with 4 spines; 2 lateral spines, each crossing, oriented in opposite directions; anteriormost spines forming a forked structure, close, nearly parallel, projecting to the

right side; posterior lobe consisting of 4 spines; 2 large lateral spines, spine on right side bent at distal end, other 2 spines smaller, arising near bases of larger lateral spines, oriented in opposite directions. Aedeagal apodeme straight, barely curving; slender, long, length  $2\times$  width; distal end barely flared, deeply notched; 2 processes on basal portion, heavily sclerotized, projecting laterally. Hypandrium simple, of uniform thickness, apex curving up slightly. Ejaculatory apodeme not studied. Head and thorax measurements: ( $n = 5$ ; Am 52, 59, 89, 116, 710) FL/FW 0.83 (0.77–0.92), EL/EW 1.32 (1.15–1.42), EL/CW 18.91

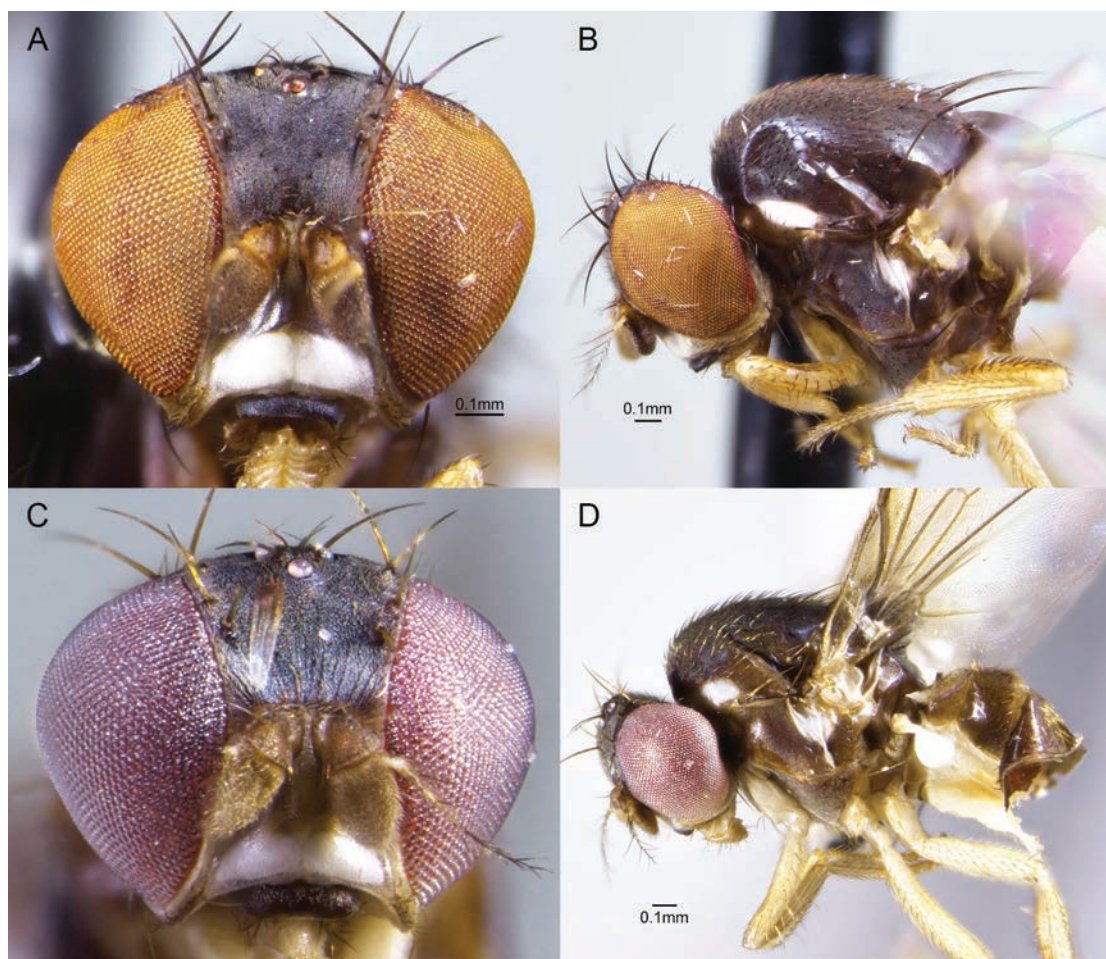


FIG. 10. Heads and lateral views, A. *alboguttata* species group. A–B. *A. lineiventris* Máca (Am 499). C–D. *A. steyskali* Máca (Am 416).

(16.5–22.33), FML/FMW 0.33 (0.28–0.37), PR/RR 0.56 (0.45–0.62), ThL 1.24 (1.15–1.29 mm).

**TYPE MATERIAL:** **Holotype:** male: 12 mi. N. Silver City, N.M. [New Mexico], [33.019248, -108.263582], MR Wheeler, Aug. 1950, “2051,” Am 55 [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** 12 mi. N. Silver City, N.M. [New Mexico], MR Wheeler, Aug. 1950, “2051,” 4♂ (Am 52\*, 57\*, 59\*, 61\*, AMNH).

**OTHER MATERIAL EXAMINED:** USA: **Arizona:** Cave Creek nr. Portal, 1951-06, leg. M.R. Wheeler and W.B. Heed, 1♂ (Am 116\*, AMNH); Cochise Co.,

Vicinity of SWRS, nr. Cave Creek, 31.882018, -109.206636, 2019-07-19, leg. L.E. Jones and J.L. Hughes, 1♂ (Am 710\*, AMNH); Ramsey Canyon Huachua Mts., 1951-06, leg. M.R. Wheeler and W.B. Heed, 2157.11, 1♂ (Am 89\*, AMNH). **New Mexico:** Mill Canyon Magdalena Mts., S. Magdalena, 1951-06-26 through 1951-06-27, leg. W.B. Heed and M.R. Wheeler, 2171.9, 1♂ (Am 78\*, AMNH).

**ETYMOLOGY:** Formed from *anti*, Greek for “opposite,” and *tormentum*, from *A. tormentum*. In reference to the chiral variance of the inner paraphyses of this species, as compared to *A. tormentum*.

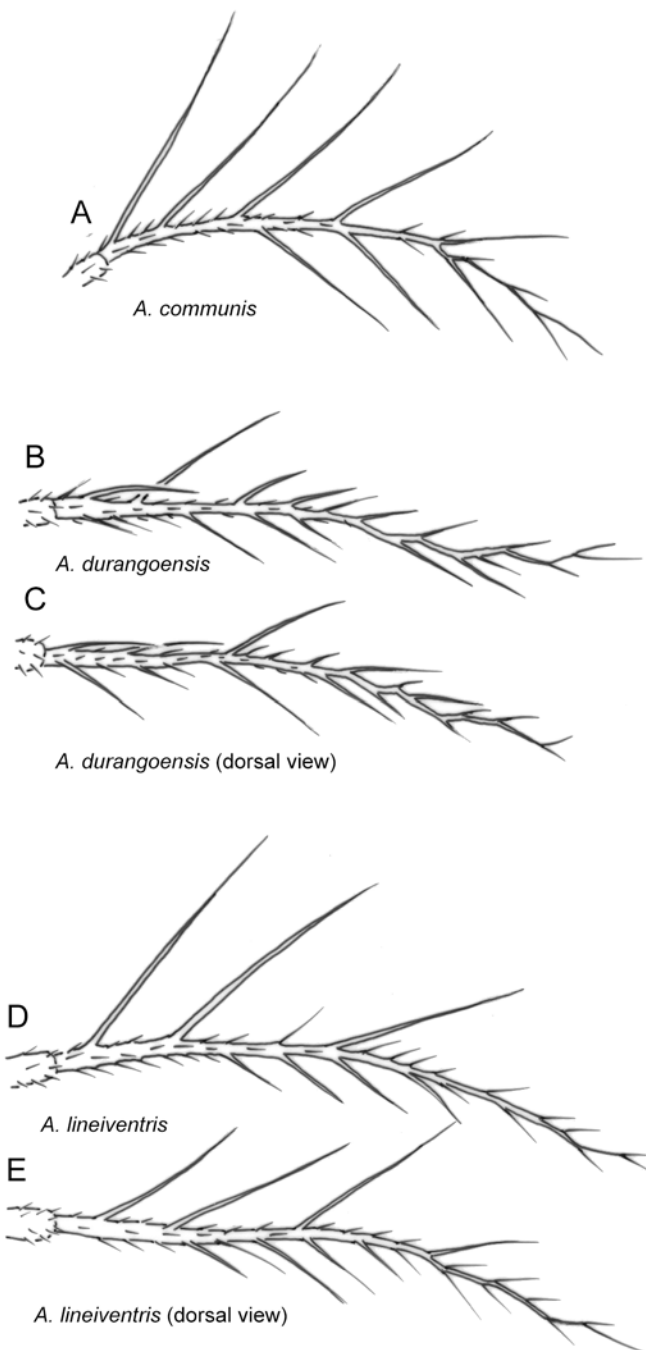


FIG. 11. Aristae, *A. alboguttata* species group. **A.** *A. communis* Chen and Steyskal. **B–C.** *A. durangoensis*. **D–E.** *A. lineiventris* Máca. Not to same scale.

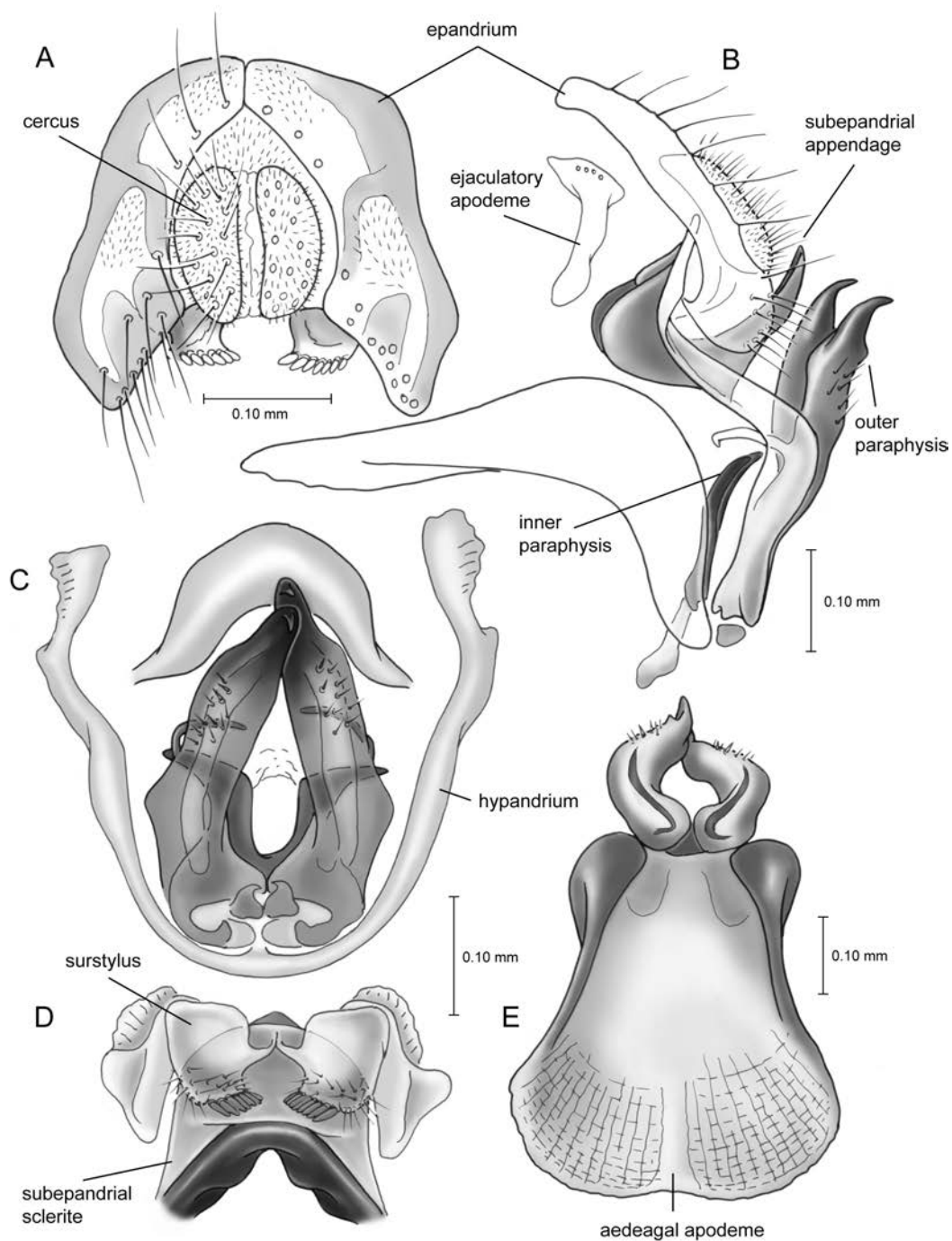


FIG. 12. Male terminalia, *A. communis* Chen and Steyskal. A. Epandrium and cerci. B. Lateral view. C. Ventral view. D. Surstyli and subepandrial sclerite. E. Aedeagal apodeme. (Am 176).

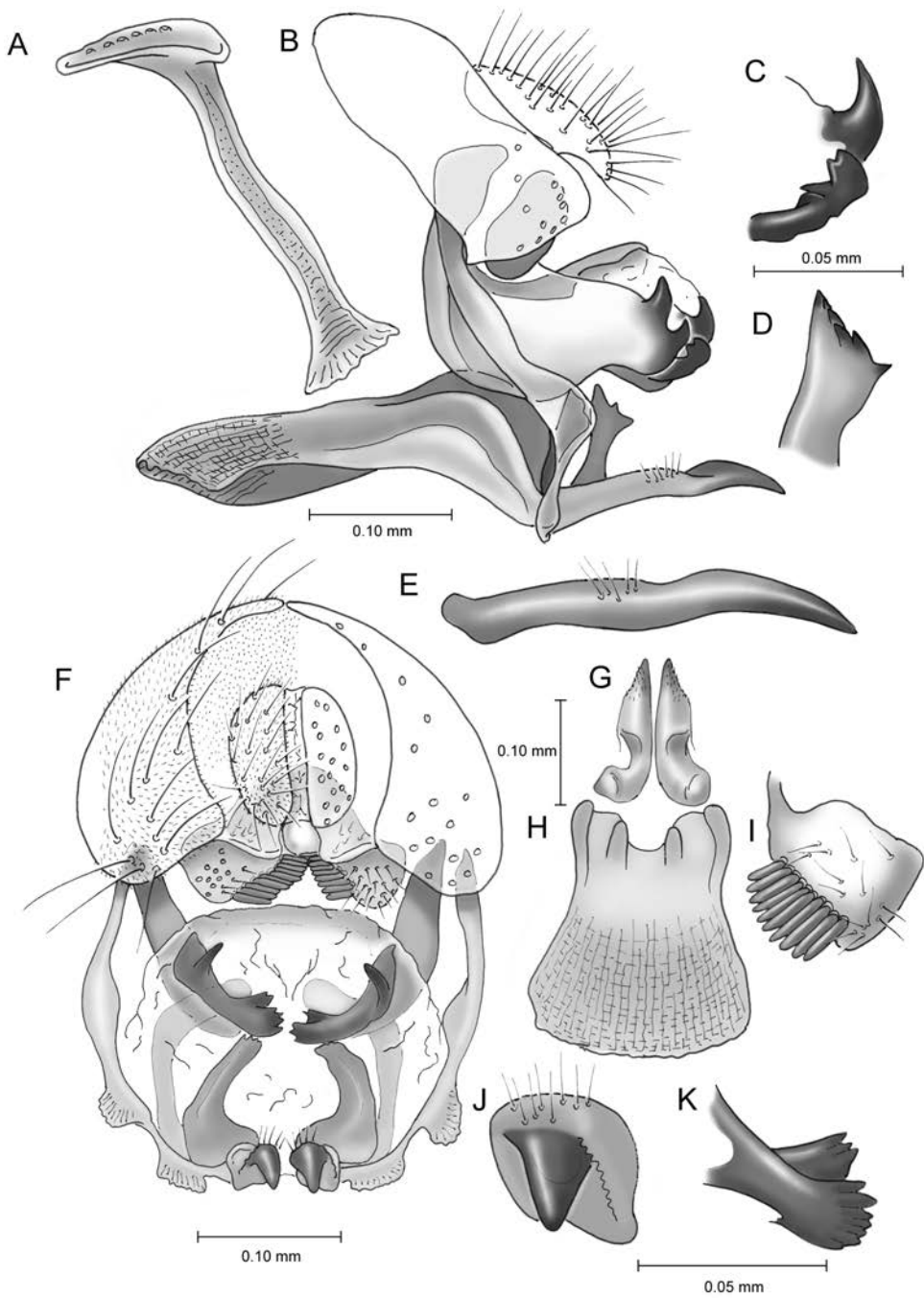


FIG. 13. Male terminalia, *A. durangoensis*. A. Ejaculatory apodeme. B. Lateral view. C. Subepandrial appendage, distal margin. D. Inner paraphysis, apex. E. Outer paraphysis, entire. F. Posterior view. G. Outer paraphyses, ventral view. H. Aedeagal apodeme. I. Surstylus. J. Outer paraphysis, distal end (posterior view). K. Subepandrial appendage. (Am 1520, holotype).

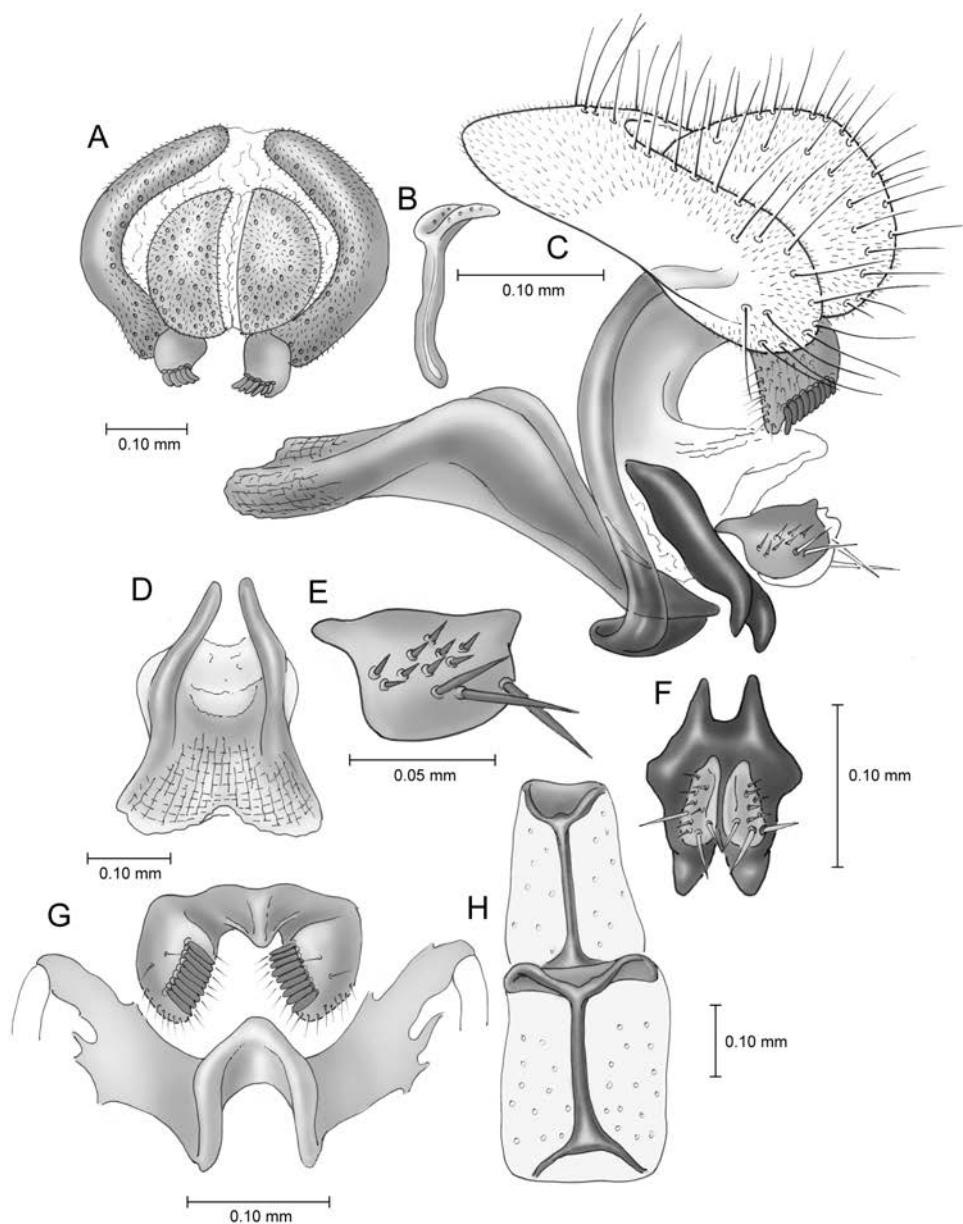


FIG. 14. Male terminalia, *A. lineiventris* Máca. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Aedeagal apodeme. **E.** Outer paraphysis, lateral. **F.** Inner paraphysis (dark) and outer paraphyses, dorsal view. **G.** Surstyli and subepandrial sclerite. **H.** Male sternites 6 (above) and 5 (below). (Am 749).

**DISTRIBUTION:** This species is known only from the sky islands and mountains of south-western Arizona and central New Mexico.

**COMMENTS:** *Amiota antitortum* is very closely related to *A. tortum*, a species with

a similar distribution and often collected in the same series. In this case, each species represents a mirror image of the other in regard to the inner paraphysis, the only instance in this study when chirality was expressed in

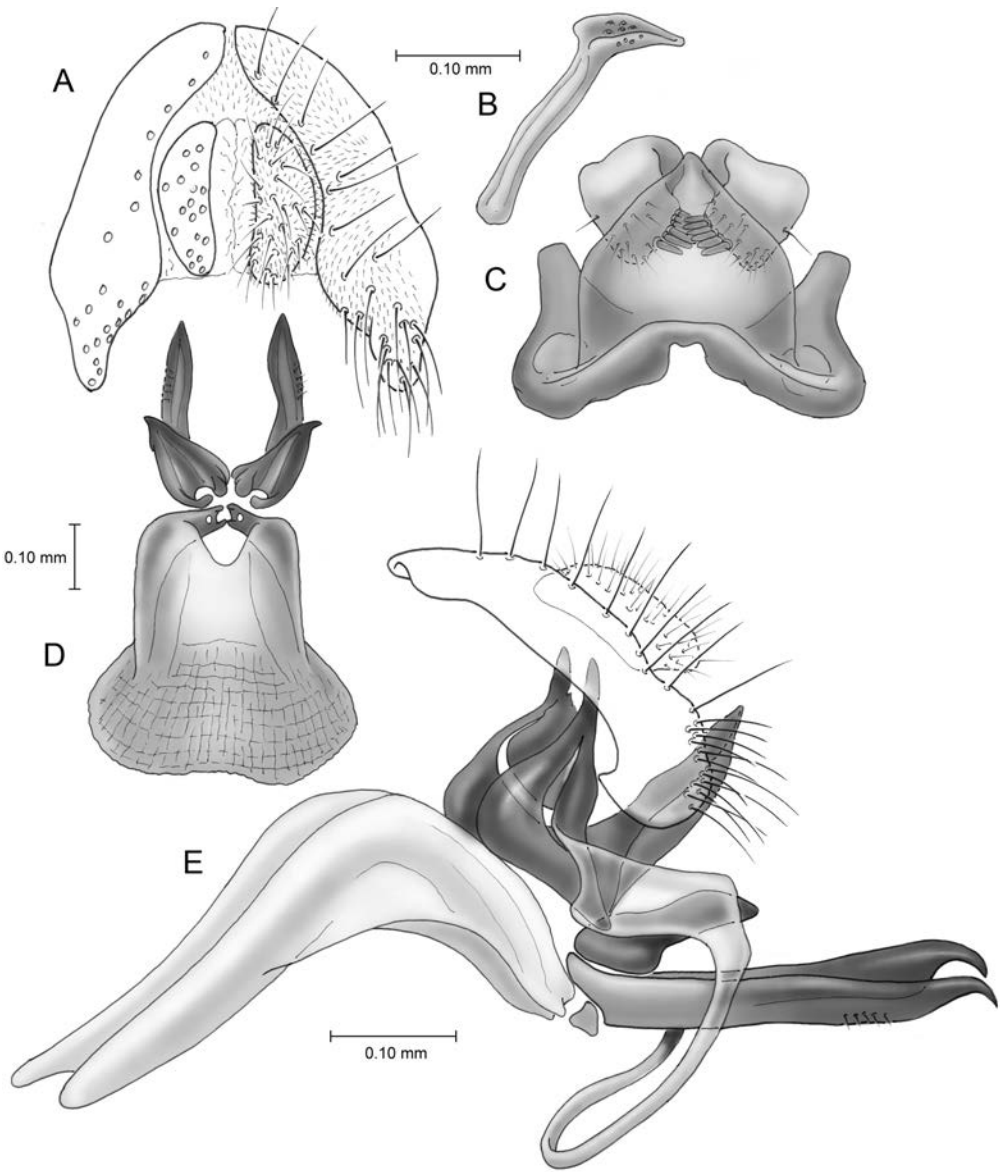


FIG. 15. Male terminalia, *A. steyskali* Máca. A. Epandrium and cerci. B. Ejaculatory apodeme. C. Surstyli and subepandrial sclerite. D. Dorsal view. E. Lateral view. (Am 25).

more than one structure. *Amiota antitormen-*  
*tum* is easily separated by the distinctive  
forked structure with close and nearly parallel  
spines, which are oriented to the right side of  
the fly. This species exhibits the characteristic  
behavior of attraction to the eyes and face  
common to many *Amiota*.

*Amiota brayi*, sp. nov.

Figures 16C–D, 19B, 21, 83B

DIAGNOSIS: Small fly (ThL 1.05–1.17 mm),  
dark brown; cheek very narrow (EL/CW  
20.30–31); frons narrow (FL/FW 0.80–0.91),  
nearly black; male genitalia complex, relatively

small; cercus long, pendulous; outer paraphysis virtually symmetrical, broad and laterally flattened (no large, perpendicular spine present), preapical dorsal claw long, strongly curved, and sclerotized, extending slightly beyond tip of outer paraphysis; inner paraphyses composed of 2 lobes, asymmetrical, with 5 sclerotized, curved, interdigitate spines; posterior lobe with 3 spines, pointed right; anterior lobe with 2 spines, pointing left.

**DESCRIPTION:** Small fly (ThL 1.05–1.17 mm), dark brown, legs light yellow. Cheek very narrow (EL/CW 20.30–31), yellow to brown. Katapisternum lighter than remaining pleuron. Frons narrow (FL/FW 0.80–0.91), black, rather shiny. Facial marking small, width 0.3× length. Palp yellow. Arista: Very long, plumose; longest branch D2; A.R. 0.51; 5 long dorsal, 2 long ventral branches, none pointed mediad/laterad; arista trunk with medium microtrichia along most of length. Male genitalia: Epandrium dorsally complete, fused at midline and grading into membrane surrounding cercus. Cercus long, pendulous, dorsally grading into surrounding membrane (other margins discrete); cerci occupy most of space surrounded by epandrium. Surstylus roughly oval shaped, middle region with scattered setulae along prensisetae margin, finer setulae near proximal end; 7 prensisetae, apices blunt, smaller medially; prominent fingerlike process adjacent to most lateral prensiseta, originating anteriorly to prensisetae, covered in setulae. Subepandrial sclerite a narrow, transverse strip; subepandrial appendage absent. Outer paraphysis symmetrical, long, slender, laterally flattened (no large, perpendicular spine present); distal end rounded, with several scattered sensilla; preapical dorsal claw heavily sclerotized, long and curved (extended nearly to tip of paraphysis). Inner paraphyses composed of 2 lobes; asymmetrical, grading into outer paraphysis, with 5 sclerotized, curved, interdigitate spines; posterior lobe with 3 spines; anterior lobe with 2 spines, pointing left. Aedeagal apodeme wide, nearly as wide as long; distal end widely flared,

distal lobes forming angled joints with midsection, deep concave depression on distal end; strong flanges running along lateral margins to base. Hypandrium simple, U-shaped, thickness consistent. Ejaculatory apodeme small, length 0.5× that of the epandrium. Head and thorax measurements: (n = 5; Am 185, 322, 400, 646, 1226) FL/FW 0.86 (0.80–0.91), EL/EW 1.31 (1.22–1.146), EL/CW 28.36 (20.30–31), FML/FMW 0.33 (0.30–0.41), PR/RR 0.53 (0.45–0.60), ThL 1.12 (1.05–1.17 mm).

**TYPE MATERIAL:** **Holotype:** male: ARKANSAS: Logan Co. Magazine Mtn., [35.167210, -93.644199], 2750 ft., D. Grimaldi, VII/6/92, Am 322, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** ARKANSAS: Logan Co. Magazine Mtn., 2750 ft., D. Grimaldi, VII/6/92, 2♂ (Am 344\*, 362\*, AMNH).

**OTHER MATERIAL EXAMINED:** **USA: Illinois:** Hardin Co., Shawnee Nat. For., 37.594631, -88.382478, 2018-08-08, Leg. J.L. Hughes and L.E. Jones, swept around head, 1♂ (Am 645\*, 646\*, AMNH). **Missouri:** Perryville, 1956-07, [collector unknown], 3♂ (Am 184\*, 185\*, 187\*, AMNH). **North Carolina:** Highlands, Wilson's Gap, 3100' 1957-05-25, leg. J.R. Vockeroth, "Paratype," [never published], 1♂ (Am 1376, CNC). **Tennessee:** Great Smoky Mtns. Nat. Park, Husky Gap Trail, 35 40 N, 83 32 "W, 2001-05-30 through 2001-06-04, leg. J. Skevington and J.M. Cumming, Malaise Trail, 1♂ (Am 1226, CNC). **Virginia:** Prince William Co., 0.5 km NE Thorofare Gap, vic. Haymarket, 1966-06-25, leg. P.H. Arnaud Jr., 1♂ (Am 400\*, CAS).

**ETYMOLOGY:** Named for James R. Bray, Jr. (1968–), bryologist extraordinaire and professor of biology at Blackburn College in Carlinville, IL. In appreciation for serving as mentor of the first author while he was an undergraduate at Blackburn, and for introducing him to taxonomy and botany. James Bray and *A. brayi* are both native to the Ozarks.

**DISTRIBUTION:** *Amiota brayi* inhabits a small band stretching from the Ozarks to the Mid-Atlantic, although by far most collections have been centered in the Ozarks and adjacent southern Illinois.

COMMENTS: This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

***Amiota cruciatum*, sp. nov.**

Figures 16E–F, 19C, 22, 83C

DIAGNOSIS: Small fly (ThL 1.11–1.24 mm), dark brown; male genitalia very lightly sclerotized with exception of inner and portion of outer paraphyses; inner paraphyses asymmetrical and composed of 2 lobes, each lobe with 3 spines, anterior lobe of inner paraphyses bearing 2 spines, forming a forked structure, spines close and nearly parallel; aedeagal apodeme slightly curved, lightly sclerotized, the distal end squared; similar to *A. tormentum* and *A. antitortum*, but male genitalia in *A. cruciatum* much more lightly sclerotized and differing in shape of aedeagal apodeme.

DESCRIPTION: Small fly (ThL 1.11–1.24 mm), dark brown, grading lighter ventrally; legs yellow. Frons dark brown, nearly black; numerous hairs on frons, scattered and golden. Characteristic markings on face and postpronotal lobe faded. Haltere bright lemon yellow. Palp yellow. Arista: Medium plumose; longest branch D2; A.R. 0.42; 4 long and 1 short dorsal, 2 ventral branches, none pointed mediad/laterad; arista trunk with short microtrichia along entire length. Male genitalia: Epandrium split medially, distinct from surrounding membrane; numerous setae clustered on ventral end, single line of setae ascending dorsally toward apex. Cercus somewhat pendulous, long, grading dorsally into surrounding membrane. Surstylus with 11 prenisetae, apices blunt, closely spaced; lobe arising anterior to most lateral prenisetae, extending ventrally. Subepandrial sclerite simple; no subepandrial appendage present, just a weakly sclerotized, narrow shelf. Outer paraphysis laterally flattened; distal end rounded with a sclerotized, preapical-dorsal claw, pointed posteriorly; ca. 20 scattered setulae on lateral surface; 2 heavily sclerotized spines proximal to distal claw,

perpendicular to paraphysis, several sensilla between proximal spines and inner paraphysis. Inner paraphysis consisting of 2 lobes, heavily sclerotized, arrayed with asymmetrical spines; anterior lobe with 3 spines, the 2 anteriormost spines forming a forked structure, spines close and nearly parallel; posterior lobe with 3 spines. Aedeagal apodeme not strongly sclerotized, almost translucent, distal end square shaped and lightly concave, the base 3/4 the length. Hypandrium simple, thickness even throughout. Ejaculatory apodeme very small, 1/3 the length of the epandrium. Head and thorax measurements: (n = 5; Am 76, 98, 105, 120, 122) FL/FW 0.85 (0.75–1), EL/EW 1.48 (1.43–1.55), EL/CW 16.79 (12.40–20.33), FML/FMW 0.33 (0.28–0.40), PR/RR 0.6 (0.45–0.77), ThL 1.16 (1.11–1.24 mm).

TYPE MATERIAL: **Holotype:** male: Ramsey Canyon, Huachua Mts., Arizona, [31.448243, -110.307832], MR Wheeler and WB Heed, June 1951, 2157:11, Am 97, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** Ramsey Canyon, Huachua Mts., Arizona, MR Wheeler and WB Heed, June 1951, 2157:11, 3♂ and 3♀ (Am 79, 85, 99\*, 104, 105\*, 106\*, 107, AMNH)

OTHER MATERIAL EXAMINED: **USA: Arizona:** Ramsey Canyon Huachua Mts., 1951-06, leg. M.R. Wheeler and W.B. Heed, 2157.11, 8♂ and 6♀ (Am 80\*, 81, 82, 83\*, 84, 86, 87\*, 88\*, 96, 98, 100, 101\*, 107\*, 108, AMNH); 1951-06, leg. M.R. Wheeler and W.B. Heed, 1♂ and 1♀ (Am 118, 119, AMNH); 1951-06-15, [no collector], 1♂ and 2♀ (Am 90, 91, 95\*, AMNH); Roundup Campground, Madera Canyon Rec. Area Coronado Nat'l. For., 1951-06-16 through 1951-06-17, leg. W.B. Heed and M.R. Wheeler, 2160.8, 1♂ and 1♀ (Am 74\*, 75\*, AMNH); Rustler Park Camp, 1951-06, leg. M.R. Wheeler and W.B. Heed, 2155.10, 1♂ (Am 120\*, AMNH); 20 mi. SW Safford, 1951-06, leg. W.B. Heed and M.R. Wheeler, 1♂ and 1♀ (Am 122\*, 123\*, AMNH). **New Mexico:** Mill Canyon Magdalena Mts., S. Magdalena, 1951-06-26 through 1951-06-27, leg. M.R. Wheeler and W.B. Heed, 2170.9, 1♂ and 1♀ (Am 76\*, 77, AMNH).

**ETYMOLOGY:** From *cruciat*, Latin for “tortured.” Used as a noun in apposition in reference to the mass of twisting spines of the inner paraphyses, which resemble an instrument of torture.

**DISTRIBUTION:** *Amiota cruciatum* is found in the mountainous regions of Arizona and New Mexico.

**COMMENTS:** It is unknown whether *Amiota cruciatum* is attracted to the eyes and face as other *Amiota*.

*Amiota incurva*, sp. nov.

Figures 17A–B, 19D, 23, 84A

**DIAGNOSIS:** Medium-sized fly (ThL 1.28–1.44 mm), black; arista long, plumose; outer paraphysis large, laterally flattened, with apical hook curving inward, proximal appendage long, heavily sclerotized, perpendicular to paraphysis, forming a “0” in dorsal/ventral views; inner paraphyses symmetrical, each composed of a lobe with 3 spines, all curving inward medially, one spine overlaying the others and pointing anteriorly.

**DESCRIPTION:** Medium-sized fly (ThL 1.28–1.44 mm), black; legs light yellow. Frons black dorsally, fading to brown ventrally. Facial marking large, depth 0.5× width, semicircular. Cheek whitish gray posteriorly. Palp brown. Arista: Long, plumose; longest branch D1; A.R. 0.53; 4 long dorsal, 2 long ventral branches, none pointed mediad/laterad; arista trunk with short microtrichia along entire length. Male genitalia: Epandrium complete at dorsal midline, this margin graded into membrane below. Cercus large, slightly crescentic, dorsally grading into membrane and epandrium; occupying most of space surrounded by epandrium. Surstylus oval; 10 prenisetae, apices blunt, closely arranged, comblike; with large, lateral fingerlike lobe adjacent to, and extending beyond, prenisetae; scattered setulae along distal margin and process. Subepandrial sclerite a simple plate, without a subepandrial appendage. Paraphyses symmet-

rical or nearly so, heavily sclerotized. Outer paraphysis large, laterally flattened, with apical hook curving inward; proximal appendage long, perpendicular to paraphysis, forming a “0” in dorsal/ventral views. Inner paraphyses symmetrical, each composed of a lobe with 3 spines, all curving inward medially; one spine overlaying the others and pointing anteriorly. Aedeagal apodeme large, midsection and base wide and quadrangular (not constricted), length 1.5× width, slightly curved in lateral view, distal end slightly flared beyond midsection with shallow emargination. Hypandrium evenly narrow, U-shaped, small bulging gonopod in posterior view. Ejaculatory apodeme not studied. Head and thorax measurements: (n = 5; Am 377, 440, 713, 716, 1425) FL/FW 0.84 (0.75–0.96), EL/EW 1.32 (1.26–1.40), EL/CW 21.81 (12.80–38), FML/FMW 0.38 (0.36–0.42), PR/RR 0.53 (0.41–0.60), ThL 1.38 (1.28–1.44 mm).

**TYPE MATERIAL:** **Holotype:** male: Sunnyside Canyon, Huachuca Mts., Ariz., [31.339651, -110.491677], VII-9-40, D.E. Hardy, Am 440, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH).

**OTHER MATERIAL EXAMINED:** **Mexico: Baja California:** Sierra La Laguna, 1770–1850m, 1977-08-29, leg. E. Fisher and R. Westcott, collected from flight trap near stream, 1♂ (Am 377\*, CAS). **Chiapas:** 20–25 mi NE Huixtla, 3000', 1969-06-01, leg. H.J. Teskey, 1♂ (Am 1425\*, CNC); 20–25 mi N Huixtla, 3000', 1969-06-01, leg. B.V. Peterson, 1♂ (Am 1266\*, CNC). **Hidalgo:** Jacala 7 mi NE, 4600', 1954-07-27, leg. J.G. Chillcott, “Holotype” [not published], 1♂ (Am 1374\*, CNC). **USA: Arizona:** Cochise Co., campground nr. SWRS, 31.872506, -109.233923, 2019-07-19, leg. L.E. Jones and J.L. Hughes, swept around head, 1♂ (Am 713\*, AMNH); Cochise Co., Vicinity of SWRS, 31.882018, -109.206636, 2019-07-18, leg. L.E. Jones and J.L. Hughes, swept around head, 1♂ (Am 716\*, AMNH); Madera Cyn, Santa Rita Mts., 4–6000', 1962-07-12, leg. H.E. Milliron, 1♂ (Am 1213\*, CNC).

**ETYMOLOGY:** Formed from *in* and *curva*, Latin in feminine form for “curving inward.” In

reference to the spines of the paraphyses which all curve medially.

**DISTRIBUTION:** *Amiota incurva* has a large distribution, from southeastern Arizona in the United States, throughout Mexico, from Baja California to Chiapas.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota mariae* Máca, 2003

Figures 17C–D, 19E, G, 24, 84B

*Amiota mariae* Máca, 2003: 268 (original description); Brake and Bächli, 2008: 253 (world catalog).

**DIAGNOSIS:** Medium to large fly (ThL 1.44–1.59 mm); dark brown, almost black; dorsal half of frons black, ventral half of frons medium brown; outer paraphysis laterally flattened, with preapical dorsal hook that protrudes beyond apex of paraphysis, proximal spine perpendicular to paraphysis; inner paraphyses asymmetrical, heavily sclerotized, with 2 hooklike lobes directed laterally in opposite directions, each of these inner paraphyses with 4 spines.

**DESCRIPTION:** Medium to large fly (ThL 1.44–1.59 mm), dark brown almost black, grading slightly lighter ventrally, legs yellow. Katepisternum lighter than remaining pleuron. Dorsal half of frons and orbital plate black, ventral half of frons medium brown. Eyes bright cherry red to wine colored. Facial marking small, depth 0.3× width. Cheek of moderate depth (EL/CW 16–20.75), yellowish. Palp yellow. Arista: Long, plumose; longest branch D3; A.R. 0.46; 4 long dorsal branches, 2 long and 1 short ventral branches; D2 pointed laterad, V2 pointed mesad; arista trunk with medium-length microtrichia over entire length. Male genitalia: Epandrium not split medially, ventral margin in this area discrete; ventral third of epandrium with clustered setae, single line of setae in line ascending dorsally to apex. Cercus almost crescentic, margins discrete

from surrounding membrane. Surstylus nearly triangular; 14 prenisetae, apices blunt, nearly of equal size, comblike; distal half with scattered setulae; small, slender lobe arising behind apical most preniseta. Subepandrial sclerite with large, broad subepandrial appendage deeply notched at base, apex pyramidal, roughly scoop shaped. Outer paraphysis long, heavily sclerotized, laterally flattened, the distal half with 6–8 scattered sensilla; vertical proximal spine 1/3 from base, perpendicular to paraphysis; slender preapical dorsal claw present, extended beyond apex of paraphysis. Inner paraphyses complex, asymmetrical, heavily sclerotized; with 2 hooklike lobes directed laterally in opposite directions, each with small spine; each of these paraphyses with 4 spines, as figured. Aedeagal apodeme with constriction in middle, base nearly as wide as the distal end, width 3/4 times the length, distal end flared, less sclerotized than the basal half. Hypandrium simple, of even thickness, nearly V-shaped in ventral view. Ejaculatory apodeme short, 1/2 the length of epandrium. Head and thorax measurements: (n = 5; Am 389, 603, 640, 692, 705) FL/FW 0.77 (0.72–0.82), EL/EW 1.39 (1.28–1.57), EL/CW 18.23 (16–20.75), FML/FMW 0.38 (0.30–0.65), PR/RR 0.53 (0.45–0.58), ThL 1.51 (1.44–1.59 mm).

**TYPE MATERIAL:** **Holotype:** male: As reported by Máca (2003): “Canada, Quebec: Lac Roddic, 16 km S Maniwaki, 23.6.1991, leg. M. Barták” [not examined]. Coll. J. Máca, to be deposited in National Museum of Prague, Czech Republic (NMPC).

**OTHER MATERIAL EXAMINED:** **Canada:** **Ontario:** Chaffey's Locks Queens Univ. Bio. Stn., 1980-09-12, leg. S.A. Marshall, tree wound, 3♂ (Am 603\*, 612, 636\*, DEBU); Ferris Provincial Park, Drumlin Trail, 2003-05-01 through 2003-05-15, leg. P.D. Careless, 1♂ (Am 628\*, DEBU); Noelville, 1974-08-10, leg. R.E. Roughley, 1♂ (Am 549\*, DEBU); Ottawa, 1946-06-12, leg. G.E. Shewell, “Paratype,” [never published], 1♂ (Am 1365, CNC); 1989-09-20, leg. J.R. Vockeroth, 1♂ (Am 1236\*, CNC); 1989-09-21, leg. J.R. Vockeroth, 1♂ (Am 1235\*, CNC); 1991-08-31, leg. J.R. Vockeroth, Ex

damp shaded ditch in Acer wood, 1 ♂ (Am 1255\*, CNC); Ottawa, Lwr. Beechwood Cem., 1999-09-03, leg. J.R. Vockeroth, Acer wd. Aerial sweep, 1 ♂ (Am 1249, CNC); Ottawa, Monfort Hosp. wood, 1993-08-07, leg. J.R. Vockeroth, aerial sweep, 1 ♂ (Am 1247, CNC); 1993-08-16, leg. J.R. Vockeroth, aerial sweep, 1 ♂ (Am 1276, CNC); Ottawa, Rockcliffe, Rockwood, 2007-07-18, leg. J.R. Vockeroth, 7pm, aerial sweep, CNC Diptera #160444, 1 ♂ (Am 1283\*, CNC); Purpleville, 1961-07-25, leg. G.K. Morris, 1 ♂ (Am 555\*, DEBU); Rattlesnake Pt. Conservation Area, 43 28 N, 79 55 W, forest, 2010-06-19, leg. B.J. Sinclair, 1 ♂ (Am 1280\*, CNC). **Quebec:** Abbotsford, 1936-08-30, leg. G.E. Shewell, "Paratype - No. 8017 Paratype," [not published], 9 ♂ (Am 1364\*, 1366-1373, CNC); 1937-09-30, leg. G.E. Shewell, "Paratype," [not published], 1 ♂ (Am 1363\*, CNC); Duncan Lake nr. Rupert, 1988-08-08, leg. J.F. McAlpine, hovering at ear, 1 ♂ (Am 1408\*, CNC); Gatinéau Co., Marsham Twp., Hilltop near Duncan Lake, 45 40 53 N, 76 03 01 W, 2001-07-21, leg. J and A Skevington, D.M. Wood, 1 ♂ (Am 1278\*, CNC); Gatineau Park, Meech Trail, 45 31 37 N, 75 54 43 W, 2011-07-09, leg. O. Lonsdale, 1 ♂ (Am 1240\*, CNC); Gatineau Park, Waterfall trail, 45 28 42 N, 75 51 6 W, 2013-09-01, leg. J.M. Cumming, CNC287593, 1 ♂ (Am 1199\*, CNC); Old Chelsea, 1955-09-20, leg. J.F. McAlpine, 1 ♂ (Am 1387\*, CNC); Old Chelsea, Summit King Mtn., 1965-06-20, leg. D.M. Wood, 9 ♂ (Am 1295\*, 1460, 1463\*, 1472\*, 1473, 1477, 1537\*, 1538, 1540\*, CNC). **USA: Arkansas:** Logan Co., Magazine Mt., 2750 ft., 1992-07-06, leg. D. Grimaldi, 1 ♂ (Am 337\*, AMNH). **New York:** Niagara Falls, 1911-09-04, leg. M.C. van Duzee, 1 ♂ (Am 389\*, CAS); **Michigan:** Marquette Co., Huron Mtns., Huron Mtn. Club property vicinity, 46.874950, -87.891717, 2018-07-06 through 2018-07-12, leg. T. Werner, 40 ♂ (Am 679\*, 681\*, 682\*, 684\*, 686-702\*, 704-708\*, 727\*, 731\*, 732\*, 1054, 1055, 1061, 1067, 1068, 1074\*, 1077, 1079-1081, 1088, AMNH). **Virginia:** Giles Co., Cascade Falls, 2001-05-19, leg. O. Lonsdale, 37 21 0 N, 80 36 30 W, debu01007851, 1 ♂ (Am 640\*, DEBU); Floyd Co., #1, Mile 175.4 Blue Ridge Parkway, 1960-06-23, leg. G.W. Byers, 1 ♂ (Am 436\*, SEMC).

**DISTRIBUTION:** This species was originally described from a single specimen collected in Canada (Quebec). It seems primarily abundant in the Great Lakes Region (Michigan and Ontario), although single specimens have been

found in the Mid-Atlantic and the Ozarks, suggesting a larger range.

**COMMENTS:** *Amiota mariae*, as treated here, may constitute a species complex comprised of several species. Dissections reveal not only chiral variants, but varying degrees of sclerotization among specimens. External characters include eyes varying from bright cherry red to wine colored as well as variation in size and number of preapical and apical setae on the legs. DNA barcodes may be useful in helping to determine this. This species exhibits the characteristic behavior of attraction to the eyes and face common in many *Amiota*.

*Amiota texas*, sp. nov.

Figures 17E-F, 19F, 25, 84C

**DIAGNOSIS:** Medium-sized fly (ThL 1.21 mm), dark brown; epandrium dorsally complete, ventral lobes curved inward; cerci large; aedeagal apodeme small, translucent, and poorly developed; outer paraphysis linear, well developed, laterally flattened; large subapical sclerotized spine, perpendicular to paraphysis, distal tip with irregular serrations; inner paraphyses highly asymmetrical, composed of 2 lobes, anterior most lobe with 3 heavily sclerotized spines, posterior lobe with 4 spines.

**DESCRIPTION:** Medium-sized fly (ThL 1.21 mm), dark brown, legs dark yellow. Frons dark brown, lighter ventrally. Facial marking small, width 0.3× length. Cheek small (EL/CW 34), yellowish. Palp dark brown. Arista: Medium, plumose; longest branch D4; A.R. 0.41; 4 long dorsal, 2 long ventral branches, none pointed mediad/laterad; arista trunk with medium microtrichia along whole length. Male genitalia: Epandrium narrow (especially dorsally), dorsal bridge complete though faint, nearly grading into surrounding membrane, with prominent ventral lobes that turn inward. Cercus large, oval, distinct from surrounding membrane. Surstylus rounded, 14 prensisetae, apices blunt, all of equal size and spacing; short lobe arising behind ven-

tralmost prensiseta (vs. distal to prensisetae); many long, prominent setulae around midregion, forming row underneath prensisetae. Outer paraphysis linear, well developed, laterally flattened, each with a medial unsclerotized spine on distal end, facing posteriorly; large, sclerotized spine arising subapically, perpendicular to paraphysis, distal tip with irregular serrations. Inner paraphyses highly asymmetrical; composed of 2 lobes, anterior most lobe with 3 heavily sclerotized spines, posterior lobe with 4 spines; forming a mass of twisting spines. Aedeagal apodeme small, translucent, poorly developed. Hypandrium U-shaped, simple. Ejaculatory apodeme not studied. Head and thorax measurements: ( $n = 1$ , Am 438) FL/FW 0.92, EL/EW 1.30, EL/CW 34, FML/FMW 0.25, PR/RR 0.54, ThL 1.21 mm.

TYPE MATERIAL: **Holotype:** male: Davis Mts, Tex., [30.745919, -104.088850], IV-17-54, LD Beamer, Am 438, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: Named for Texas (United States), the state of the type locality. Used as a noun in apposition.

DISTRIBUTION: *Amiota texas* is currently only known from west Texas.

COMMENTS: This species is similar to *Amiota wheeleri*, also from West Texas. It is likely that this holotype is of a young individual, not fully sclerotized, but given the numerous differences in the paraphyses it is reliably distinct from that species.

### *Amiota tormentum*, sp. nov.

Figures 18A–B, 19H, 26, 85A

DIAGNOSIS: Small to medium-sized fly (ThL 1.10–1.30 mm), nearly black; arista with branches sparse and shorter than in *A. antitortum*; inner paraphysis with asymmetrical spines in mirror image of *A. antitortum*, anteriormost

spines forming forked structure, spines close and nearly parallel, oriented to the left side, other differences with *A. antitortum* listed under that species; also similar to *Amiota cruciatum*, but *A. cruciatum* differing by the smaller and less sclerotized male genitalia.

DESCRIPTION: Small to medium-sized fly (ThL 1.10–1.30 mm), nearly black, slightly lighter ventrally; legs yellow. Frons black, dark brown just above ptilinal margin. Cheek small, rather bronze. Palp brown. Arista: Medium plumose; longest branch D1; A.R. 0.33; 4 long dorsal, 1 long ventral branch, none pointed mediad/laterad; arista trunk with medium microtrichia along most of its length. Male genitalia: Epanthrium fused, indistinct, not grading into surrounding membrane. Cercus distinct, oval shaped, not parallel to neighboring cercus; dorsal membranous region above large, triangular. Surstylus almost triangular, covered in setulae, especially the lateral half; 9 prensisetae, apices blunt, closely arranged; small fingerlike projection along most lateral prensisetae. Subepandrial sclerite broad, almost trapezoidal, base deeply notched. Outer paraphysis laterally flattened, symmetrical; distal end rounded, with small heavily sclerotized preapical dorsal claw, arising internally; large spine proximal to distal end, perpendicular to paraphysis, curving slightly medially. Inner paraphyses consisting of 2 lobes; anterior lobe with 4 spines; 2 lateral spines, each crossing, oriented in opposite directions; anteriormost spines forming a forked structure, close, nearly parallel, projecting to the left side; posterior lobe consisting of 4 spines; 2 large, opposite, lateral spines; prominent spine bent at distal end, other 2 spines smaller, arising near bases of larger lateral spines, oriented in opposite directions. Aedeagal apodeme very straight, not curving; long, width  $0.6\times$  length; distal end not widely flared, shallowly notched. Hypandrium simple, U-shaped, of relatively uniform thickness. Ejaculatory apodeme very small, slightly longer than  $0.25\times$  length of the epanthrium. Head and thorax measurements: ( $n = 5$ ; Am 53, 56, 113, 451, 459) FL/FW 0.83 (0.70–0.96), EL/

EW 1.39 (1.27–1.56), EL/CW 21.06 (18.33–22), FML/FMW 0.32 (0.26–0.36), PR/RR 0.53 (0.50–0.66), ThL 1.24 (1.10–1.30 mm).

**TYPE MATERIAL:** **Holotype:** male: 12 mi N. Silver City, N.M. [New Mexico], [33.019248, -108.263582], MR Wheeler, Aug 1950, 2051, Am 53, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratype:** 12 mi N. Silver City, N.M. [New Mexico], MR Wheeler, Aug 1950, 2051, 1 ♂ (Am 56\*, AMNH).

**OTHER MATERIAL EXAMINED:** **Arizona:** Cave Creek nr. Portal, 1951-06, leg. M.R. Wheeler and W.B. Heed, 3 ♂ (Am 111\*, 113\*, 115\*, AMNH). **New Mexico:** Tajique, 1940-06-25, leg. D.E. Hardy, 1 ♂ (Am 459\*, SEMC); 1941-06-25, leg. R.H. Beamer, 1 ♂ (Am 451\*, SEMC).

**ETYMOLOGY:** From *tormentum*, Latin for “torment,” in reference to the mass of twisting spines of the male genitalia.

**DISTRIBUTION:** This species is known only from the sky islands and mountains of southwestern Arizona and central New Mexico.

**COMMENTS:** *Amiota tormentum* is very closely related to *A. antitormentum*, a species with a similar distribution and often collected in the same series. In this case, each species represents a mirror image of the other with regard to the inner paraphysis, the only instance in this study when chirality was found expressed in more than one structure. *Amiota tormentum* is easily separated by the distinctive forked structure with close and nearly parallel spines, which are oriented to the left side of the animal, and by the arista (with fewer, shorter branches). It is unknown whether this species is lachryphagous, but due to its very close relationship with *Amiota antitormentum*, which is lachryphagous, it can safely be assumed to be so as well.

*Amiota wheeleri*, sp. nov.

Figures 18C–D, 19I, 27, 85B

**DIAGNOSIS:** Medium-sized fly (ThL 1.18 mm), dark brown to somewhat black dorsally; outer

paraphysis long, laterally flattened, with apical hook, large dorsal spine perpendicular to paraphysis, left spine long, tapered to point, [right spine broken in holotype]; inner paraphyses asymmetrical, heavily sclerotized, each with 3 large, twisting spines; aedeagal apodeme narrow, nearly flat, distally flared, distal margin deeply notched.

**DESCRIPTION:** Medium-sized fly (ThL 1.18), dark brown, grading black dorsally, legs yellow. Frons black. Characteristic markings faded [likely due to preservation of holotype]. Palp yellow. Tergites 1 and 2 lightly colored. Arista: long, plumose; longest branch D1; A.R. 0.48; 3 long dorsal, 2 long ventral branches, none pointed mediad/laterad; arista trunk with short to medium microtrichia, including on apical half. Male genitalia: Epandrium with narrow dorsal connection, dorsal incision indistinct, grading into surrounding membrane; setae clustered on ventral lobe, with a line of single setae ascending dorsally to apex. Cercus long, oval, distinct from surround membrane. Surstylus wide, paddle shaped, middle region and ventral margin with scattered setulae; 13 prenisetae, apices blunt, of equal size; fingerlike lobe adjacent to lateralmost preniseta. Subepandrial sclerite broad, wide, prominent notch creating posterior apex, without any appendage. Outer paraphysis long, laterally flattened, distal end rounded; heavily sclerotized, preapical, curved dorsal claw, attached on inner surface of paraphysis, sensilla lining rounded margin at distal end; large proximal spine, perpendicular to paraphysis, heavily sclerotized, oriented dorsally; left appendage slightly sinuous, tapering to point; right appendage shorter, the distal end serrated (possibly broken); proximal to long appendages, 7–8 sensilla on lateral side as well as dorsally. Inner paraphyses asymmetrical, heavily sclerotized; each with 3 large, twisting spines. Aedeagal apodeme long and narrow, the distal end widely flared, deeply notched, width at apex lobes 0.7× length of aedeagal apodeme. Hypandrium U-shaped, simple, lateral arms thick in ventral. Ejaculatory apodeme not examined. Head and thorax measurements: (n = 1, Am 73) FL/FW 0.76, EL/

EW 1.45, EL/CW 10.16, FML/FMW 0.43, PR/RR 0.77, ThL 1.18 mm.

**TYPE MATERIAL:** **Holotype:** male: 10 mi. N. Ft. Davis, Texas, [30.781638, -103.895047], MR Wheeler, WB Heed, June 1951, "2174.6," Am 73, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** Named for Marshall R. Wheeler (1917–2010), graduate of Blackburn College in Carlinville, Illinois, and professor of biology at the University of Texas at Austin, who collected many specimens used in this revision, and for his many contributions to drosophilid systematics.

**DISTRIBUTION:** *Amiota wheeleri* is currently only known from the mountains of West Texas.

**COMMENTS:** This species is apparently of close relation to *Amiota texas*, which is also found in the mountains of West Texas. The lack of white spots on the holotype is probably due to preservation techniques.

*Amiota zaliskoi*, sp. nov.

Figures 18E–F, 19J–K, 28, 85C

**DIAGNOSIS:** Small to medium-sized fly (ThL 0.98–1.38 mm); dark brown, glossy; facial marking small, width 0.3× length; subepandrial sclerite cantilevered, compartmentalizing surstyli; outer paraphyses laterally flattened, with short subapical dorsal hook and pair of large, symmetrical, dorsomedial spines; inner paraphysis composed of 4 asymmetrical spines, including large, prominent one with preapical tooth, extending over complex.

**DESCRIPTION:** Small to medium-sized fly (ThL 0.98–1.38 mm), almost black, slightly glossy, grading lighter ventrally; legs yellow. Frons black, shiny ventrally, especially ventrolateral corners. Cheek small (EL/CW 9.6–13.75), yellow to brown. Facial marking small, width 0.3× length. Palp brown. Arista: Medium, plumose; longest branch D3; A.R. 0.38; 4 long dorsal, 2 long ventral branches; D4

pointed laterad, V1 mediad; arista trunk with long microtrichia along entire length. Male genitalia: Epandrium fused at midline, this margin faintly grading into surrounding membrane. Cercus long, pendulous, nearly diamond-shaped; dorsal margins grading into surrounding membrane. Surstylus rounded; 11 prenisetae, apices blunt, closely arranged, comblike; distinctive paddle-shaped process, curving dorsomedially, extending beyond prenisetae; distal end of process with rough, textured cuticle; row of setulae along process, curving medially in semicircular pattern to midregion of surstylus. Subepandrial sclerite distinctive; cantilevered, distal corners curving downward slightly; central membrane forming septum, surrounding surstylus. Outer paraphysis long, laterally flattened, distal end rounded; very small preapical dorsal apical hook, arising on mesal surface; 2 large, heavily sclerotized, perpendicular spines present, proximal to preapical dorsal hook, with sensilla between; 4–5 sensilla in row between large spine and inner paraphysis. Inner paraphysis composed of 4 asymmetrical spines; prominent spine, large, with preapical tooth, extending over complex. Aedeagal apodeme slightly longer than wide; distal end only slightly flared, lobes distinct; distal notch very small, shallow. Hypandrium simple, of relatively uniform thickness, anterior end narrowed. Ejaculatory apodeme not studied. Head and thorax measurements: (n = 5; Am 29, 32, 529, 638, 1168) FL/FW 0.77 (0.70–0.85), EL/EW 1.29 (1.17–1.40), EL/CW 11.2 (9.6–13.75), FML/FMW 0.27 (0.24–0.30), PR/RR 0.58 (0.45–0.77), ThL 1.25 (0.98–1.38 mm).

**TYPE MATERIAL:** **Holotype:** male: NEW YORK: Tompkins Co., Texas Hollow, [42.386486, -76.773090], VII/26/83, D. Grimaldi and L.L. Pechuman, flying about head, Am 32, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** NEW YORK: Tompkins Co., Texas Hollow, VII/26/83, D. Grimaldi and L.L. Pechuman, flying about head, 3 ♂ (Am 21, 29\*, 30\*, AMNH).

**OTHER MATERIAL EXAMINED:** **Canada:** **Ontario:** Algonquin Provincial Park, Swan Lake Station, Scott Lake Survey, 1995-05-29 through

1995-06-16, leg. S.A. Marshall, A transect bracket. Pans on debarked snag, 1♂ (Am 576, DEBU). Lambton Co., Port Franks, 1996-08-02, leg. J. Skevington, 1♂ (Am 638\*, DEBU). **Quebec:** Old Chelsea, 1959-09-29, leg. J.R. Vockeroth, 1♂ (Am 1437\*, CNC); 1150', 1966-07-05, leg. D.D. Monroe, 1♂ (Am 1258\*, CNC); 1150', 1966-07-08, leg. D.D. Monroe, 1♂ (Am 1259\*, CNC); 1150', 1966-08-09, leg. D.D. Monroe, 1♂ (Am 1261\*, CNC); Old Chelsea, King Mt., 1969-08-13, leg. B.V. Peterson, 1♂ (Am 1582\*, CNC); Old Chelsea, Summit King Mtn., 1965-06-20, leg. D.M. Wood, 2♂ (Am 1462\*, 1541\*, CNC); Summit King Mt. Old Chelsea, 1980-06-23, leg. K.N. Barber, 1♂ (Am 529\*, DEBU). **USA: New York:** Monroe Co., Rochester, Highland Pk., 43.132600, -77.602784, 2018-09-17, leg. John Jaenike, 1♂ (Am 1168\*, AMNH). **North Carolina:** Wayah Bald, 5300', 1957-07-14, leg. J.G. Chillcott, "Paratype," [never published], 1♂ (Am 1375\*, CNC).

**ETYMOLOGY:** Named for Edward Zalisko (1958–), outstanding teacher and professor of biology at Blackburn College in Carlinville, Illinois. In appreciation for introducing the first author to phylogenies and evolution while he was an undergraduate at Blackburn. Zalisko once said in class, "I am the world's authority on something that absolutely nobody cares about!" a sentiment now understood by the first author.

**DISTRIBUTION:** *Amiota zaliskoi* is found in the Great Lakes region, but one record as far south as North Carolina is known.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common in many *Amiota*.

#### THE CERVITES SPECIES GROUP (NEW GROUP)

**DIAGNOSIS:** Large flies (*A. elsaltoensis*, sp. nov., small); dark black-brown, with typical white markings, but also with frons dark and relatively shiny on dorsal portion, a silvery band along ptilinal margin on ventral third; arisal branches short, at base only; Male genitalia: Very complex, outer and inner paraphyses with multiple, slender spines.

**NEARCTIC SPECIES:** *Amiota cervites*, sp. nov., *A. elsaltoensis*, and *A. multiplex*, sp. nov.

**COMMENTS:** All members of this species group are known only from Durango State in Mexico, two from the holotypes.

#### *Amiota cervites*, sp. nov.

Figures 29A–B, 30A–B, 31, 86A

**DIAGNOSIS:** Large fly (ThL 1.39–1.48 mm), dark brown, nearly black; thorax and abdomen glossy; frons blackish brown on rest of frons, ventral third shiny, silvery; spines of outer paraphyses forming a cross-shaped structure (in posterior view), the most ventral portion consisting of an anterior, posterior, and lateral spine; dorsal spine with a lateral spine as well as a bifurcated posterior spine; inner paraphysis small and cuplike.

**DESCRIPTION:** Large fly (ThL 1.39–1.48 mm), dark brown, nearly black; legs dark yellow. Thorax and abdomen glossy. Frons shiny, with silvery band along ptilinal margin on ventral third. Cheek whitish to light brown. Palp brown. Tergite 1 lightly colored. Arista: Short to medium, plumose, most branches decumbent; longest branch D1–D2; A.R. 0.31; 3 dorsal, 0 ventral branches; branches D1–3 pointed mediad; arista trunk with long microtrichia grading shorter toward apex. Male genitalia: Epandrium dorsally separated, margins in this area discrete from membrane; row of long setae along posterolateral margin. Cercus oval shaped, long though not pendulous, ventral margin extending approximately to lower level of epandrium; most margins discrete from surrounding membrane (except for dorsal most portion); setae long. Surstylus curved, lateral convex; cluster of setulae along preapical-ventral margin; 15 prenisetae, apices blunt, closely arranged, comblike. Subepandrial sclerite large, subepandrial appendage arising from a thin stalk, expanding into a large scoop-shaped structure, as wide as long; moderately sclerotized. Outer paraphyses complex, virtually symmetrical (except for 2 dorsal spines): entire complex approximately cross shaped; ventralmost portion with anterior, posterior, and lateral spines; anterior portion with spine oriented toward the opposite direction of the lateral appendage; anteroventral spine

with two sensilla near midpoint, on tiny tubercles; dorsal portion of outer paraphysis with pair of longer lateral spines and pair of bifurcated posterior spines; paraphysial complex heavily sclerotized, except bases of pair of posterolateral spines (which are membranous). Inner paraphysis small, heavily sclerotized, simple and cuplike with anterior rim; lying lateral to outer paraphysis. Aedeagal apodeme long, width  $0.60 \times$  length, moderately sclerotized; curved  $90^\circ$  in lateral view. Hypandrium approximately following contours of cross-shaped outer paraphyses in ventral view, forming 3 lobes; the most anterior lobe thinner than the lateral lobes, with a small, rounded projection at the apex; in lateral view hypandrium gently S-shaped, without lobe on posterior margin. Ejaculatory apodeme half the length of the epandrium. Head and thorax measurements: (n = 5; Am 1267, 1447, 1526, 1530, 1532) FL/FW 0.75 (0.72–0.79), EL/EW 1.23 (1.17–1.29), EL/CW 13.29 (11.6–17.25), FML/FMW 0.26 (0.24–0.28), PR/RR 0.55 (0.45–0.58), ThL 1.43 (1.39–1.48 mm).

**TYPE MATERIAL:** **Holotype:** male: 14 mi SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June "26" 1964, J.F. McAlpine, attracted to man, Am 1526, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC). **Paratypes:** 14 mi. SW El Salto, Dgo. [Durango] MEX., 8000', June "26" 1964, J.F. McAlpine, attracted to man, 6♂ (Am 1447\*, 1484\*, 1495\*, 1512\*, 1524\*, 1532\*, CNC).

**OTHER MATERIAL EXAMINED:** **Mexico:** **Durango:** 10 mi W. El Salto, 9000', 1964-06-08, leg. J.F. McAlpine, attracted to man, 1♂ (Am 1267, CNC); 1964-06-12, leg. J.F. McAlpine, 2♂ (Am 1530\*, 1555\*, CNC); 14 mi. SW El Salto, 8000', 1964-06-09, leg. J.F. McAlpine, attracted to man, 3♂ (Am 1498\*, 1523\*, 1528\*, CNC).

**ETYMOLOGY:** Formed from *cervus*, Latin for "deer." Meaning "deerlike," in reference to the posterior view of the male genitalia, which resemble a deer skull.

**DISTRIBUTION:** *Amiota cervites* is currently only known from the state of Durango in Mexico.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota elsaltoensis*, sp. nov.

Figures 29C–D, 30C–D, 32, 86B

**DIAGNOSIS:** Small fly (ThL 0.97 mm), nearly black; frons black dorsally, ventral third silvery near lateral corners; outer paraphysis long, linear, tapering to a point, 3 pairs of slender, dorsal spines curved inward; base of inner paraphysis with 3 sets of medially pointed lobes, terminating in 3 pairs of dorsally pointed appendages, 2 apical sets fused at base, forming a semicircular inner region.

**DESCRIPTION:** Small fly (ThL 0.97 mm), nearly black, fading slightly to dark brown ventrally; legs yellow. Frons black dorsally, ventral third silvery in lateral corners. Cheek relatively wide (EL/CW 11.83), whitish gray posteriorly. Palp yellow. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branch D3; A.R. 0.28; 4 dorsal, 1 ventral branch; branch D4 pointed mediad; arista trunk with medium microtrichia nearly to apex. Male genitalia: Epandrium split medially, margins not grading into surrounding membrane; ventral lobes very long in posterior view, extending well beyond surstyli. Cercus semicircular, not grading into surrounding membrane; dorsal membranous area large, triangular. Surstylus triangular or wedge-shaped; 12 short prensisetae, apices blunt; numerous scattered setulae along lateral margin on ventral third; small lobe on apical-lateral corner not extending beyond prensisetae. Subepandrial sclerite simple, tapering to an acute point; lacking subepandrial appendage. Outer paraphysis large and distinctive: long; linear, slightly sinuous in shape, especially distal third; apex tapered to blunt point; 5–7 sensilla clustered subapically; dorsally with 3 equally spaced pairs of slender spines, each pair curved medially, overlapping; base of outer paraphysis in lateral view with a dorsoposteriorly pointed

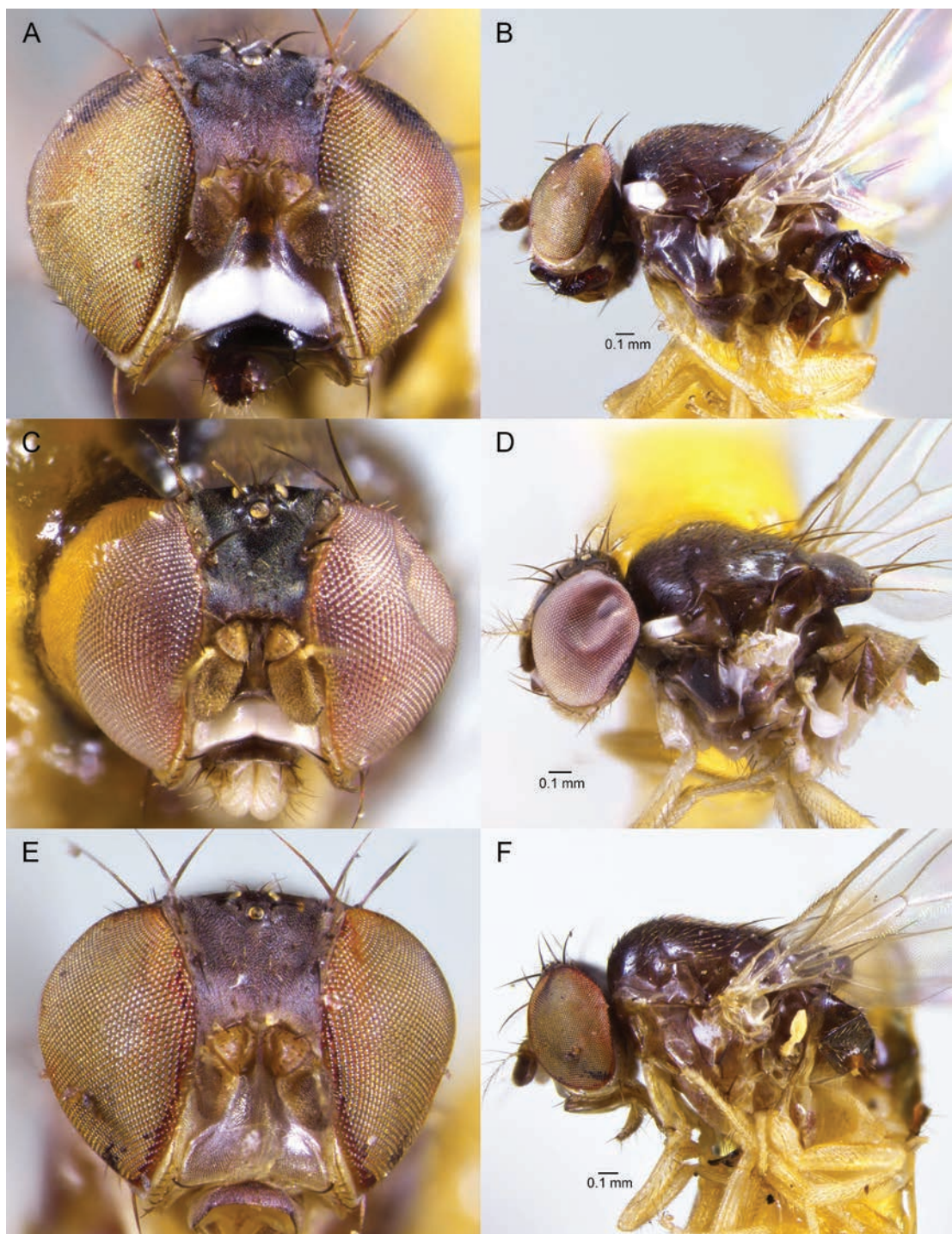


FIG. 16. Heads and lateral views, *A. mariae* species group. A–B. *A. antitortum*, sp. nov. (Am 55, holotype, lateral image flipped). C–D. *A. brayi*, sp. nov. (Am 322, holotype). E–F. *A. cruciatum*, sp. nov. (Am 83, lateral image flipped). Lack of white spots is likely an effect due to preservation.

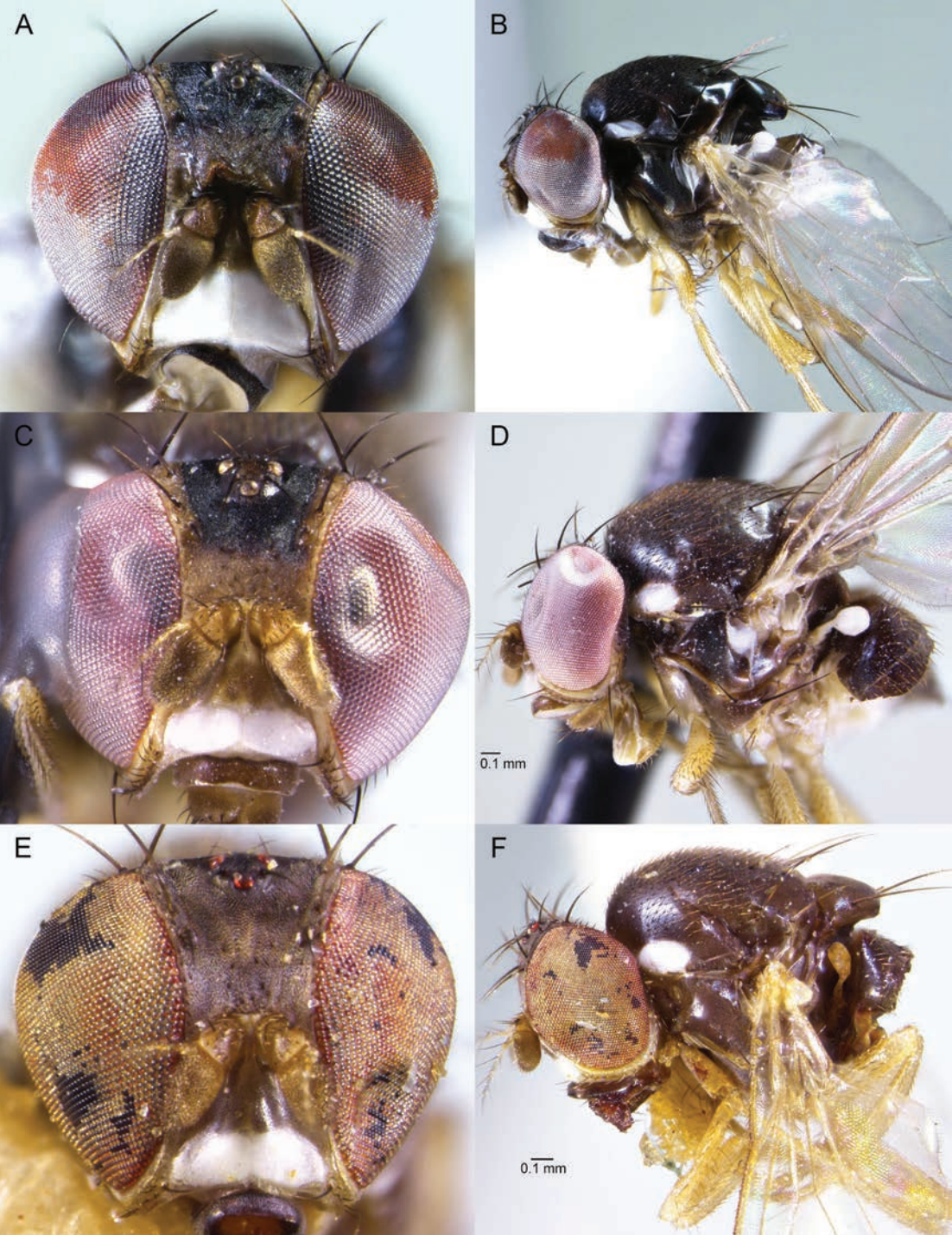


FIG. 17. Heads and lateral views, *A. mariae* species group. A–B. *A. incurva*, sp. nov. (Am 716). C–D. *A. mariae* Máca (Am 603). E–F. *A. texas*, sp. nov. (Am 438, holotype).

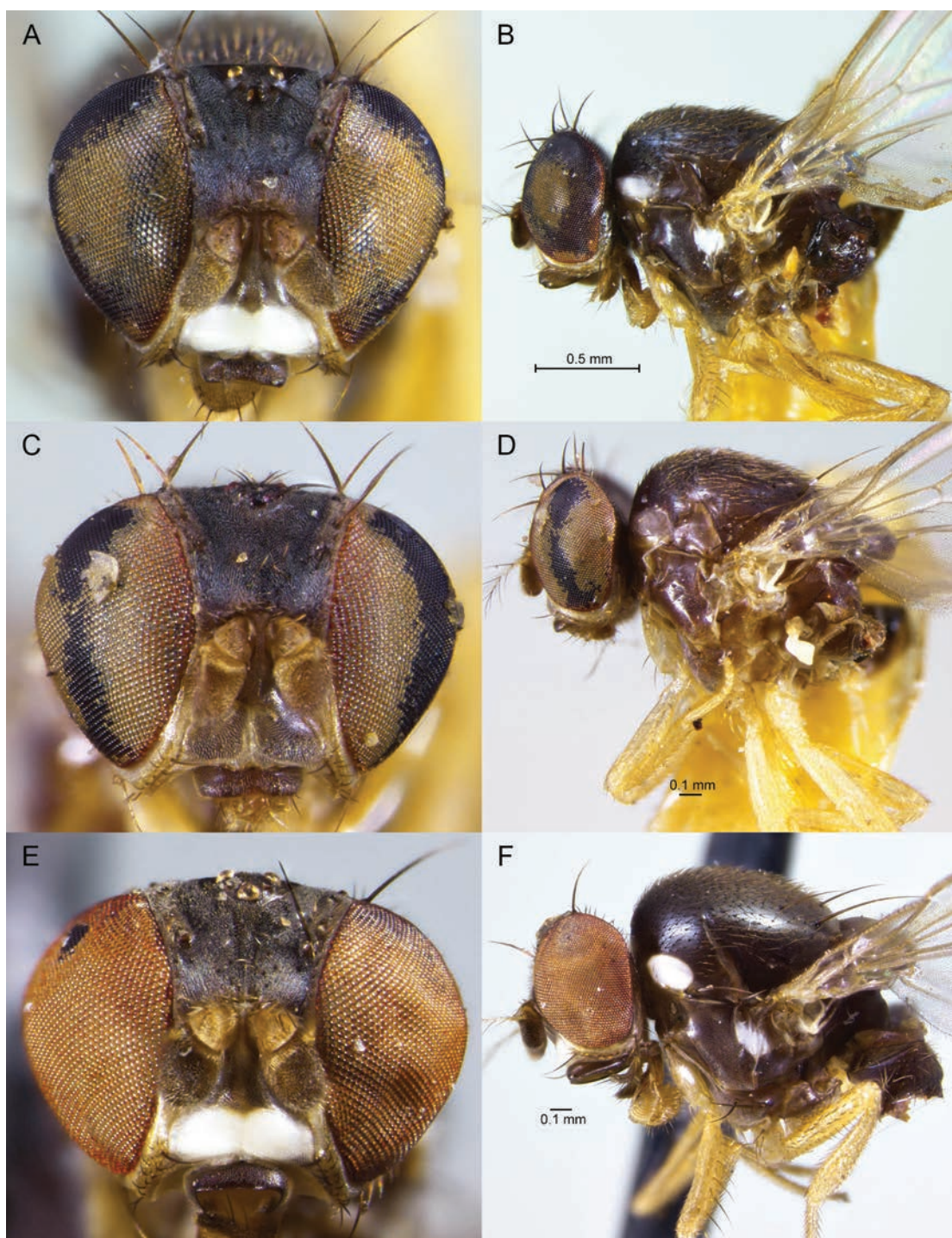


FIG. 18. Heads and lateral views, *A. mariae* species group. **A–B.** *A. tormentum*, sp. nov. (Am 53, holotype, lateral image flipped). **C–D.** *A. wheeleri*, sp. nov. (Am 73, holotype, lateral image flipped). Lack of white spots is likely an effect due to preservation. **E–F.** *A. zaliskoi*, sp. nov. (Am 529).

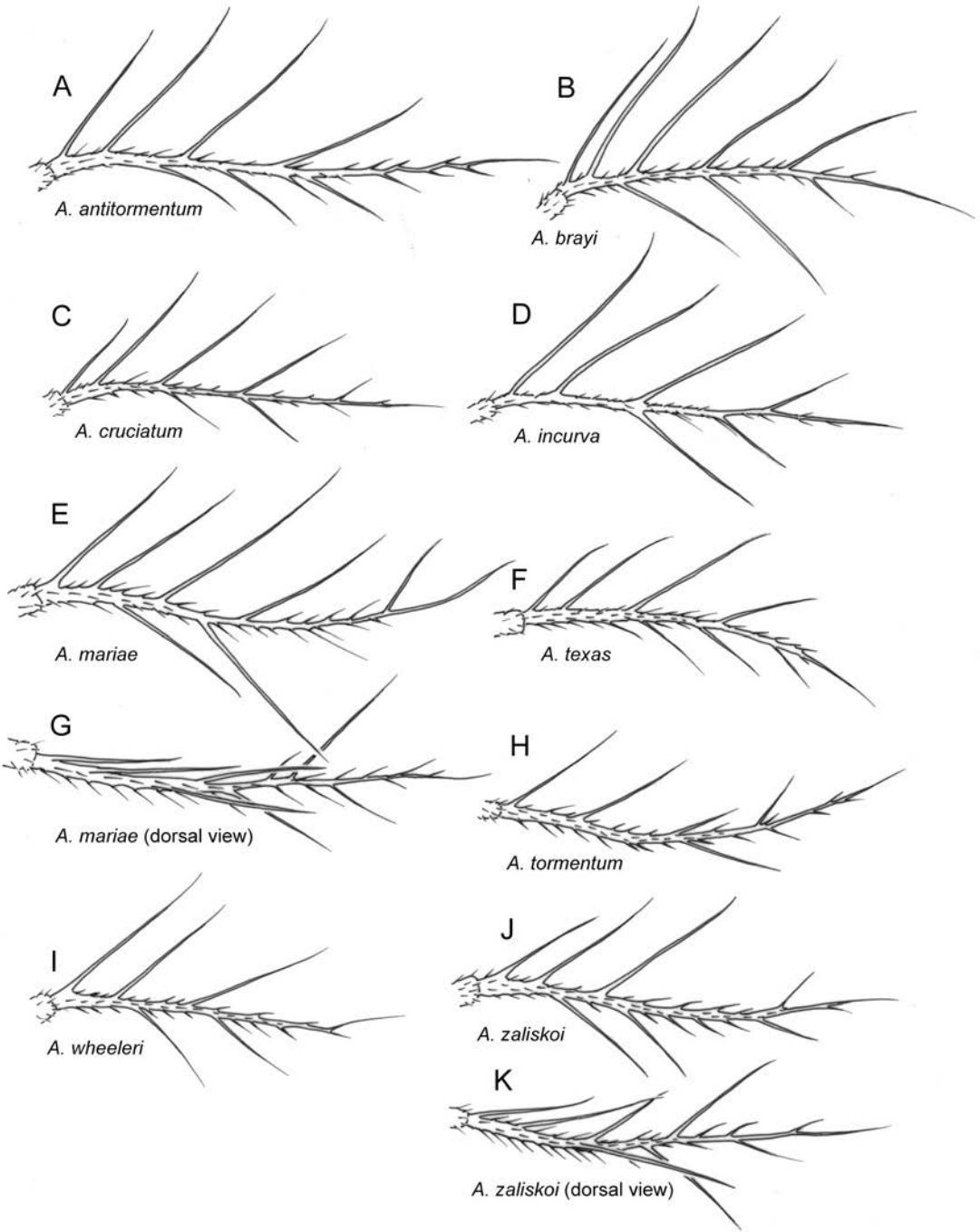


FIG. 19. Aristae, *A. mariae* species group. A. *A. antitortum*. B. *A. brayi*. C. *A. cruciatum*. D. *A. incurva*. E, G. *A. mariae* Máca. F. *A. texas*. H. *A. tormentum*. I. *A. wheeleri*. J–K. *A. zaliskoi*. Not to same scale.

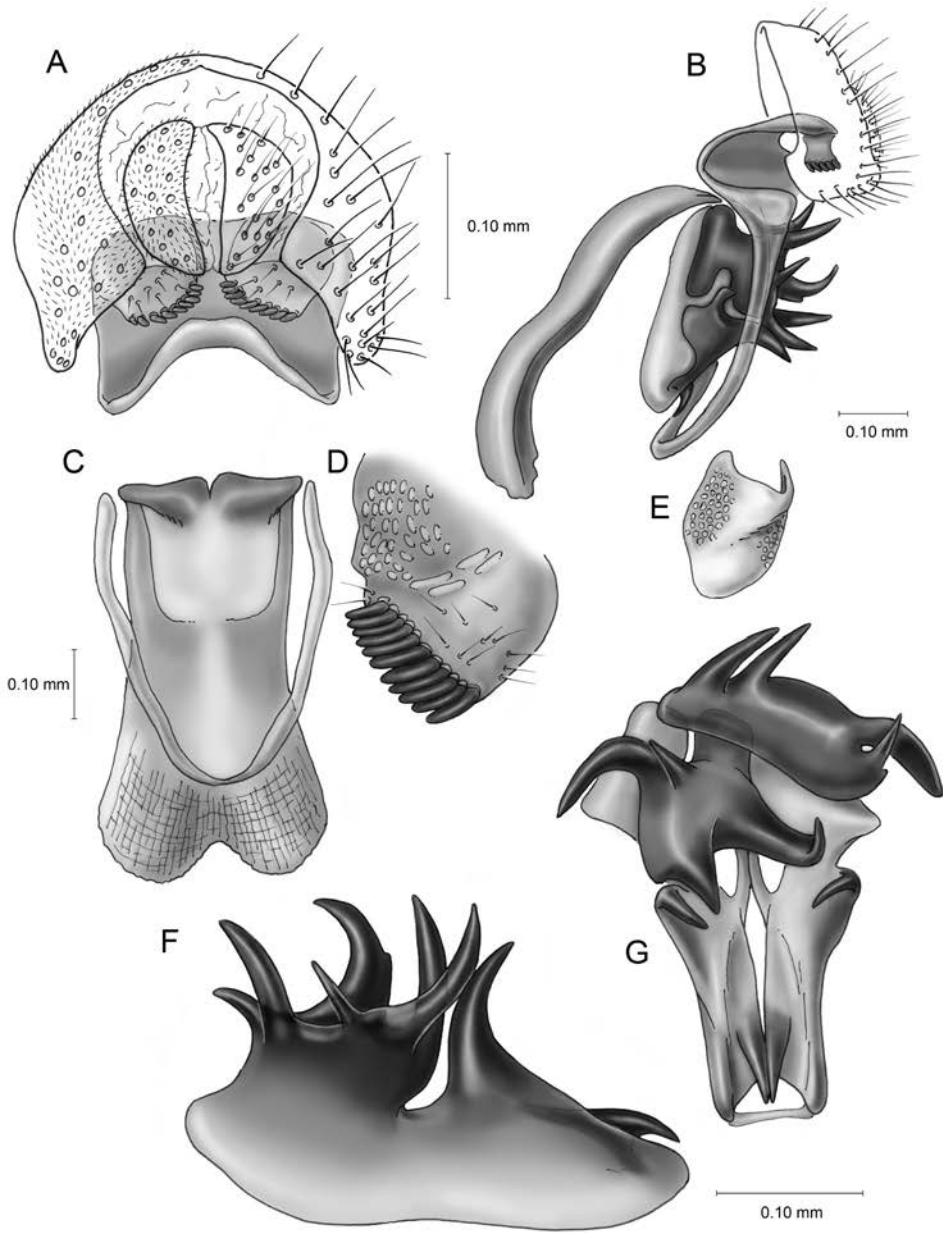


FIG. 20. Male terminalia, *A. antitortum*. **A.** Epandrium and cerci, subepandrial sclerite shaded. **B.** Lateral view. **C.** Aedeagal apodeme and hypandrium, ventral view. **D.** Surstylus. **E.** Sternite 6 sac. **F.** Paraphyses, lateral view. **G.** Paraphyses, posterior view. (Am 710).

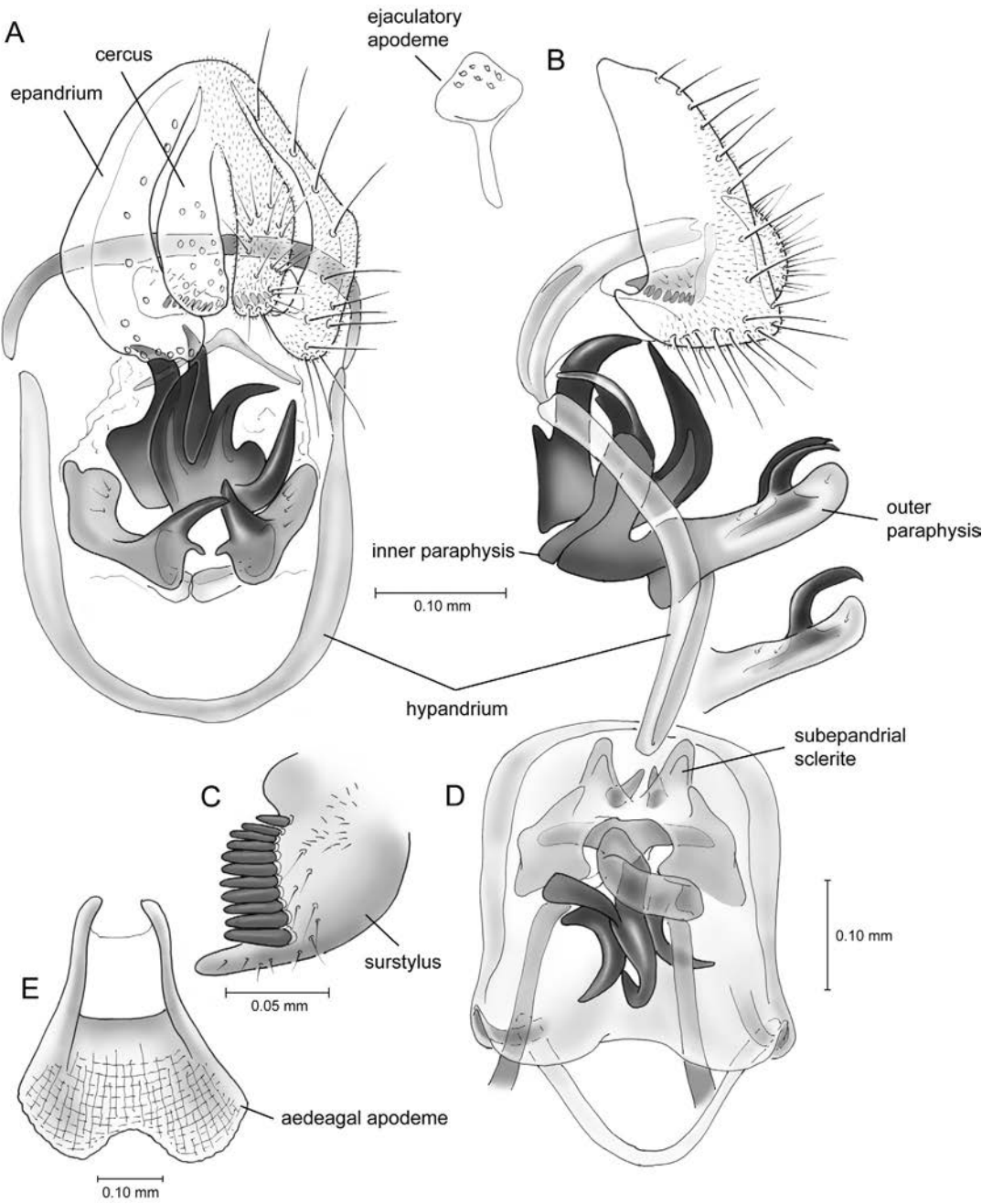


FIG. 21. Male terminalia, *A. brayi*. **A.** Posterior view of entire complex. **B.** Lateral view. **C.** Surstylus **D.** Subepandrial sclerite, paraphyses, and hypandrium, dorsal view. **E.** Aedeagal apodeme. (Am 322, holotype).

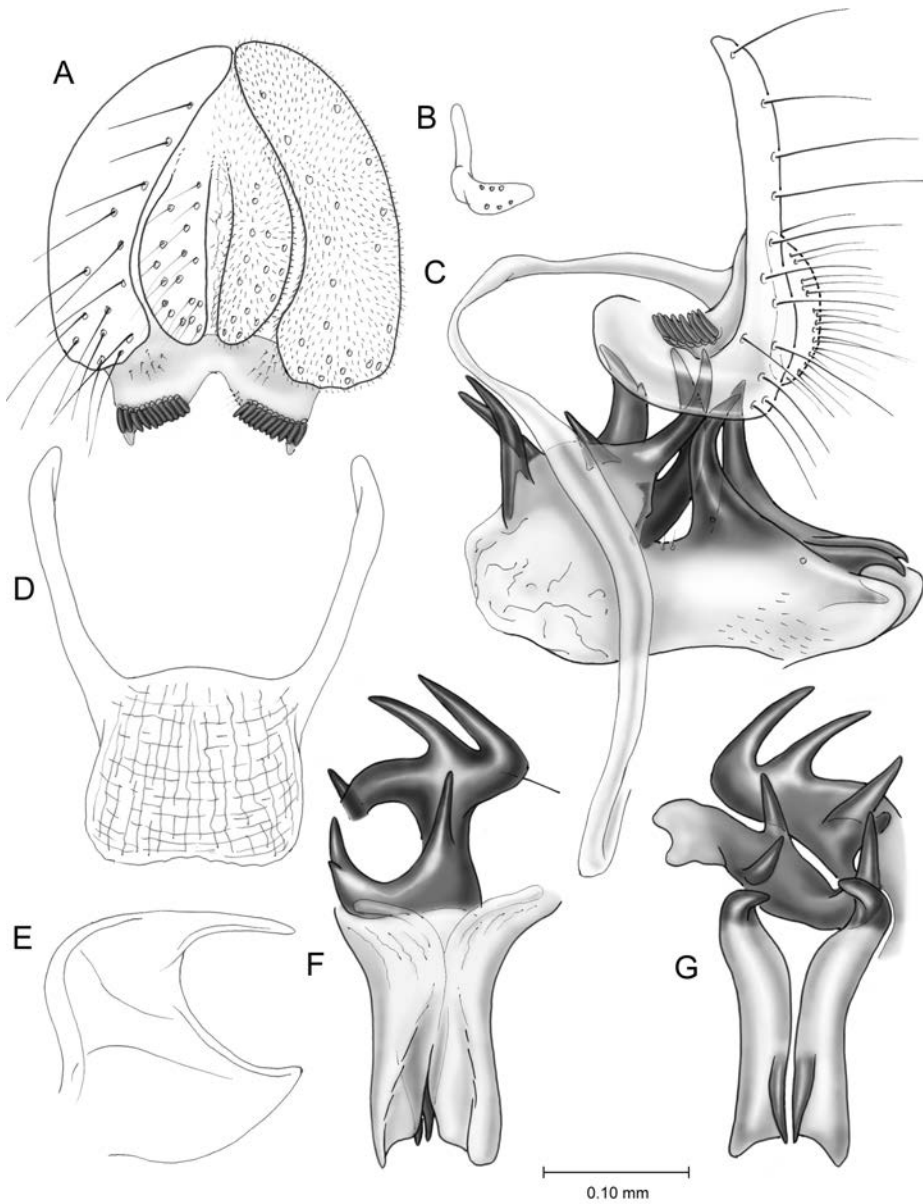


FIG. 22. Male terminalia, *A. cruciatum*. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Aedeagal apodeme. **E.** Subepandrial sclerite, lateral. **F.** Paraphyses, ventral view. **G.** Paraphyses, dorsal view. (Am 97).

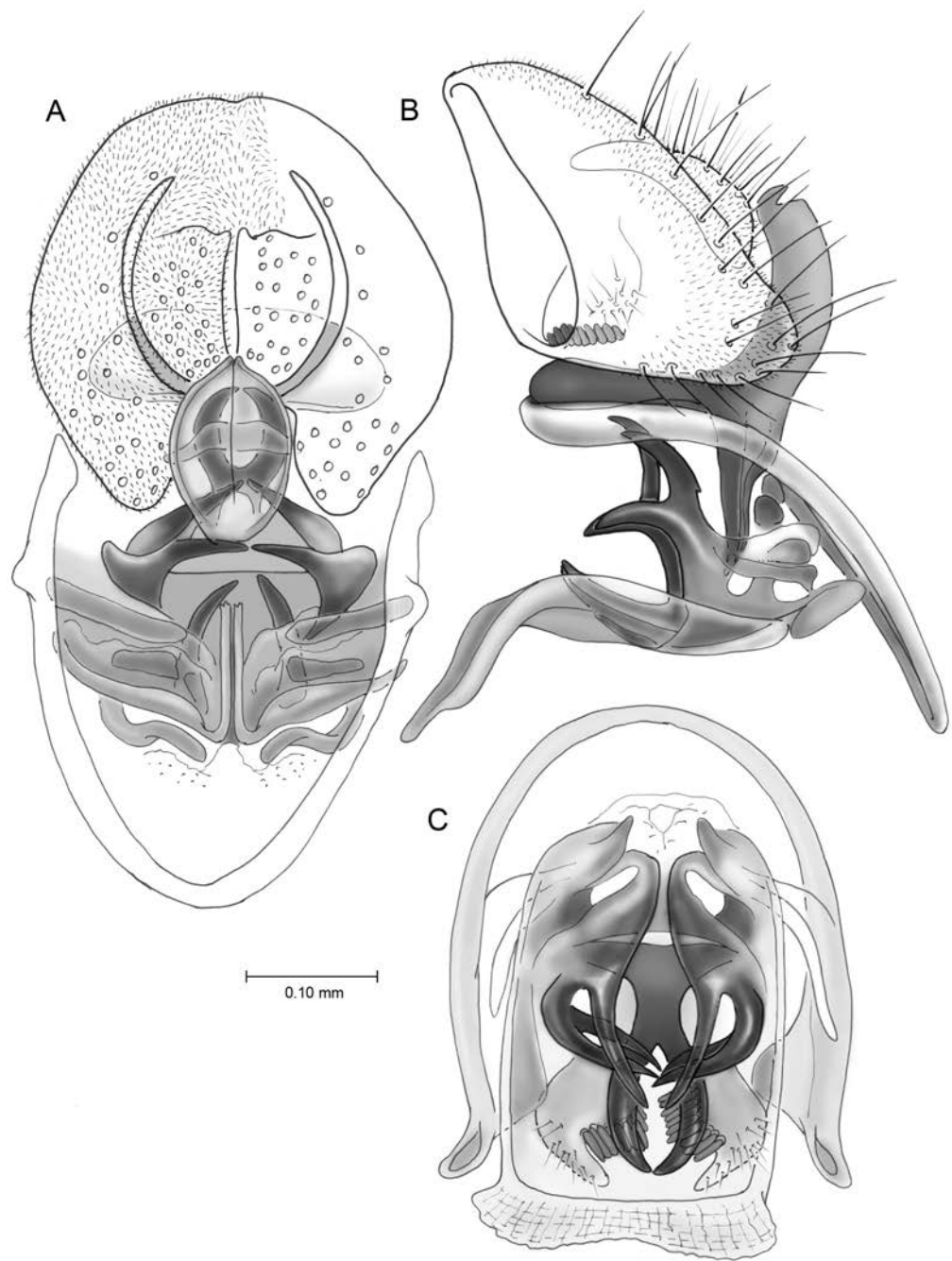


FIG. 23. Male terminalia, *A. incurva*. A. Posterior view. B. Lateral view. C. Ventral view. (Am 440, holotype).

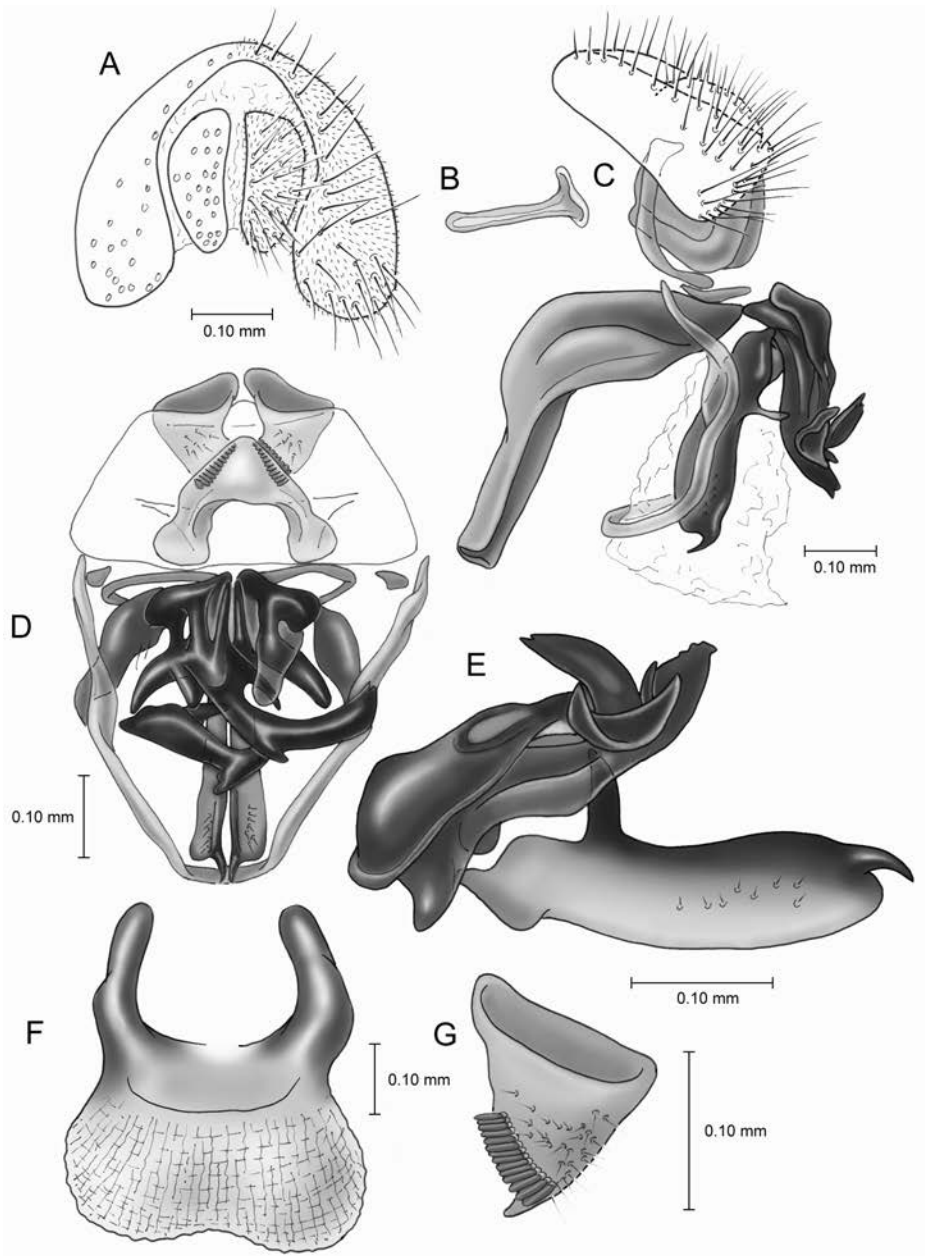


FIG. 24. Male terminalia, *A. mariae* Máca. A. Epandrium and cerci. B. Ejaculatory apodeme. C. Lateral view. D. Ventral view. E. Paraphyses, lateral view. F. Aedeagal apodeme. G. Surstylus. (Am 695).

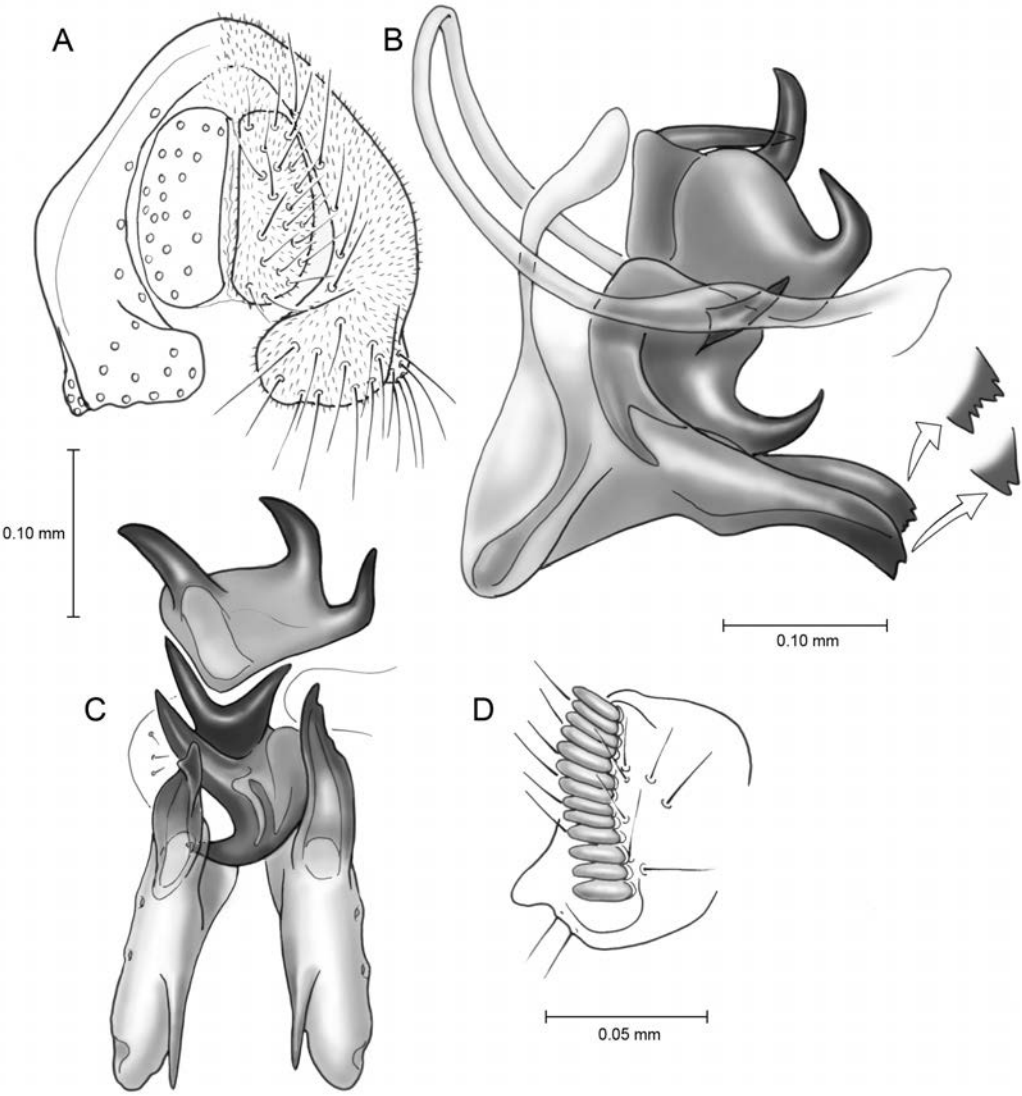


FIG. 25. Male terminalia, *A. texas*. **A.** Epandrium and cerci. **C.** Paraphyses and hypandrium, lateral view. **D.** Paraphyses, dorsal view. **D.** Surstylus. (Am 438, holotype).

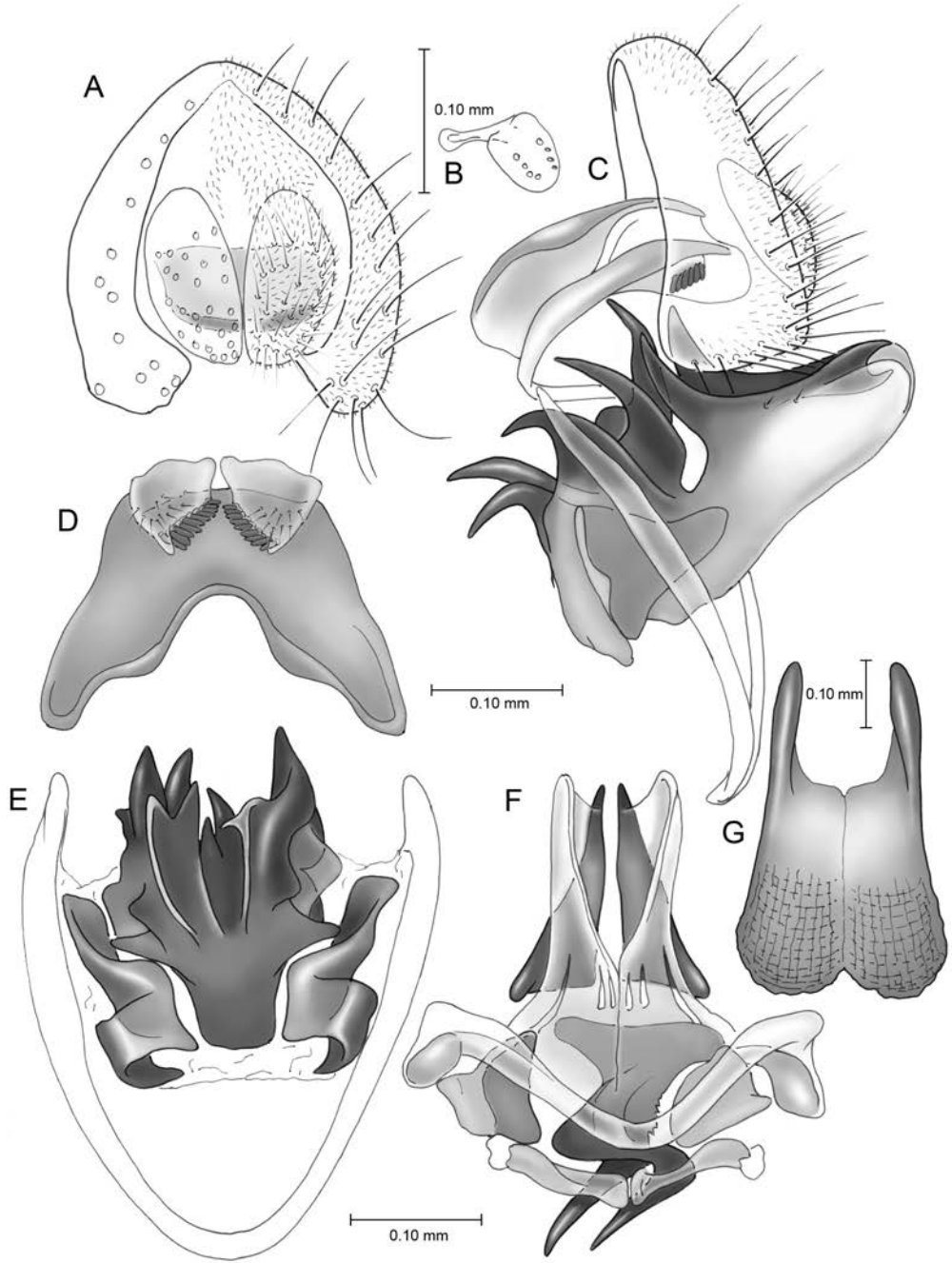


FIG. 26. Male terminalia, *A. tormentum*. **A.** Epandrium and cerci (subepandrial sclerite shaded). **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Surstyli and subepandrial sclerite. **E.** Paraphyses and hypandrium, posterior view. **F.** Ventral view. **G.** Aedeagal apodeme. (Am 53, holotype).

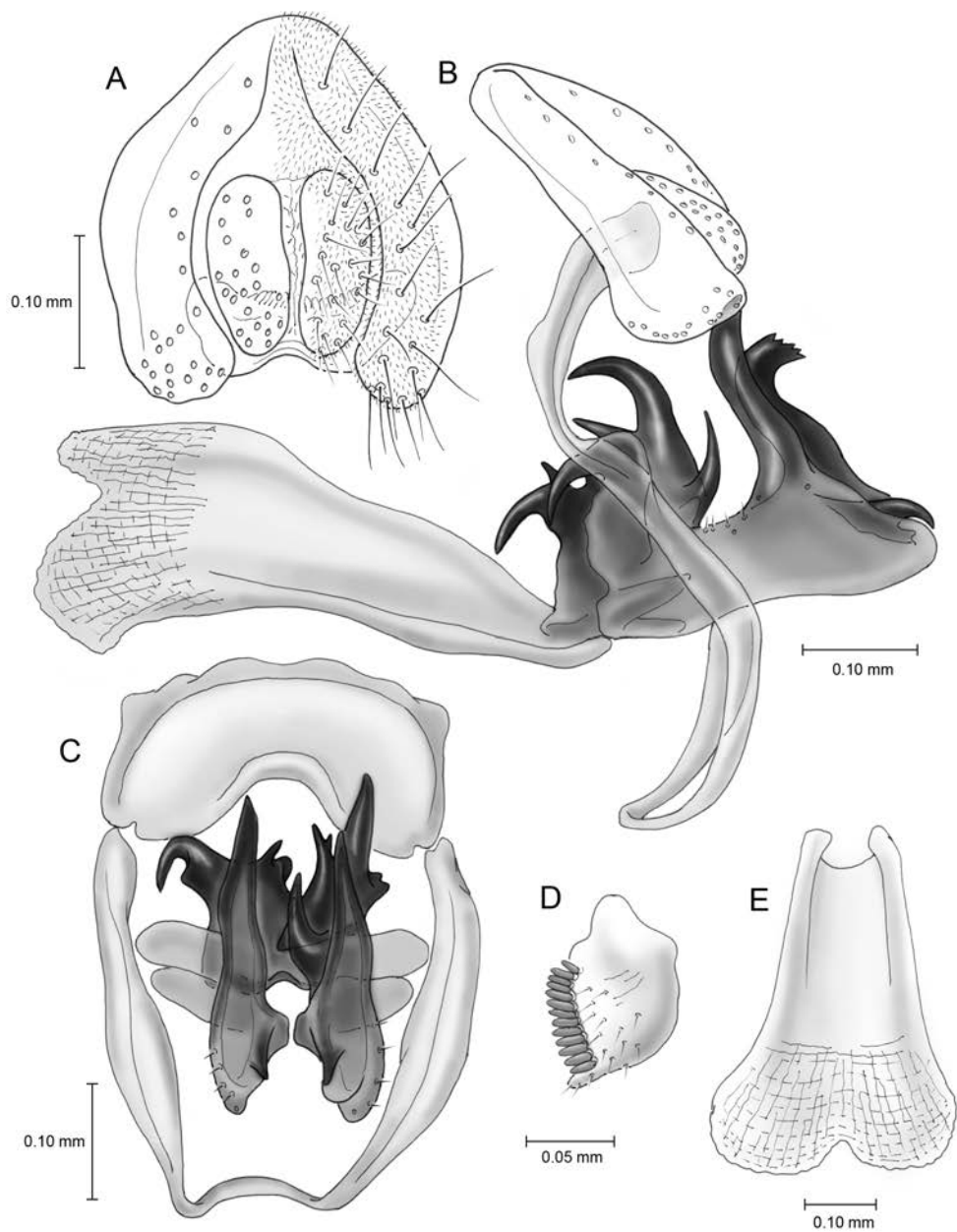


FIG. 27. Male terminalia, *A. wheeleri*. **A**. Epandrium and cerci. **B**. Lateral view. **C**. Hypandrium, paraphyses, subepandrial sclerite, posterior view. **D**. Surstylus. **E**. Aedeagal apodeme. (Am 73, holotype).

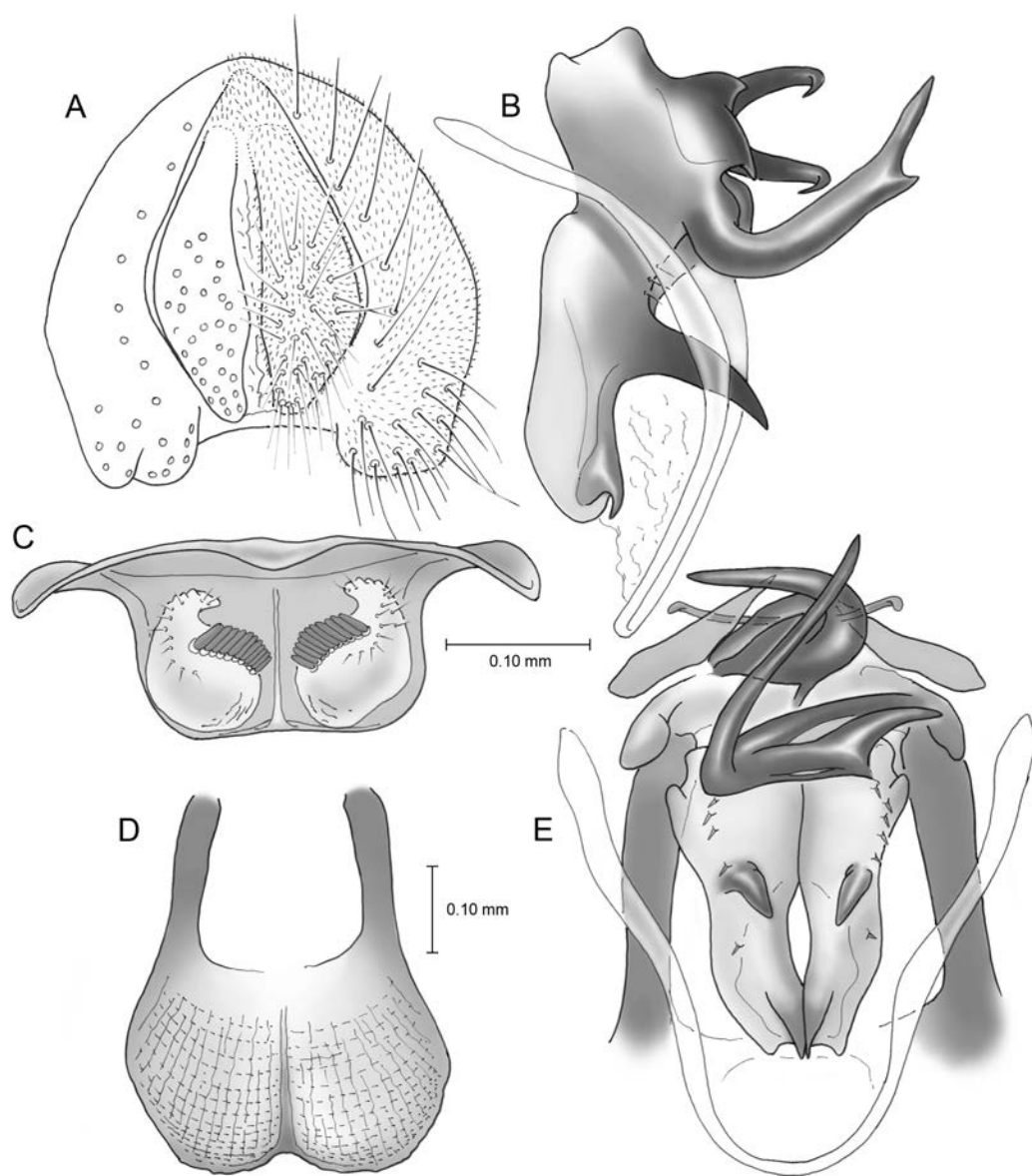


FIG. 28. Male terminalia, *A. zaliskoi*. **A.** Epandrium and cerci. **B.** Lateral view. **C.** Surstyli and subepandrial sclerite. **D.** Aedeagal apodeme. **E.** Posterior view. (Am 32, holotype).

spine, base cuplike, intersecting perpendicularly with a strongly hooked appendage. Inner paraphysis base with 3 pairs of basal lobes, pointed medially; distal portion with 3 pairs of appendages pointed dorsally; posterior pairs fused at base, forming a semicircular shape; basalmost pair of appendages simple, with a

small lateral spine. Aedeagal apodeme 1.25× longer than wide, broad and shieldlike in lateral view, not strongly bent; lateral margins slightly constricted at middle; distal end flared as wide as base with a shallow concave depression/emargination. Hypandrium U-shaped; lateral arms thickened with a distinctive gonopod;

stalk small, expanding at the apex to a wide oval pad. Ejaculatory apodeme small,  $0.4\times$  length of epandrium, barely sclerotized. Head and thorax measurements: ( $n = 1$ , Am 1455) FL/FW 0.59, EL/EW 1.25, EL/CW 11.83, FML/FMW 0.26, PR/RR 0.54, ThL 0.97 mm.

TYPE MATERIAL: **Holotype**: male: 14 mi. SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June "26" 1964, J.F. McAlpine, attracted to man, Am 1455, [specimen glued to pin, dissected]. Deposited in the Canadian National Collection (CNC).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: Derived from El Salto, city in Durango State of Mexico, a productive locality for *Amiota*.

DISTRIBUTION: *Amiota elsaltoensis* is currently known only from the holotype in the vicinity of El Salto within the state of Durango.

COMMENTS: This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

### *Amiota multiplex*, sp. nov.

Figures 29E–F, 30E–F, 33, 86C

DIAGNOSIS: Large fly (ThL 1.65 mm), black; frons silvery on ventral half, especially ventrolateral corners; epandrium tall, dorsally complete, cerci situated low; outer paraphysis heavily sclerotized, consisting of 2 lobes with 5 pairs of narrow, curved spines; inner paraphyses small, clavate, distal end setose, covered in 6–8 fine setulae; ejaculatory apodeme small.

DESCRIPTION: Large fly (ThL 1.65 mm), black, legs dark yellow. Frons dark and rather shimmering, especially at ventrolateral corners. Cheek somewhat deep for size (EL/CW 9.25); anterior half dark yellow, posterior half brown. Palp yellow. Arista: Very short, plumose, branches decumbent; longest branch D1; A.R. 0.24; 3 dorsal, 0 ventral branches; branch D3 pointed mediad; arista trunk with medium-length microtrichia nearly to apex.

Male genitalia: Epandrium tall, height  $\sim 1.25\times$  width; fused at midline, not grading into surrounding membrane; ventral lobes setose, line of setae along medial margin of epandrium. Cercus position low, with large triangular-shaped membranous region above; pendulous, not grading into surrounding membrane; slightly narrowed ventrally. Surstylus wide at base, tapered distally; ventral half with very long, fine scattered setulae; 8 short prenisetae, apices blunt. Subepandrial sclerite rounded, U-shaped with an acute, mucronate point; inner margin thickened; subepandrial appendage not well developed. Outer paraphysis heavily sclerotized; consisting of 2 large lobes with a thickened lip on posterior margin; 5 pairs of zygomorphic appendages; most apical pair slender, sinuous, pointed posteriorly; second pair arising medially to apical pair, oriented laterally; third pair ventral to apex, appendages curved, oriented posteriorly; fourth pair arising proximally, curved downward, oriented ventrally; fifth pair most proximal, sinuous, slender, oriented anteriorly; 2 appendages arising between fourth and fifth pairs, each oriented laterally, crossing midline. Inner paraphysis clavate, slender; distal end expanded to rounded pad, setose, with 6–8 fine setulae. Aedeagal apodeme nearly bent at  $90^\circ$  angle; basal region with widely flared flanges; middle region constricted; distal end round, with a minute medial cleft running to the midpoint, but no significant emargination. Hypandrium U-shaped, width consistent; apex notched, accommodating paraphyses; lateral arm with a small, thickened swelling. Ejaculatory apodeme very small,  $0.25\times$  length of the epandrium, barely sclerotized. Head and thorax measurements: ( $n = 1$ , Am 1552) FL/FW 0.75, EL/EW 1.14, EL/CW 9.25, FML/FMW 0.31, PR/RR 0.60, ThL 1.65 mm.

TYPE MATERIAL: **Holotype**: male: 11 mi. E. El Salto, Dgo. [Durango] MEX., [23.785100, -105.536622], June 13, 1964, J.F. McAlpine, 8000', Am 1552, [pinned specimen, dissected]. Deposited in the Canadian National Collection (CNC).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: From Latin, meaning "complex, multilayered," in reference to the outer paraphysis.

DISTRIBUTION: *Amiota multiplex* is known only from Durango State in Mexico.

COMMENTS: It is unknown whether this species is attracted to the face and eyes as other *Amiota*.

#### THE AVIPES SPECIES GROUP (NEW GROUP)

DIAGNOSIS: Mostly medium-sized flies (*A. biacuminis* large); dark black-brown to light golden-honey color; typical white markings, faded in some species, entirely absent in *A. minor*; arisal branches short, mostly on basal half, or longest branches on basal half and grading shorter apicad; frons dark, dull, with faint silvery pollinosity in some species. Male genitalia: Outer paraphysis short, with two apical lobes; inner paraphysis lost; ventral epandrial sclerite large and recurved.

NEARCTIC SPECIES: *Amiota avipes*, sp. nov., *A. biacuminis*, *A. forceps*, sp. nov., *A. minor* (Malloch), *A. onyx*, sp. nov., *A. pseudominor*, and *A. uniacuminis*, sp. nov.

COMMENTS: All members of the *avipes* species group are known only from Mexico, with the exception of *A. minor* (Malloch), which is found throughout the United States, north of Mexico.

#### *Amiota avipes*, sp. nov.

Figures 34A–B, 37A, 38B, E, G, I, 87A

DIAGNOSIS: Medium-sized fly (ThL 1.17–1.24 mm), dark blackish brown fading lighter ventrally; facial marking thin, width 0.25× length; characteristic markings on postpronotal lobe and under wing base small, fading near margins; surstylus with short secondary row of 4 prenisetae; outer paraphyses symmetrical, short, stout, heavily sclerotized, with 2 short apical spines, winglike basal projec-

tion, pointed laterally; inner paraphysis lost; length of ejaculatory apodeme equal to height of epandrium.

DESCRIPTION: Medium-sized fly (ThL 1.17–1.24 mm), dark blackish brown fading to lighter ventrally, including katepisternum; legs light yellow. Characteristic markings on postpronotal lobe and under wing base small, fading near margins. Frons dark blackish brown, black near ptilinal suture, overall with faint bluish pollinosity. White facial marking thin, width 0.25× length. Cheek relatively wide (EL/CW 9.5–11), yellowish. Palp yellow. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branch D4; A.R. 0.35; 7 dorsal branches, grading to shortest one apically; 3–4 short ventral branches; no branches pointed significantly mediad or laterad; arista trunk with medium-length microtrichia to apex. Male genitalia: Epandrium dorsally complete, ventral margin in this area graded into membrane below; row of ~6 setae leading near posterior margin. Cercus long, pendulous, dorsally grading into membrane and epandrium; lateral margins of cercus discrete; cercus large, occupying virtually all space surrounded by epandrium. Surstylus with even row of 8–9 prenisetae, apices blunt; second row of 4 prenisetae dorsally, apices slightly pointed, widely spaced; setulae along ventral margin and midpoint of surstylus. Subepandrial sclerite well developed; subepandrial appendage pyramidal, pointed at tip. Outer paraphysis laterally flattened, heavily sclerotized, short, stout, with 2 pointed apical lobes and small group of sensilla at base of lower lobe; low carina immediately basal to group of sensilla; winglike basal projection, with faint distal striations, oriented laterally. Inner paraphysis lost. Aedeagal apodeme constricted on all sides, curved 90° in lateral view; basal margins wider than distal end. Hypandrium circular, apex with small gap; lateral arms thick, bulging outward anteriorly and posteriorly; membranous connection with 2 pairs small membranous lobes between lateral arms and paraphyses. Ejaculatory apodeme as long as height of epandrium, stalk thick. Head

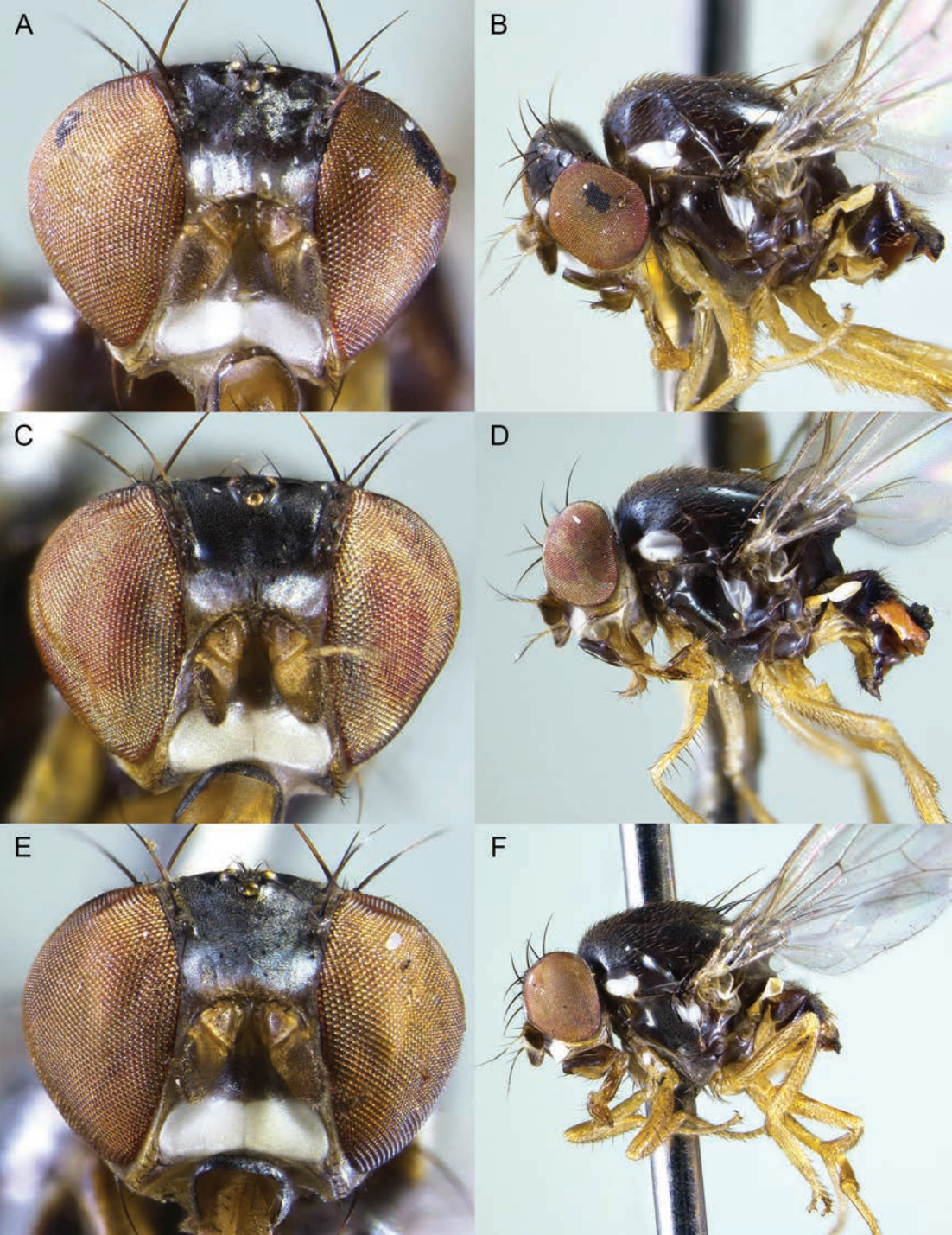


FIG. 29. Heads and lateral views, *A. cervites* species group. A–B. *A. cervites*, sp. nov. (Am 1526, holotype). C–D. *A. elsaltoensis*, sp. nov. (Am 1455, holotype). E–F. *A. multiplex*, sp. nov. (Am 1552, holotype).

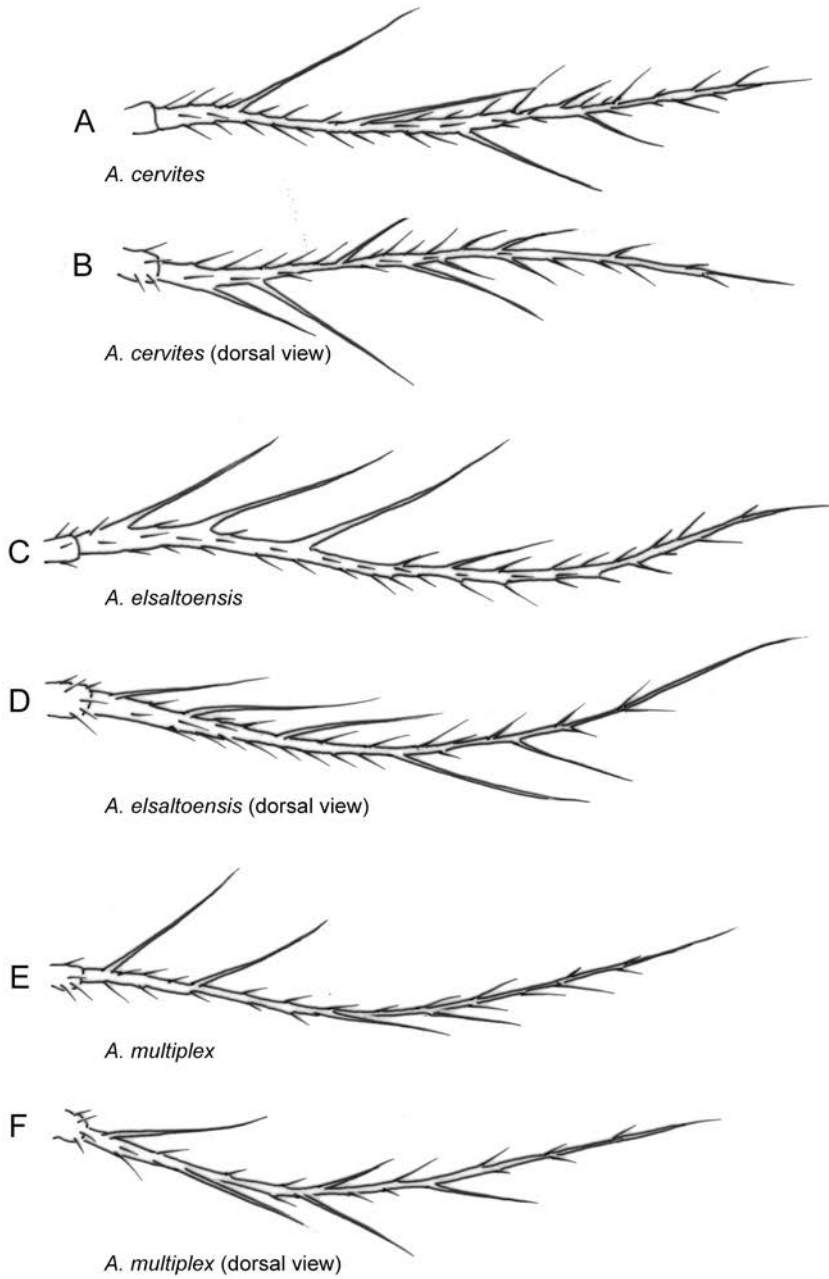


FIG. 30. Aristae, *A. cervites* species group. A-B. *A. cervites*. C-D. *A. elsaltoensis*. E-F. *A. multiplex*. Not the same scale.

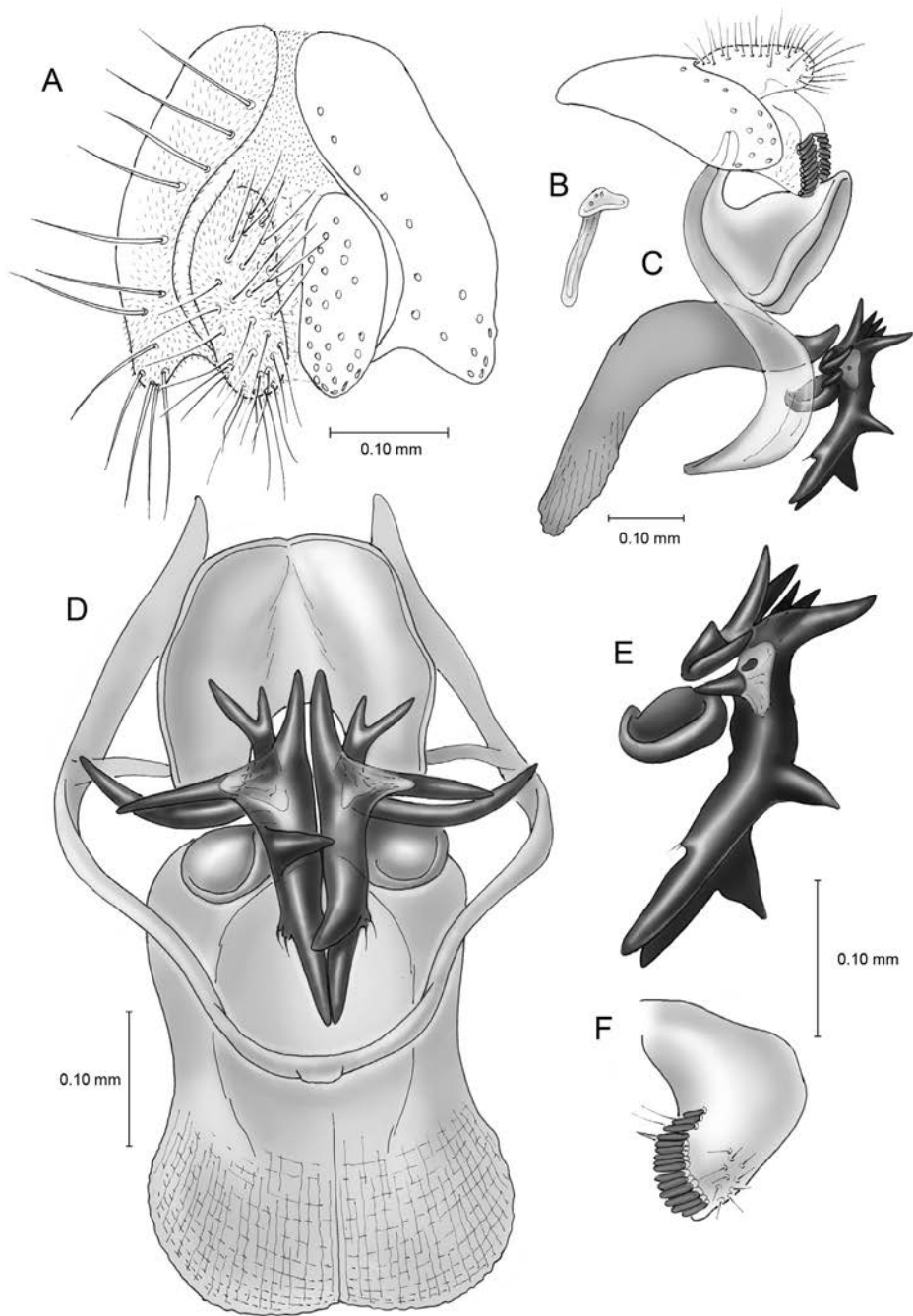


FIG. 31. Male terminalia, *A. cervites*. A. Epandrium and cerci. B. Ejaculatory apodeme. C. Lateral view. D. Ventral view. E. Paraphyses, lateral view. F. Surstylus. (*Am* 1526, holotype)

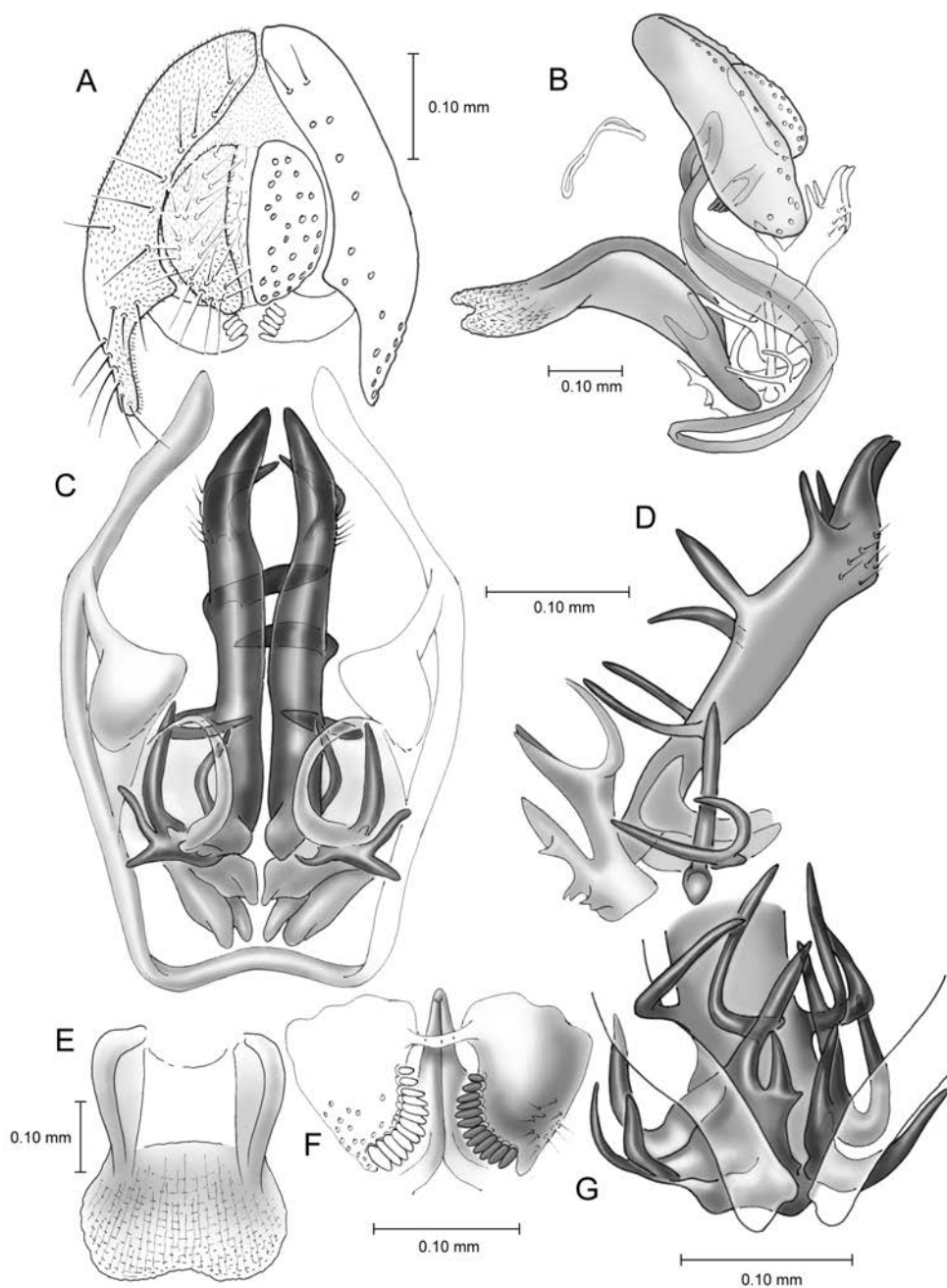


FIG. 32. Male terminalia, *A. elsaltoensis*. **A.** Epandrium and cerci. **B.** Lateral view with ejaculatory apodeme. **C.** Hypandrium and paraphyses, ventral view. **D.** Paraphyses, lateral view. **E.** Aedeagal apodeme. **F.** Surstyli. **G.** Paraphyses, dorsal view. (Am 1455, holotype).

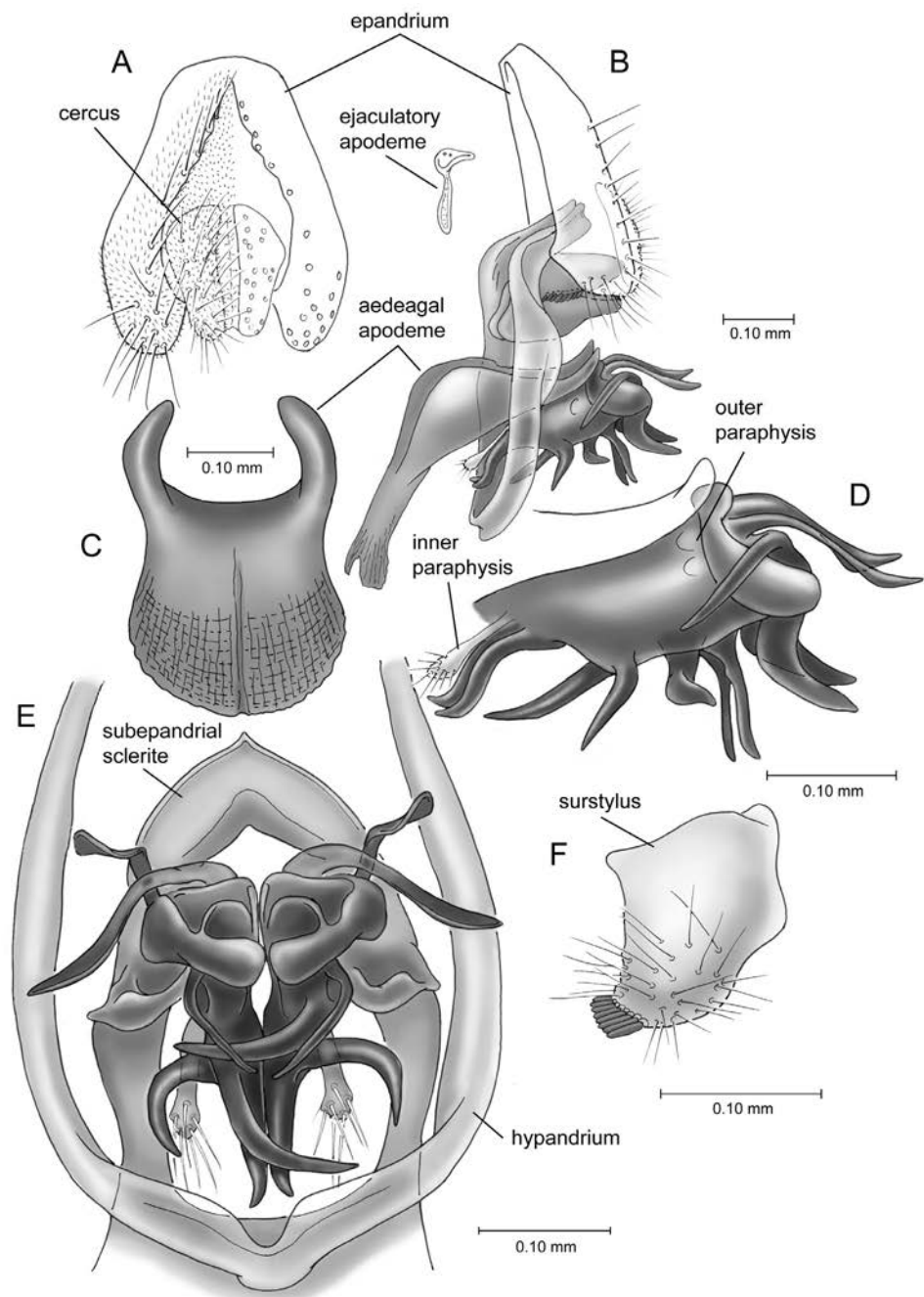


FIG. 33. Male terminalia, *A. multiplex*. A. Epandrium and cerci. B. Lateral view. C. Aedeagal apodeme. D. Paraphyses, lateral view. E. Posterior view. F. Surstylus. (Am 1552, holotype).

and thorax measurements: ( $n = 3$ ; Am 1453, 1496, 1514) FL/FW 0.50 (0.45–0.53), EL/EW 1.27 (1.25–1.29), EL/CW 10.3 (9.5–11), FML/FMW 0.26 (0.23–0.29), PR/RR 0.48 (0.44–0.50), ThL 1.20 (1.17–1.24 mm).

TYPE MATERIAL: **Holotype**: male: 14 mi. SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June "26" 1964, J.F. McAlpine, attracted to man, Am 1453, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC). **Paratypes**: 14 mi. SW. El Salto, Dgo. [Durango] MEX., 8000', June "9" 1964, J.F. McAlpine, attracted to man, 2♂ (Am 1496\*, 1514\*, CNC).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: Formed from Latin *avis* for "bird" and *pes* for "foot." Used as a noun in apposition. In reference to the paraphyses, in lateral view, resembling an outstretched bird's foot.

DISTRIBUTION: *Amiota avipes* is currently only known from Durango State.

COMMENTS: This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

### *Amiota biacuminis*, sp. nov.

Figures 34C–D, 37B; 39D–F, H–J, Q; 87B

DIAGNOSIS: Large fly (ThL 1.52–1.74 mm), dark blackish brown, including entire pleura; white spots typical of genus present; cheek deep, yellow; belongs to complex of species that includes *A. uniacuminis* and *A. forceps*, all with short outer paraphyses that are pincerlike in lateral view; inner paraphysis lost; subepandrial appendage well developed, protruding, apex triangular with an apical "nipple"; hypandrium with 1 or 2 small, wrinkled lobes; *Amiota biacuminis* distinguished from other species as follows: Arista plumosity shorter; lower lobe of outer paraphysis with apex rounded (vs. bifid); surstylus with fewer prensisetæ (7 vs. 12–14); hypandrium with two wrinkled lobes flanking apex (vs. 1).

DESCRIPTION: Large fly (ThL 1.52–1.74 mm), dark blackish brown, pleura entirely dark (including katapisternum); legs yellow. Characteristic markings typical of genus present. Frons dark brown, fading to light brown at margins and orbital plate. Cheek very deep (EL/CW 6.18–7.5), yellowish. Facial marking large, depth 0.25× width. Palp brown. Tergites 1 and 2 lightly colored. Arista: Short, plumose; longest branch D3; A.R. 0.27; 3 longer dorsal, 1 short dorsal, 3 very short ventral branches preapically; no branches pointed significantly mediad or laterad; arista trunk with medium-length microtrichia, bare on apical third. Male genitalia: Epandrium complete dorsally, ventral margin in this area evanescent, graded into membrane below. Cercus of moderate size, nearly grading with surrounding membrane, but margins discrete and faint. Surstylus oval shaped; 7 long prensisetæ, apices blunt, closely arranged, comblike; setulae along ventral margin; row of medially projecting setulae dorsal to prensisetæ. Subepandrial sclerite well developed; subepandrial appendage present, triangular in full ventral view, broad at base and tapering to small, nipplelike point. Outer paraphysis heavily sclerotized, compressed laterally, pincerlike in lateral view, with 2 lobes: upper lobe slender and pointed, lower lobe thicker with apex rounded. Inner paraphysis lost. Aedeagal apodeme slightly rectangular, width 0.80× length, the basal lateral margins heavily sclerotized; with slightly lateral constriction, anterior margin with faint emargination. Hypandrium roughly squared, inner margin more sclerotized; apex with two flattened, wrinkled, paramedian lobes; lateral arm with large swollen gonopod, ventrally pointed. Ejaculatory apodeme long, length equal to depth of epandrium. Head and thorax measurements: ( $n = 5$ ; Am 1420, 1449, 1481, 1485, 1515) FL/FW 0.47 (0.43–0.51), EL/EW 1.28 (1.17–1.39), EL/CW 6.57 (6.18–7.5), FML/FMW 0.26 (0.24–0.28), PR/RR 0.46 (0.36–0.50), ThL 1.60 (1.52–1.74 mm).

TYPE MATERIAL: **Holotype**: male: 14 mi. SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June "9" 1964, J.F. McAl-

pine, attracted to man, Am 1485, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC). **Paratypes:** 14 mi. SW. El Salto, Dgo. [Durango] MEX., June "9" 1964, J.F. McAlpine, attracted to man, 2♂ (Am 1486\*, 1522\*, CNC); 14 mi. SW. El Salto, Dgo. [Durango] MEX., 8000', June "26" 1964, J.F. McAlpine, attracted to man, 4♂ (Am 1449\*, 1457\*, 1481\*, 1494\*, CNC).

**OTHER MATERIAL EXAMINED:** **Mexico: Chiapas:** 16 mi. NW Comitán, 5000', 1969-05-18, leg. H.J. Teskey, (Am 1420\*, CNC). **Durango:** 24 mi W La Ciudad, 7000', 1964-06-25, leg. J.F. McAlpine, 1♂ (Am 1515\*, CNC).

**ETYMOLOGY:** Formed from Latin *bi-* for "two" and *acuminis* for "sharp point," in reference to the two points on the apex of the hypandrium.

**DISTRIBUTION:** *Amiota biacuminis* is known from the states of Durango and Chiapas in Mexico.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota forceps*, sp. nov.

Figures 34E–F, 37C; 39A, N–P, S; 87C

**DIAGNOSIS:** Small fly (ThL 1.15 mm), dark blackish brown; frons slightly shiny ventrally, with a bluish pruinescence, dark dorsally; white spots characteristic of genus present; similar to species in a complex including *A. uniacuminis* and *A. biacuminis* (defined under *A. biacuminis*), but differing from those species by the following: outer paraphysis with upper and lower lobes of equal length (vs. upper one longer), upper lobe slender, pointed, lower lobe flared at apex, truncate; hypandrium nearly square, apex notched, with small rounded, median lobe; prensisetae long, very slender, and densely packed, 14 prensisetae present (vs. 12 much shorter ones in *A. uniacuminis* and 7 stout ones in *A. biacuminis*).

**DESCRIPTION:** Small fly (ThL 1.15 mm), dark blackish brown, fading ventrally, including katapisternum; legs light yellow. Characteristic markings typical of genus present. Frons slightly

shiny; dorsal portion almost black; ventral portion below with slight bluish pruinescence. Cheek relatively deep (EL/CW 10.66), yellowish. Palp yellow. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branch D1; A.R. 0.32; 5 dorsal branches grading to shortest apically, 3–4 very short ventral branches; no branches pointed significantly mediad laterad; arista trunk with medium-length microtrichia, bare on apical third. Male genitalia: Epandrium dorsally complete, ventral margin near this area grading into membrane below; lateral portions with numerous setae of medium length along most of length; ventral margin with small, medial emargination. Cercus with margins distinct, overall shape subcircular, with large membranous region dorsal to cercus. Surstylus oval shaped, with scattered setulae around midregion; 14 prensisetae, long, slender, apices blunt, closely packed. Subepandrial sclerite well developed, laterally slightly compressed; subepandrial appendage triangular middle portion slightly constricted, apex dull point. Outer paraphysis with 2 lobes of equal length in lateral view: upper lobe linear, straight, pointed; lower lobe thicker, truncate, with 2 small terminal points. Inner paraphysis lost. Aedeagal apodeme with very similar proportions to *A. biacuminis* and *A. uniacuminis*. Hypandrium roughly square inner margin more sclerotized; apex notched on inner margin; opposite this a small, flat, faintly wrinkled lobe. Ejaculatory apodeme not studied. Head and thorax measurements: (n = 1, Am 1452) FL/FW 0.49, EL/EW 1.39, EL/CW 10.66, FML/FMW 0.22, PR/RR 0.40, ThL 1.15 mm.

**TYPE MATERIAL:** **Holotype:** male: 14 mi. SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June "26" 1964, J.F. McAlpine, attracted to man, Am 1452, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** From *forceps*, Latin for "pincers," in reference to the paraphyses of the male genitalia in lateral view. Used as a noun in apposition.

**DISTRIBUTION:** *Amiota forceps* is currently known from Durango State in Mexico.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota minor* (Malloch, 1921)

Figures 35A–B, 37D, F, 40, 88A

*Phortica minor* Malloch, 1921: 312 (original description).

*Amiota minor* (Malloch), 1924: 30 (comb. nov. by Malloch and male genitalia figured); Wheeler, 1949: 260 (discussion); Wheeler, 1952: 169 (discussion and key to Nearctic species); Wheeler, 1965: 761 (Nearctic catalog); Wheeler and Takada, 1971: 226 (male genitalia figured); Máca, 2003: 263–264 (discussion and male genitalia figured); Brake and Bächli, 2008: 253 (world catalog).

**DIAGNOSIS:** Very small to medium-sized fly (ThL 0.95–1.23 mm); light honey-golden to dark brown in color, abdomen dark brown or almost black; characteristic white markings of genus entirely absent or very faint; middle tibia with comb of ~10 setae; outer paraphysis forming forked structure (in lateral view); inner paraphysis lost; aedeagal apodeme broad and almost circular.

**DESCRIPTION:** Very small to medium-sized fly (ThL 0.95–1.23 mm); light honey-golden to dark brown in color, abdomen dark brown or almost black; legs yellow to nearly white. Characteristic white markings of genus on face, beneath wing base, and postpronotal lobe entirely absent or very faint. Frons dark brown, nearly black, except orbital plate. Cheek small (EL/CW 13.25–20.33), variable in coloration. Palp yellow to brown. Katepisternum lighter than rest of pleuron. Middle tibia with comb composed of ~10 setae, length of longest setae ~0.7× width of tibia. Tergite 1 lightly colored. Arista: Long, plumose; longest branch D4; A.R. 0.48; 4 long dorsal, 3 shorter ventral branches; branch V1 pointed anteriad,

V2 pointed mediad; arista trunk with medium-length to long microtrichia. Male genitalia: Epandrium dorsally complete, fused at midline and grading into membrane surrounding cerci. Cercus relatively large, oval shaped, fused dorsally with surrounding membrane (most margins are discrete); large gap laterally, no obvious membrane between cercus and epandrium. Surstylus short, handlike; 4–7 short prensisetae, apices blunt, arranged on rounded edge; widely spaced, space size increasing laterally. Subepandrial sclerite large, broad, and with upturned subepandrial appendage having a pair of ostia. Outer paraphysis forming a forked structure (as seen in lateral view); left and right side appear unfused in anterior view: well sclerotized; with 1 spine directed forward, the other backward, plus a thicker, lobelike structure dorsally. Inner paraphysis lost. Aedeagal apodeme broad, width nearly equal to length; distal end circular, concave depression absent. Hypandrium simple, with apical notch. Ejaculatory apodeme 0.5× depth of epandrium. Head and thorax measurements: (n = 5; Am 39, 230, 242, 365, 720) FL/FW 0.63 (0.56–0.77), EL/EW 1.38 (1.26–1.45), EL/CW 17.04 (13.25–20.33), FML/FMW 0.33 (0.25–0.45), PR/RR 0.49 (0.30–0.62), ThL 1.08 (0.95–1.23 mm).

**TYPE MATERIAL:** **Holotype:** male: “Dubois, June 5, 20,” [white label, computer printed] INHS Insect Collection 238.816, [red label] “Holotype, *Phortica minor* Malloch, ♂,” [38.220808, -89.211255], [glued to point, not dissected], [examined]. Deposited in the Illinois Natural History Survey (INHS). **Paratypes:** Du Bois Ill., June 3, 1919, Am 1611, [blue label] PARATYPE “*Phortica minor* Malloch ♂,” [examined]. Deposited in the Illinois Natural History Survey (INHS); Dubois, August 12, 1920, [not seen in collection], sex unknown. Deposited in the Illinois Natural History Survey (INHS).

**OTHER MATERIAL EXAMINED:** **Canada: Manitoba:** Max Lake, Turtle Mtn. For. Res., 1958-07-30, leg. J.G. Chillcott, 1 ♀ (Am 1433, CNC). **New Brunswick:** Priceville, 1971-07-20, leg. B.V. Peterson, 1 ♂ (Am 1442, CNC); Renous, 1965-07-11, leg.

D.M. Wood, 1 ♂ (Am 1573, CNC). **Ontario:** Algonquin Province Park, Scott Lake, 1994-08-06, leg. S.A. Marshall, maple forest sweep, 1 ♂ (Am 566\*, DEBU); Algonquin Provincial Park, W.R.S., 1994-06-28, leg. R. Bonduriansky, [not female as label suggests], 1 ♂ (Am 606, DEBU); 1994-07-15, [collector unknown], 1 ♂ (Am 605, DEBU); Bruce Co., Bruce Peninsula National Park, High Dump Trail, 2000-07-07, leg. S. Paiero, debu00079793, sweep, 1 ♂ (Am 618, DEBU); Bruce Co., Dunks Bay, 2000-07-23 through 2000-07-27, leg. S.A. Marshall, swarming face, debu00079592, 1 ♂ (Am 616, DEBU); 2000-07-23 through 2000-07-27, leg. S.A. Marshall, debu00079460, 1 ♂ (Am 620, DEBU); 2000-07-23 through 2000-07-28, leg. S.A. Marshall, debu00079468, 1 ♂ (Am 617, DEBU); Grand Bend, 1939-07-05, leg. G.E. Shewell, 1 ♂ (Am 1341, CNC); Lanark Co., N. Burgess Twp., 1967-06-11, leg. D.M. Wood, 4 ♂ (Am 1569–1572, CNC); Leeds Co., Chaffey's Locks, 1973-06-21, leg. P. Ward, attracted to *Homo sapiens*, 3 ♂ (Am 1574–1576, CNC); Mer Bleue, 2014-08-23, leg. O. Lonsdale, CNC380700, 1 ♂ (Am 1198, CNC); Lyn, 1926-08-10, leg. G.S. Walley, 1 ♂ (Am 1338, CNC); Near Picton, 1970-07-07, leg. J.F. McAlpine, 2 ♂ (Am 1195, 1196, CNC); Noellville, 1974-08-10, leg. R.E. Roughley, 4 ♂ and 1 ♀ (Am 548\*, 550\*, 551, 552\*, 553, 554, DEBU); Ottawa, 1974-08-18, leg. J.R. Vockeroth, 1 ♂ (Am 1578, CNC); 1974-08-21, leg. J.R. Vockeroth, 1 ♂ (Am 1298, CNC); 1994-09-13, leg. J.R. Vockeroth, damp second-growth, *Acer-Betula* wood, 1 ♀ (Am 1394, CNC); Picton, 1970-07-07, leg. J.F. McAlpine, 2 ♂ (Am 1558, 1559, CNC); Sandbanks Pk, nr Picton, 1970-07-01, leg. J.F. McAlpine, 5 ♂ (Am 1562, 1563, 1565, 1566, 1568, CNC); Simcoe, 1939-06-26, leg. G.E. Shewell, 2 ♂ (Am 1339, 1340, CNC); Smith's Bay, Nr. Picton, 1970-01-07, leg. J.F. McAlpine, 8 ♂ (Am 1181, 1182, 1184, 1186, 1188, 1191, 1192, 1208, CNC); S. March, 1962-06-16, leg. J.R. Vockeroth, 1 ♂ (Am 1533, CNC). **Quebec:** Abbotsford, 1937-06-14, leg. G. Shewell, 3 ♂ (Am 1332–1334, CNC); 1936-08-30, leg. G. Shewell, 1 ♂ (Am 1323, CNC); 1934-07-24, leg. C.E. Bourgalt, 1 ♂ (Am 1307, CNC); Aylmer, 1924-06-27, leg. C.H. Curran, 2 ♂ (Am 1306, 1322, CNC); 1924-08-08, leg. C.H. Curran, C.H. Curran Collection Acc. 31144, 1 ♂ (Am 373, AMNH); Duncan Lake nr. Rupert, 1988-08-08, leg. J.F. McAlpine, hovering at my ear, 7 ♂ (Am 1400, 1401, 1403–1407, CNC); Hull, 1965-08-05, leg. B.V. Peterson, 1 ♂ (Am 1579, CNC);

Knowlton, 1929-07-05, leg. L.J. Milne, 2 ♂ (Am 1320, 1321, CNC); 1929-08-01, leg. L.J. Milne, 1 ♂ (Am 1337, CNC); Norway Bay, 1938-08-31, leg. G.E. Shewell, 1 ♂ (Am 1336, CNC); Old Chelsea, 1959-07-21, leg. J.R. Vockeroth, 3 ♂ (Am 1203–1205, CNC); 1965-06-20, leg. D.M. Wood, 8 ♂ (Am 1459, 1461, 1467, 1475, 1478, 1479, 1535, 1536, CNC). **USA:** **Alabama:** Clay Co., Talladega Nat. For., 33.443496, -85.839339, 2018-08-15, leg. L.E. Jones, swept around head, 1 ♂ (Am 924, AMNH); Haleyville, 1953-07-06, leg. M.R. Wheeler, 2 ♂ (Am 237\*, 238\* [dissection missing], AMNH); Lawrence Co., Bankhead Nat. For., 34.308325, -87.395084, 2018-08-15, leg. L.E. Jones, swept around head, 11 ♂ (Am 910, 911, 914–922, AMNH); Wilson Dam F.Q., 1942-07-12, leg. J.N. Belkin, 2 ♂ (Am 668, 669, LACM); Winston Co., Bankhead Nat. For., 34.285427, -87.396155, 2018-08-15, leg. L.E. Jones, swept around head, 14 ♂ and 1 ♀ (Am 895–909, AMNH). **Arizona:** Cochise Co., campground nr. SWRS, 31.872506, -109.233923, 2019-07-18, leg. L.E. Jones and J.L. Hughes, swept around head, 3 ♂ (Am 720\*, 1052, 1053\*, AMNH); Cochise Co., Vicinity of SWRS, 31.882018, -109.206636, 2019-07-18, leg. L.E. Jones and J.L. Hughes, swept around head, 8 ♂ (Am 1043–1046, 1047\*, 1049–1051, AMNH); 2019-07-19, leg. L.E. Jones and J.L. Hughes, swept around head, 6 ♂ (Am 1036–1041, AMNH); 2019-07-18, leg. J.L. Hughes and L.E. Jones, swept around head, 2 ♂ (Am 1034, 1035, AMNH); 2019-07-19, leg. J.L. Hughes and L.E. Jones, swept around head, 6 ♂ (Am 1028–1033, AMNH). **Arkansas:** Garland Co., Ouachita Nat. For., 34.540121, -93.352490, 2018-08-09, leg. L.E. Jones and J.L. Hughes, swept around head, 4 ♂ (Am 654\*, 844–846, AMNH); 2018-08-08, leg. J.L. Hughes and L.E. Jones, swept around head, 1 ♂ (Am 847, AMNH); Logan Co., Magazine Mt. 2750 ft., 1992-07-06, leg. D. Grimaldi, 8 ♂ (Am 328\*, 332, 338\*, 346\*, 352\*, 354\*, 357, 365\*, AMNH); 2200 ft., 1992-07-09, leg. D. Grimaldi, fr. oak sap flux, 1 ♂ (Am 350\*, AMNH); Johnson Co., Ozark National Forest, 2018-08-08, leg. L.E. Jones and J.L. Hughes, swept around head, 16 ♂ (Am 653\*, 822–824, 827–838, AMNH); 2018-08-08, leg. J.L. Hughes and L.E. Jones, swept around head, 4 ♂ (Am 840–843, AMNH). **District of Columbia:** Rock Creek Park, 1957-06-01, leg. P.H. Arnaud Jr., 1 ♂ (Am 396, CAS); 1957-06-09, leg. P.H. Arnaud Jr., 1 ♂ (Am 395, CAS). **Georgia:** Black Rock Mt. S.P., 1953-07-04, leg. M.R.

- Wheeler, 10♂ (Am 213, 216, 218\*, 219\*, 220, 223, 224, 225\*, 230\*, 231, AMNH); Holcomb crk., 1957-08-01, leg. W.R. Richards, 1♂ (Am 1329, CNC); Rabun Co., 1957-07-13, leg. W.R. Richards, 1♂ (Am 1325, CNC). **Idaho:** 4.5 mi N. Moscow Ida. Hgwy 95, 1954-07-28, leg. R. Moree, 1♂ (Am 407\*, WSU). **Illinois:** Carlinville, 1955-06-22, leg. M.R. Wheeler, 2♂ (Am 233\*, 250, AMNH); Equality, 1951-09-11, [collector unknown], 1♂ (Am 239\*, AMNH); Hardin Co., Shawnee Nat. For., 37.594631, -88.382478, 2018-08-08, leg. L.E. Jones and J.L. Hughes, swept around head, 9♂ and 1♀ (Am 754, 760, 766, 769, 775, 777, 780, 784, 787, 789, AMNH); 2018-08-08, leg. J.L. Hughes and L.E. Jones, swept around head, 8♂ (Am 792-795, 799, 800, 810, 812 AMNH); St. Clair Co., Stemler Cave Woods, 38.464886, -90.155530, 2019-05-24, leg. L.E. Jones, swept around head, 9♂ (Am 997-1004, 1090, AMNH); 2018-05-30, leg. C.R. Sopow and L.E. Jones, 2♂ (Am 1177, 1178, AMNH); 2018-05-30, leg. L.E. Jones and C.R. Sopow, 2♂ (Am 1179, 1180, AMNH); Union Co., Trail of Tears State Forest, 37.499757, -89.11340117, 2018-8-08, leg. L.E. Jones and J.L. Hughes, swept around head, 13♂ (Am 651\*, 652\*, 801-806, 809, 814-817, AMNH); 2018-8-08, leg. J.L. Hughes and L.E. Jones, swept around head, 3♂ (Am 818, 819, 821, AMNH). **Indiana:** Harrison Co., O'Bannon Woods St. Pk., 38.194962, -86.267880, 2018-08-14, leg. L.E. Jones, swept around head, 4♂ (Am 890-893, AMNH); Perry Co., Hoosier Nat. For., 38.195597, -86.613230, 2018-08-14, leg. L.E. Jones, swept around head, 22♂ (Am 866-887, AMNH); Posey Co., Murphy's Park, New Harmony, 1967-08-02, leg. H.B. Leech, 1♂ (Am 386, CAS). **Kentucky:** Rowan Co., Daniel Boone Nat. For., Sheltoe Trace trail 100, 38 23 07 N, 83 24 58 W, 2013-05-23, leg. J.M. Cumming, 1♂ (Am 1285, CNC). **Louisiana:** Rapides Par., Kisatchie Nat. For., 31.261073, -92.634975, 2018-08-10, leg. L.E. Jones and J.L. Hughes, swept around head, 5♂ (Am 849-853, AMNH). **Maine:** Mt. Desert I., 1948-07, leg. M.R. Wheeler and T.C. Hsu, 1890.7, A. acadia, [genitalia on slide], 1♂ (Am 248\*, AMNH); Mt. Katahdin, 1968-07-04, leg. D.M. Wood, 2♂ (Am 1220, 1221, CNC); Mt. Katahdin, Hunt Trail, 16-2400', 1968-07-01 through 1968-07-06, leg. D.M. Wood, 2♂ (Am 1217, 1218, CNC); Vanceboro, 1965-07-09, leg. D.M. Wood, 1♂ (Am 1219, CNC). **Michigan:** Delta Co., Escanaba, 45.732003, -87.081676, 2018-06, leg. T. Werner, 3♂ (Am 1094-1096, AMNH); 2018-08-27 through 2018-08-31, leg. T. Werner, 1♂ (Am 1092, AMNH); Marquette Co., Huron Mtns., Huron Mtn. Club property vicinity, 46.874950, -87.891717, 2018-07-06 through 2018-07-12, leg. T. Werner, 12♂ (Am 683\*, 1057, 1059, 1060, 1062, 1066, 1071, 1073, 1075, 1076, 1078, 1082, AMNH); Wayne Co., 1961-07-10, leg. G. Steyskal, 2♂ (Am 1308, 1309, CNC); 20 mi NE St. Ignace, Acadia, 1948-08-02 through 1948-08-03, leg. M.R. Wheeler and T.C. Hsu, 1903.6, 1♂ (Am 211\*, AMNH). **Mississippi:** Marshall Co., Wall Doxey St. Pk., 34.661856, -89.462140, 2018-08-12, leg. L.E. Jones and J.L. Hughes, swept around head, 6♂ and 2♀ (Am 856-863, AMNH); 2018-08-12, leg. J.L. Hughes and L.E. Jones, swept around head, 1♂ (Am 864, AMNH); Yalobusha Co., George P. Cossar State Park, leg. L.E. Jones and J.L. Hughes, 1♂ (Am 854, AMNH). **Missouri:** Carter Co., Ridge road at Road C, 4.5 mi SW of Van Buren, 1967-08-04, leg. H.B. Leech, 1♂ (Am 380, CAS); Lithium, 1952-09-05, [collector unknown], 1♂ (Am 229, AMNH); 1955-06-29, leg. M.R. Wheeler, 1♂ and 1♀ (Am 227\*, 228, AMNH); St. Fran. Co., St. Francois St. Pk., 37.973473, -90.529404, 2019-05-24, leg. L.E. Jones, swept around head, 6♂ (Am 1005-1010, AMNH); Williamsville, 1955-07-06, leg. E.C. Becker, 1♂ (Am 1330, CNC). **Nebraska:** Elkhorn River 2 mi E. Oakdale, 1950-08-21 through 1950-08-22, leg. M.R. Wheeler and Stephens, 2068.14, 3♂ (Am 234, 235\*, 236\*, AMNH). **New Jersey:** Lebanon State Forest, 1958-08-19, leg. Evan and Beneway, 1♂ (Am 307, AMNH). **New York:** Bronx Co., New York Bot. Garden, 40.864029, -73.875571, 2018-08, leg. L.E. Jones and L. Li, swept around head, 2♂ and 1♀ (Am 1024, 1025, 1027, AMNH); Jeff. Co., Wellesley Is., 1963-08-22, leg. L.L. Pechuman, 2♂ (Am 39\*, 40, AMNH); Monroe Co., Rochester, Highland Pk., 43.132600, -77.602784, 2018-06-13, leg. J. Jaenike, 3♂ (Am 1174-1176, AMNH); 2018-06-28, leg. J. Jaenike, 13♂ (Am 1138-1150, AMNH); 2018-07-10, leg. J. Jaenike, 25♂ (Am 1113-1137, AMNH); 2018-07-26, leg. J. Jaenike, 16♂ (Am 1097-1112, AMNH); 2018-08-08, leg. J. Jaenike, 3♂ (Am 1163-1165, AMNH); 2018-09-04, leg. J. Jaenike, 2♂ (Am 1166, 1167, AMNH); [no date], leg. J. Jaenike, 4♂ (Am 1170-1173, AMNH); Orange Co., Black Rock Forest, 41.410629, -74.014558, 2017-09-09, leg. L.E. Jones, swept around head, 3♂ (Am 523\*, 1015, 1016, AMNH); Putnam Co., Hudson Highlands State Park, 2017-09-23, leg. L.E. Jones and C.

Liriano, swept around head, 1 ♀ (Am, 1013, AMNH); Staten Island, 1923, [collector unknown], 1 ♂ (Am 245, AMNH). **North Carolina:** Cherokee, 1957-07-25, leg. W.R. Richards, 1 ♂ (Am 1328, CNC); Franklin, 2000', 1957-06-08, leg. W.R.M. Mason, 1 ♂ (Am 1335, CNC); Graham Co., Robbinsville, 1976-06-09, leg. G.E. Bohart, 10 ♂ (Am 508-511, 512\*, 513-517, EMUS); Highlands, 1957-07-13, leg. J.G. Chillcott, 1 ♂ (Am 1326, CNC); Jackson Co., Cherokee, 2000', 1957-07-25, leg. J.G. Chillcott, 1 ♂ (Am 1324, CNC); Transylvania Co., Pisgah Nat. For., 35.290995, -82.776835, 2018-08-20, leg. L.E. Jones, swept around head, 6 ♂ and 1 ♀ (Am 989-995, AMNH). **Ohio:** Portage Co., West Branch State Park, 1988-07-17, leg. B.A. Foote, 1 ♂ (Am 311, AMNH). **South Carolina:** Anderson, 1957-07-21, leg. W.R. Richards, 1 ♂ (Am 1327, CNC); Charleston Co., Francis Marion Nat. For., 33.067907, -79.518209, 2018-08-19, leg. L.E. Jones, swept around head, 1 ♂ (Am 658\*, AMNH); Greenwood, Long Cane Creek, 1957-07-21, leg. W.R. Richards, 1 ♂ (Am 1299, CNC); Seneca, 1957-06-06, leg. W.R.M. Mason, 1 ♂ (Am 1331, CNC); Sumter Co., Poinsett St. Pk., 33.802244, -80.545550, 2018-08-19, leg. L.E. Jones, swept around head, 26 ♂ (Am 659\*, 660\*, 925-941, 943-949, AMNH). **Tennessee:** Cades Cove, GSMNP, 1953-07 through 1953-08, leg. J.M. Carpenter, 9 ♂ (Am 209, 210, 214, 215, 217, 221\*, 222\*, 226\* [dissection missing], 232, AMNH); Great Smoky Mtns. Nat. Park, near Cosby headquarters, 35 47 N, 083 13 W, 2001-05-30, leg. J.A. Skevington, CNC 699259, 1 ♂ (Am 1294, CNC); Unicoi Co., Cherokee Nat. For., 36.137782, -82.350719, 2018-08-20, leg. L.E. Jones, swept around head, 40 ♂ (Am 662\*, 663\*, 950-988, AMNH). **Texas:** Austin Aldrich Farm, 1951-05-20, leg. M.R. Wheeler, 1 ♀ (Am 249\*, AMNH); Houston Co., Davy Crockett Nat. For., 31.390387, -95.157191, 2018-08-10, leg. L.E. Jones and J.L. Hughes, swept around head, 1 ♂ (Am 848, AMNH). **Vermont:** Orleans Co., nr. Bald Mountain, near stream (Mad Brook), 1650 ft., 2016-07-19 through 2016-07-21, sweep netted in forest, leg. D. Grimaldi, 2 ♂ (Am 366, 367\*, AMNH); 2018-08-16, leg. D. Grimaldi, swept around head, 8 ♂ (Am 665\*, 1017-1023, AMNH). **Virginia:** Giles Co., Cascade Falls, 2001-05-19, leg. O. Lonsdale, 6 ♂ (Am 744-746, 748, 751, 752, DEBU); Prince William Co., 0.5 km NE Thorofare Gap, vic. Haymarket, 1966-06-25, leg. P.H. Arnaud Jr., 2 ♂ (Am 397, 398, CAS). **Washington:** Wenatchee, 1950-08, leg. M.R. Wheeler,

2191.12, 5 ♂ and 1 ♀ (Am 212\*, 240\* [genitalia on slide], 241, 242\*, 243\*, 244, AMNH).

**DISTRIBUTION:** This species may have the widest distribution of any species of *Amiota* in North America. *Amiota minor* is exceptionally common throughout Eastern North America, with western populations known from Washington State and Arizona. This species probably occurs in northern Mexico. Wheeler (1952) reported *A. minor* from Veracruz in Mexico, but these specimens have not been seen.

**COMMENTS:** *Amiota minor* as known may represent a species complex. Substantial size and color variation is seen in this species, as well as the degree of faintness in the markings of the face, wing base, and postpronotal lobe. Wheeler (1952) noted great variation in the morphology of the surstylus. Size and shape of the aedeagal apodeme varies as well, with western populations differing in some cases from those in the east. It is notable for being the only species known in the genus to lack the characteristic white markings found in the other members (although these can be faded in other members of the *avipes* species group). *Amiota minor* is the only species in the group known to have the character of the comb on the midtibia. It can form dense swarms in humid settings and can lodge itself in the eye (L.E.J., personal obs.). This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

### *Amiota onyx*, sp. nov.

Figures 35C-D, 37E, G, 38A, C-D, F, H 88B

**DIAGNOSIS:** Small to medium-sized fly (ThL 0.98-1.22 mm), medium brown, darker above grading lighter ventrally, legs yellow; white markings characteristic of genus present, spot under wing base slightly faded; outer paraphyses heavily sclerotized, symmetrical, short, forming stout, strongly curved claw, winglike basal projection, pointing laterally; inner paraphysis lost.

**DESCRIPTION:** Small to medium-sized fly (ThL 0.98–1.22 mm), medium brown body, fading ventrally; legs yellow. Characteristic markings of genus present, marking under wing base rather faint. Frons medium brown, darkening to black ventrally. Facial marking of moderate width (FML/FMW 0.26–0.29). Palp brown. Cheek yellowish. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branch D2; A.R. 0.32; 2 longer and 3 shorter dorsal, 3 short ventral branches; branches D3–5 pointed mediad, V1–3 pointed laterad; arista trunk with medium-length microtrichia nearly to apex. Male genitalia: Epandrium dorsally complete but with ventral margin in this area graded into membrane below; row of ~6 setae leading near posterior margin. Cercus long, pendulous, dorsally grading into membrane and epandrium; lateral margins of cercus discrete; cerci large, occupying virtually all space surrounded by epandrium. Surstylus with 11 prenisetae, apices blunt, evenly and densely spaced, comblike; middle region and ventral margin with setulae. Subepandrial sclerite pyramidal in posterior view, not projecting beyond epandrium. Outer paraphysis heavily sclerotized, short, forming stout hooked claw; base with small row of minute sensilla; distinctive low carina basal to sensilla; basal winglike projection, pointing laterally, the distal end with faint striations. Inner paraphysis lost. Aedeagal apodeme with all 4 margins constricted, bent nearly 90° in lateral view; basal margin slightly wider than distal end; distal end hardly expanded; marginal constrictions very shallow. Hypandrium thick, roughly square in terminal view; lateral arms very thick, bulging, with a prominent ostium. Ejaculatory apodeme 0.60× length of epandrium; stalk slightly sinuous. Head and thorax measurements: (n = 2; Am 1450, 1505) FL/FW 0.55 (0.55–0.56), EL/EW 1.31 (1.27–1.36), EL/CW 11.72 (11.20–12.25), FML/FMW 0.27 (0.26–0.29), PR/RR 0.49 (0.44–0.55), ThL 1.10 (0.98–1.22 mm).

**TYPE MATERIAL:** **Holotype:** male: MEXICO, Chis. [Chiapas] 20–25 mi. N Huixtla, [15.537566, -92.473191], 3000', 4.VI.1969, B.V. Peterson,

“Amiota (Amiota)” det. D. Grimaldi 1991, Am 1505, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC).

**OTHER MATERIAL EXAMINED:** **Mexico:** **Durango:** 14 mi. SW. El Salto, 8000', 1964-06-26, leg. J.F. McAlpine, attracted to man (Am 1450\*, CNC).

**ETYMOLOGY:** Greek for “claw,” in reference to the paraphyses that in lateral view resemble a dark, curving claw.

**DISTRIBUTION:** *Amiota onyx* is known from Durango and Chiapas State in Mexico.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota pseudominor*, sp. nov.

Figures 36A–B, 37H–I, 41, 88C

**DIAGNOSIS:** Medium-sized fly (ThL 1.23–1.27 mm), dark brown to black; similar to *Amiota minor* (Malloch), but *A. pseudominor* differing externally by white markings present under wing base and faint marking on postpronotal lobe and face; darker frons; cheek relatively deep (EL/CW 11.6–12.2), white; surstylus with distinctive secondary lobe on posterior surface; epandrium with narrow dorsal gap; pair of outer paraphyses symmetrical, forked, upper prong straight, tapered to point, lower one shorter, curved upward, less sclerotized; ejaculatory apodeme large.

**DESCRIPTION:** Medium-sized fly (ThL 1.23–1.27 mm), dark brown to black; abdomen black. Characteristic markings of the genus present, although somewhat faded. Frons dark brown, black above ptilinal suture; slightly pollinose. Facial marking large (FML/FMW 0.28–0.35), semicircular, faint. Cheek relatively deep (EL/CW 11.6–12.2), white. Palp yellow. Arista: Short, plumose; longest branch D2; A.R. 0.36; 4 dorsal branches (D1 very short), 0 long ventral branches; 3 short apical-dorsal branches pointed laterad; arista trunk with short microtrichia, bare on apical half. Male genitalia: Epandrium sepa-

rated dorsally at midline, not grading into surrounding membrane; ventral lobe with dense cluster of long setae, row of 7 setae in single row ascending to apex. Cercus small, much smaller than space surrounded by epandrium; crescentic, margins discrete, distinctively protruding well beyond posterior surface of epandrium; surrounded by large membranous area dorsally. Surstylus very distinct: secondary bulbous lobe atop middle region, triangular membranous extension with cluster of long setulae adjacent; medial margin with several long setulae; 8 long prensisetae, apices blunt, closely arranged. Subepandrial sclerite large, scoop shaped, with posterior margin pointed and projected nearly to same level as tip of outer paraphysis. Outer paraphysis forming forked structure in lateral, heavily sclerotized, 2-pronged in lateral view; dorsal prong longer, tapered to point; lower prong shorter, less sclerotized, curved upward, bearing sensilla at base. Inner paraphysis lost. Aedeagal apodeme rectangular, almost square; distal margin even, barely flared, concave depression absent. Hypandrium simple, of relatively uniform thickness; lateral arms widely expanded, bulging outward anteriorly and posteriorly. Ejaculatory apodeme large, 0.9× size of epandrium. Head and thorax measurements: (n = 2; Am 256, 257) FL/FW 0.61 (0.54–0.69), EL/EW 1.43 (1.41–1.45), EL/CW 11.9 (11.6–12.2), FML/FMW 0.63 (0.28–0.35), PR/RR 0.47 (0.45–0.50), ThL 1.25 (1.23–1.27 mm).

**TYPE MATERIAL:** **Holotype:** male: 30 klm. N Chilpancingo, Guerrero, Mex., [17.945004, -99.513764], July 1952, M Wasserman, WB Heed, “2266.19,” Am 256, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratype:** 30 klm. N Chilpancingo, Guerrero, Mex., July 1952, M Wasserman, WB Heed, “2266.19,” “A. barretti,” 1♂ (Am 257\*, AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the type series.

**ETYMOLOGY:** Formed from *pseudo*-, Greek for “false,” and *minor*, a previously described species in the genus. In reference to the deceptive nature

of the new species, with male genitalia very similar to *A. minor*, but with the characteristic external markings of the genus, although faded, which *A. minor* lacks.

**DISTRIBUTION:** *Amiota pseudominor* is currently known from Guerrero State in Mexico.

**COMMENTS:** This species, related to *A. minor* but unlike it, exhibits the characteristic markings of other members of the genus.

### *Amiota uniacuminis*, sp. nov.

Figures 36C–D; 39B, C, G, K–M, R; 89A

**DIAGNOSIS:** Medium-sized fly (ThL 1.09–1.32 mm); dark brown, legs dark yellow; characteristic markings of postpronotal lobe and face faded, marking on wing base less so; cheek relatively deep (EL/CW 8.57–10.60); similar to other species in complex, including *A. biacuminis* and *A. forceps* (defined under *A. biacuminis*), but differing from them by the following: epandrium nearly semicircular in terminal view (vs. narrowed dorsally in *A. biacuminis* and *A. forceps*); outer paraphysis with tapered, pointed upper lobe, extended well beyond level of lower lobe, lower lobe with distal end slightly expanded with 2 small points; hypandrium with prominent, wrinkled, median lobe at apex (vs. pair of such lobes in *A. biacuminis*), apex not deeply notched (vs. notched in *A. forceps*); surstylus with shorter prensisetae (~1/2 length in other species).

**DESCRIPTION:** Medium-sized fly (ThL 1.09–1.32 mm); dark brown, legs dark yellow. Katepisternum lighter than remaining pleuron. Markings on postpronotal and face faded, marking on wing base less so comparatively. Frons dark brown dorsally; light brown ventrally, concentrated in ventrolateral corners. Cheek relatively deep (EL/CW 8.57–10.60), white posteriorly. Palp brown. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branch D2; A.R. 0.38; 5 dorsal branches decreasing in length apicad, 4 short ventral branches; arisal trunk with medium-length microtrichia along entire length. Male genitalia: Epandrium wide, virtually semicircular in termi-

nal view; dorsally complete, ventral margin grading with membrane below region. Cercus pendulous, slightly crescentic, faintly grading into membrane dorsally. Surstylus with setulae on ventral half; 12 prensisetae, apices blunt, closely spaced, the innermost medial 4 slightly more spaced; prensisetae relatively short. Subepandrial sclerite well developed, compressed laterally; subepandrial appendage present, nearly triangular in full terminal view, with pointed, nipplelike tip. Outer paraphysis with upper lobe extended well beyond level of lower lobe, upper lobe tapered, pointed; lower lobe with distal end slightly expanded with 2 small points, several scattered sensilla near base. Inner paraphysis lost. Aedeagal apodeme rectangular, width  $0.80\times$  length, each margin faintly concave. Hypandrium of uniform thickness, inner margin more sclerotized; apex with a flat, rounded, slightly wrinkled lobe. Ejaculatory apodeme relatively small, half the length of the epandrium, stalk straight. Head and thorax measurements: ( $n = 3$ ; Am 254, 255, 1511) FL/FW 0.60 (0.54–0.66), EL/EW 1.30 (1.25–1.35), EL/CW 9.72 (8.57–10.60), FML/FMW 0.23 (0.19–0.26), PR/RR 0.48 (0.40–0.55), ThL 1.19 (1.09–1.32 mm).

**TYPE MATERIAL:** **Holotype:** male: 14 mi. SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June "26" 1964, J.F. McAlpine, attracted to man, Am 1511, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC). **Paratype:** 14 mi. SW. El Salto, Dgo. [Durango] MEX., 8000', June "26" 1964, J.F. McAlpine, attracted to man, 1 ♂ (Am 1412\*, CNC).

**OTHER MATERIAL EXAMINED:** **Mexico:** **Guerro:** 30 klm. N. Chilpancingo, July 1952, leg. M. Wasserman and W.B. Heed, 2266.19, 2 ♂ (Am 254\*, 255\*, AMNH).

**ETYMOLOGY:** Formed from Latin *uni-* for "one" and *acuminis* for "point." In reference to the pointed lobe at the apex of the hypandrium.

**DISTRIBUTION:** *Amiota uniacuminis* is known to inhabit a wide swath of Mexico, from Durango and Guerrero State.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

#### THE *RUFESCENS* SPECIES GROUP

**DIAGNOSIS:** Large flies; light colored, scutum dark yellow to ochre, with typical white markings; frons dull, dark yellowish to ochre/light brown; arisal branches medium to long. Male genitalia: Outer paraphysis slender, linear, simple (no spines or a pair of very small ones), with sensilla; prensisetae pointed; subepandrial sclerite strongly recurved, U-shaped.

**NEARCTIC SPECIES:** *Amiota leucostoma* Loew, *A. mcalpinei*, sp. nov., and *A. tessae*, sp. nov.

**COMMENTS:** This group was established by Chen and Toda (2001), for three Old World species: *A. magniflava* Chen and Toda, *A. rufescens* (Oldenberg), and *A. stylopyga* Wakahama and Okada. *Amiota leucostoma* Loew was added later (Chen et al., 2004). The original diagnosis was based on one of the characters we also observed, the pointed prensisetae, to which we add several additional male genitalic characters. Two Nearctic species are being added here, *A. mcalpinei* and *A. tessae*. Since species groups are informal categories there is no need to rename the group for the first species described (*A. leucostoma* Loew); taxonomic priority is not required, though generally followed.

#### *Amiota leucostoma* Loew, 1862

Figures 42A–B, 43, 44A–B, 45A–B, F–G, 89B

*Amiota leucostoma* Loew, 1862a: 230 (original description); Coquillett, 1910: 505 (designated as genotype); Sturtevant, 1921: 57 (synonymy under *Stegana humeralis*); Malloch and McAtee, 1924: 41, plate VIII, figs. 6–8 (male genitalia figured); Wheeler, 1949: 260–261 (discussion); Wheeler, 1952: 169 (key to Nearctic species); Wheeler, 1965:

761 (Nearctic catalog); Chen, 2004: 66 (inclusion in species group); Brake and Bächli, 2008: 253 (world catalog).

*Phortica leucostoma* (Loew): Malloch, 1921: 312 (comb. nov. by Malloch).

**DIAGNOSIS** Large fly (ThL 1.72–1.94 mm), light brown to light golden-honey in color, abdomen dark brown to almost black, overall coloration similar to *A. minor*, except with characteristic white markings of genus; outer paraphysis long, swordlike, with small lateral spine 1/3 from apex; inner paraphysis more heavily sclerotized, hooked strongly medially, with small preapical tooth; aedeagal apodeme curved 90° in lateral view, distal end widely flared, with a wide shallow concave depression. *Amiota leucostoma* is very similar to *A. mcalpini* from British Columbia, *A. tessae* from the Great Lakes region, and *A. rufescens* (Oldenberg) from Europe, but *A. leucostoma* can be easily separated by the presence of a lateral spine on the outer paraphysis.

**DESCRIPTION:** Large fly (ThL 1.72–1.94 mm), light brown to light golden honey, seta black; abdomen dark brown to almost black, legs yellow; coloration similar to *A. minor* (Malloch), except with characteristic white markings of genus. Frons light brown, ventral half darker, with numerous scattered black setulae. Cheek yellow on anterior half, whitish yellow on posterior half. Palp yellow. Tergites 1 and 2 lightly colored. Arista: Long, plumose; longest branch D2; A.R. 0.42; 6 dorsal, 3 ventral branches; branches V1 and V2 pointed mediad, D4 pointed laterad; arista trunk with medium-length microtrichia along much of length. Male genitalia: Epandrium with gap at midline; long setae clustered at ventral portion, ascending to apex. Cercus semicircular. Surstylus pendulous, length greater than twice the width; with 9 pointed prensisetae (not rounded); distal end densely crowded with long setulae. Subepandrial sclerite with a long appendage, ventral to epandrium, the distal end rounded,

bent strongly upward. Outer paraphysis long and swordlike; several sensilla pits scattered throughout middle portion; lateral spine 1/3 distance from apex, with sensillum just distal to spine. Inner paraphysis heavily sclerotized, curving strongly medially, with subapical tooth. Aedeagal apodeme bent 90° at midpoint; widely flared on distal end, deeply concave; almost equal in length to the outer paraphysis. Hypandrium deeply notched, web of membrane between hypandrium apex; lateral arms thickened, with a prominent bulging gonopod. Ejaculatory apodeme long, thick, length equal to the epandrium. Head and thorax measurements: (n = 5; Am 379, 399, 1202, 1314, 1319) FL/FW 0.67 (0.61–0.70), EL/EW 1.30 (1.25–1.36), EL/CW 17.72 (15–19.75), FML/FMW 0.38 (0.37–0.41), PR/RR 0.56 (0.33–0.75), ThL 1.84 (1.72–1.94 mm).

**TYPE MATERIAL:** **Holotype:** female: USA: Pennsylvania: Loew Coll., Penn., “leucostoma m.” “Type 13407,” [barcode] MCZ-ENT00013407, [leg. C.R. Osten-Sacken], [not examined, only photomicrographs reviewed]. Deposited in the Harvard Museum of Comparative Zoology, Cambridge (MCZC).

**OTHER MATERIAL EXAMINED:** **Canada: British Columbia:** Cultus Lake, 1948-07-15, leg. H.R. Foxlee, Exp No 12129-13, 1♂ (Am 1313\*, CNC); 1948-07-17, leg. H.R. Foxlee, 1♂ (Am 1312\*, CNC). **Quebec:** Aylmer, 1926-08-12, [collector unknown], 1♂ (Am 1318\*, CNC); Cottage Beaulieu [location uncertain], 1906-07-07, [collector unknown], 1♂ (Am 1319\*, CNC); Laniel, 1973-07-24, leg. F.P. Ide, 1♂ (Am 1314\*, CNC); Old Chelsea, Summit King Mtn., 1962-06-25, leg. J.R. Vockeroth, 1♂ (Am 1202\*, CNC). **USA: Illinois:** Urbana, 1916-06-26, [leg. J.R. Malloch], tree trunk, 1♂ (Am 1590, INHS); 1916-08-08, [leg. J.R. Malloch], 1♂ (Am 1589, INHS). **Maryland:** **Pennsylvania:** Valley Forge, 1912-07-15, collector unknown, 4♂ (Am 1600\*, 1603–1605\*, INHS); Montgomery Co., Cabin John, 1929-06, leg. F.R. Cole, 1♂ (Am 379\*, CAS). **Virginia:** Blacksburg, 1953-09-09, leg. M. Levitan, 1♀ (Am 297, AMNH); Prince William Co., 0.5 km NE Thorofare Gap, vic. Haymarket, 1966-06-25, leg. P.H. Arnaud Jr., 1♂ (Am 399\*, CAS).

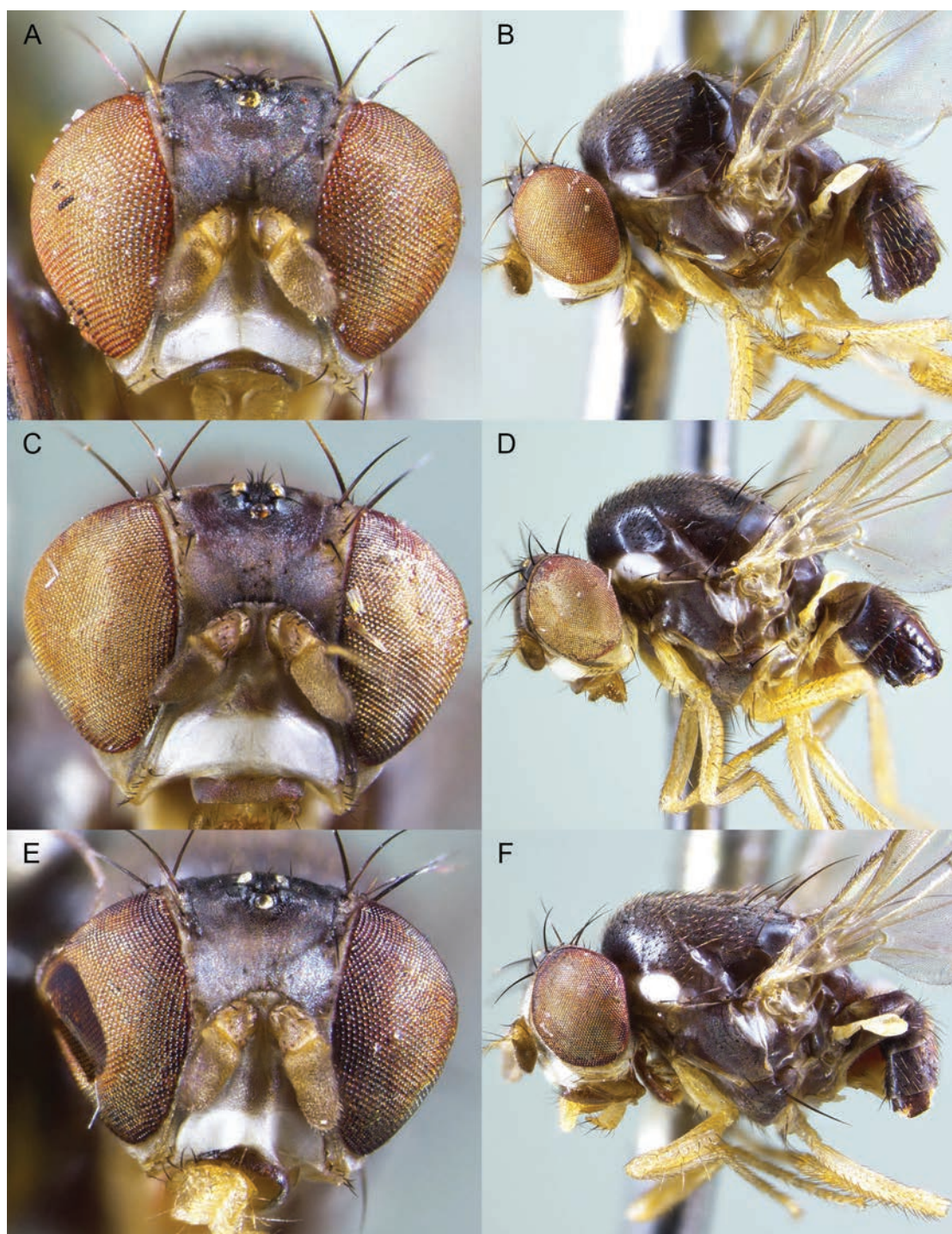


FIG. 34. Heads and lateral views, *A. avipes* species group. A–B. *A. avipes*, sp. nov. (Am 1514, paratype). C–D. *A. biacuminis*, sp. nov. (Am 1494, paratype). E–F. *A. forceps*, sp. nov. (Am 1452, holotype).

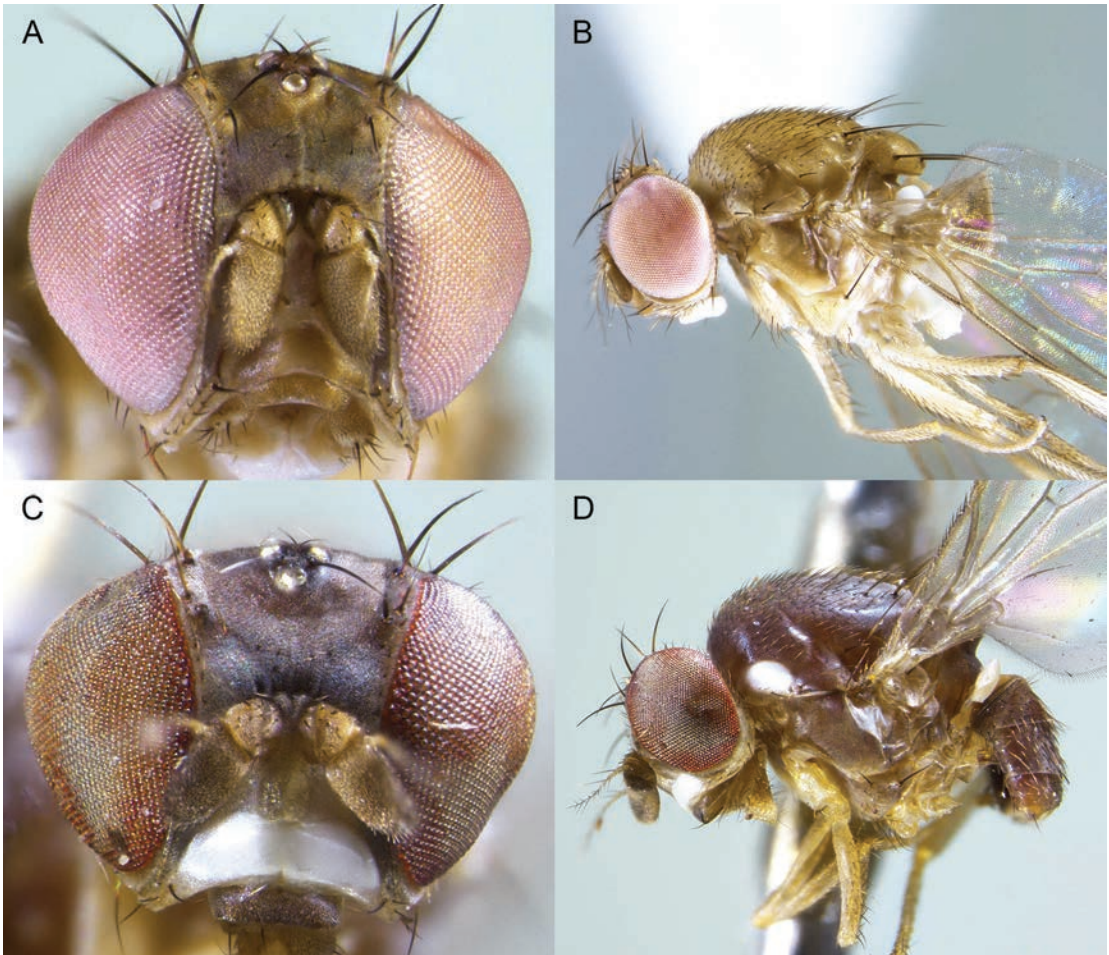


FIG. 35. Heads and lateral views, *A. avipes* species group. **A–B.** *A. minor* (Malloch) (Am 651). Lack of white spots is natural. **C–D.** *A. onyx*, sp. nov. (Am 1450).

**DISTRIBUTION:** This species is rarely collected and has a large distribution, most records from the Mid-Atlantic and eastern Canada, with one specimen collected as far west as British Columbia. The type locality is in Pennsylvania.

**COMMENTS:** *Amiota leucostoma* has long been thought to be synonymous with *A. rufescens* (Oldenberg) of Europe (Malloch and McAtee, 1924), but morphology of specimens from various localities reveals consistent differences. The holotype of *A. leucostoma* was collected in Pennsylvania (fig. 43). Wheeler (1952) erroneously referred to *A. humeralis* Loew as the type species of the genus, but *A. leucostoma* Loew was designated as so by

Coquillett (1910). It is unknown whether *A. leucostoma* is attracted to the eyes and face as is common in other *Amiota*, but this is likely given its presence in another Nearctic member of this species group, *A. tessae*.

***Amiota mcalpinei*, sp. nov.**

Figures 42C–D, 45C–E, H, 89C

**DIAGNOSIS:** Large fly (ThL 1.71 mm); medium brown to ochre, abdomen nearly black; coloration similar to *A. minor* (Malloch), except with characteristic white markings of genus; outer

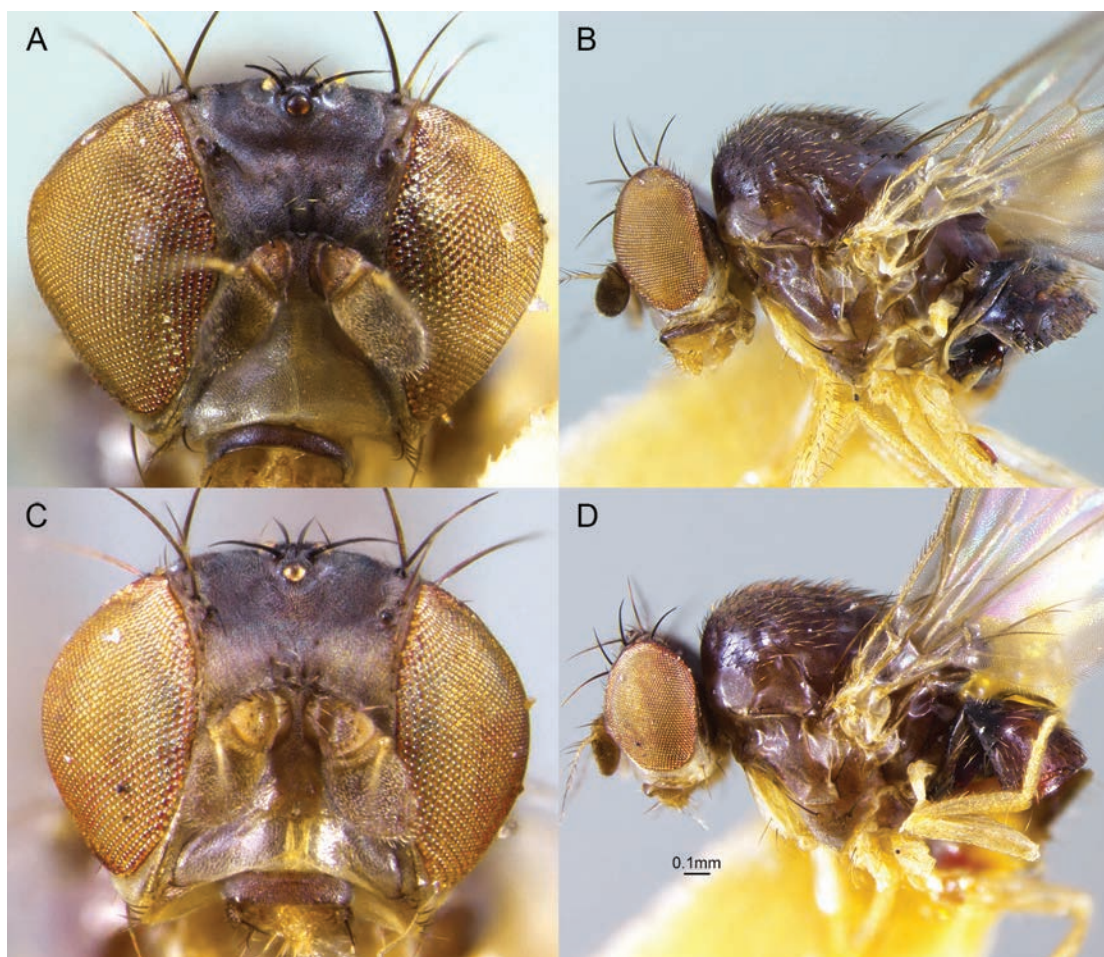


FIG. 36. Heads and lateral views, *A. avipes* species group. **A–B.** *A. pseudominor*, sp. nov. (Am 256, holotype, lateral image flipped). **C–D.** *A. uniacuminis*, sp. nov. (Am 255, lateral image flipped). Lack of white spots is likely an effect due to preservation.

paraphysis long, slender, lacking lateral spine; tapering acutely to mucronate point, lacking terminal sensillum; inner paraphysis robust, curving medially and overlapping; aedeagal apodeme lightly sclerotized; similar to other Nearctic species, but easily distinguished by lack of a lateral spine on the outer paraphysis (as in *A. leucostoma* Loew) or a terminal trichoid sensillum (as in *A. tessae*); differs from *A. rufescens* by having shorter outer paraphysis and a large, strongly hooked inner paraphysis.

**DESCRIPTION:** Large fly (ThL 1.71 mm), medium brown to ochre, uniformly so, setae

black; legs yellow; abdomen nearly black; coloration similar to *A. minor* (Malloch), except with characteristic white markings of genus. Frons blackish on dorsal half, yellow ventrally. Cheek yellow on anterior half, whitish gray on posterior half. Palp yellow. Tergites 1 and 2 lightly colored. Arista: Medium plumose; A.R. 0.3; longest branch D5, D6 points mediad; 6 long dorsal (1 short preapical), 4 shorter ventral branches; arisal trunk with medium-length microtrichia along entire length. Male genitalia: Epandrium with dorsal gap. Cercus semicircular. Surstylus pendulous, distal end covered in setulae; prenisetae

pointed (not round). Subepandrial sclerite wide; forming long subepandrial appendage, distal end rounded. Outer paraphysis long and swordlike, lightly sclerotized; midpoint with several scattered sensilla pits, distal end tapering acutely to mucronate point. Inner paraphysis a spine of medium sclerotization, curving medially; anterior hook present, overlapping with adjacent paraphysis. Aedeagal apodeme lightly sclerotized, slightly wider than long; lightly concave depression. Hypandrium U-shaped; lateral arm with a long, lobelike gonopod. Ejaculatory apodeme slender, length equal to depth of epandrium, bent at 2/3 the length from distal end. Head and thorax measurements: (n = 1, Am 1315) FL/FW 0.70, EL/EW 1.40, EL/CW 16.8, FML/FMW 0.33, PR/RR 0.50, ThL 1.71 mm.

**TYPE MATERIAL:** **Holotype:** male: Cultus Lake, B.C. [British Columbia], [49.047143, -121.979228], "8".VIII.1948, H.R. Foxlee, "*Amiota leucostoma*" d. G.Steyskal, Am 1315, [specimen glued to pin, dissected]. Deposited in Canadian National Collection (CNC).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** Named for James F. McAlpine (1922–2019), renowned dipterist at the Canadian National Collection, Ottawa, and collector of many of the Mexican specimens used in this revision.

**DISTRIBUTION:** The holotype was collected in British Columbia, but the species is likely more widespread in western Canada.

**COMMENTS:** It is unknown whether this species is attracted to the eyes and face as other *Amiota*, but this is likely the case due to its close relationship with *A. tessae*, which is known to exhibit this behavior.

*Amiota tessae*, sp. nov.

Figures 42E–F, 46, 90A

**DIAGNOSIS:** Very large fly (ThL 1.61–1.92 mm), medium brown, grading darker ventrally, abdomen nearly black; similar coloration to *A. minor*, except characteristic markings of genus

present; outer paraphysis long, heavily sclerotized, sinuous in dorsal/ventral, lacking lateral spine, trichoid sensillum on distal end; inner paraphysis short, heavily sclerotized, U-shaped in dorsal/ventral views with lateral hook, inner tips distant (not almost touching as in *leucostoma* and *mc Alpinei*).

**DESCRIPTION:** Very large fly (ThL 1.61–1.92 mm), medium brown grading darker ventrally, setation black, legs dark yellow; abdomen nearly black; coloration similar to *A. minor* (Malloch), except characteristic markings of genus present. Frons ochre, matte, with dark brown triangle, relatively broad (FL/FW 0.60–0.76). Cheek yellowish brown on anterior half, yellowish gray on posterior half. Palp yellow. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branch D2; A.R. 0.33; 4 long dorsal branches, 4 shorter ventral branches; arisal trunk with medium-length microtrichia along entire length. Male genitalia: Epandrium stout, with broad ventral lobes; separated dorsomedially, ventral lobe densely setose, lateral portion of epandrium lacking microtrichia. Cercus crescentic, margins distinct from surrounding membrane (not grading), cercus occupies most of space surrounded by epandrium. Surstylus with 12 prenisetae, slightly curved, apices pointed (not round); distal end of surstylus densely hairy. Subepandrial sclerite large, well developed, sclerotized, strongly U-shaped in lateral view; a long, phalluslike subepandrial appendage ventral to epandrium and projecting slightly beyond, distal end of appendage round, surrounded by fine membrane. Outer paraphysis long, slender and linear, heavily sclerotized, slightly sinuous in dorsal/ventral views, tapering to a point, sensillum on distal end; middle with several sensilla pits ventrally. Inner paraphysis short, heavily sclerotized, slightly C-shaped, central groove down middle, distal appendage pointed posterolaterally. Aedeagal apodeme long, bent 90° in lateral view and slightly sinuous; distal end widely flared and deeply concave. Hypandrium narrow, forming wide square, apex slightly notched; lateral arm

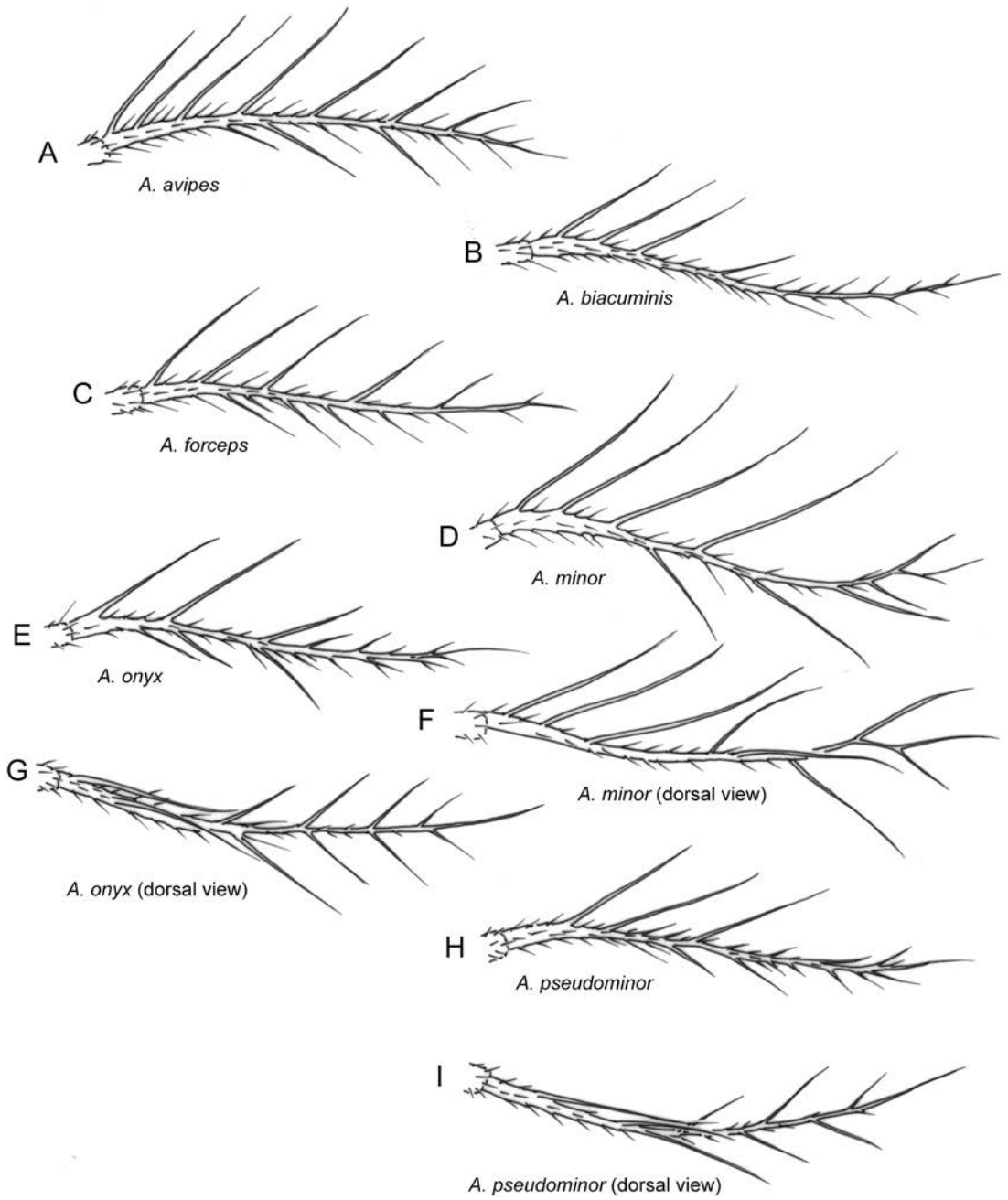


FIG. 37. Aristae, *A. avipes* species group. A. *A. avipes*. B. *A. biacuminis*. C. *A. forceps*. D, F. *A. minor* (Malloch). E, G. *A. onyx*. H–I. *A. pseudominor*. Not to the same scale.

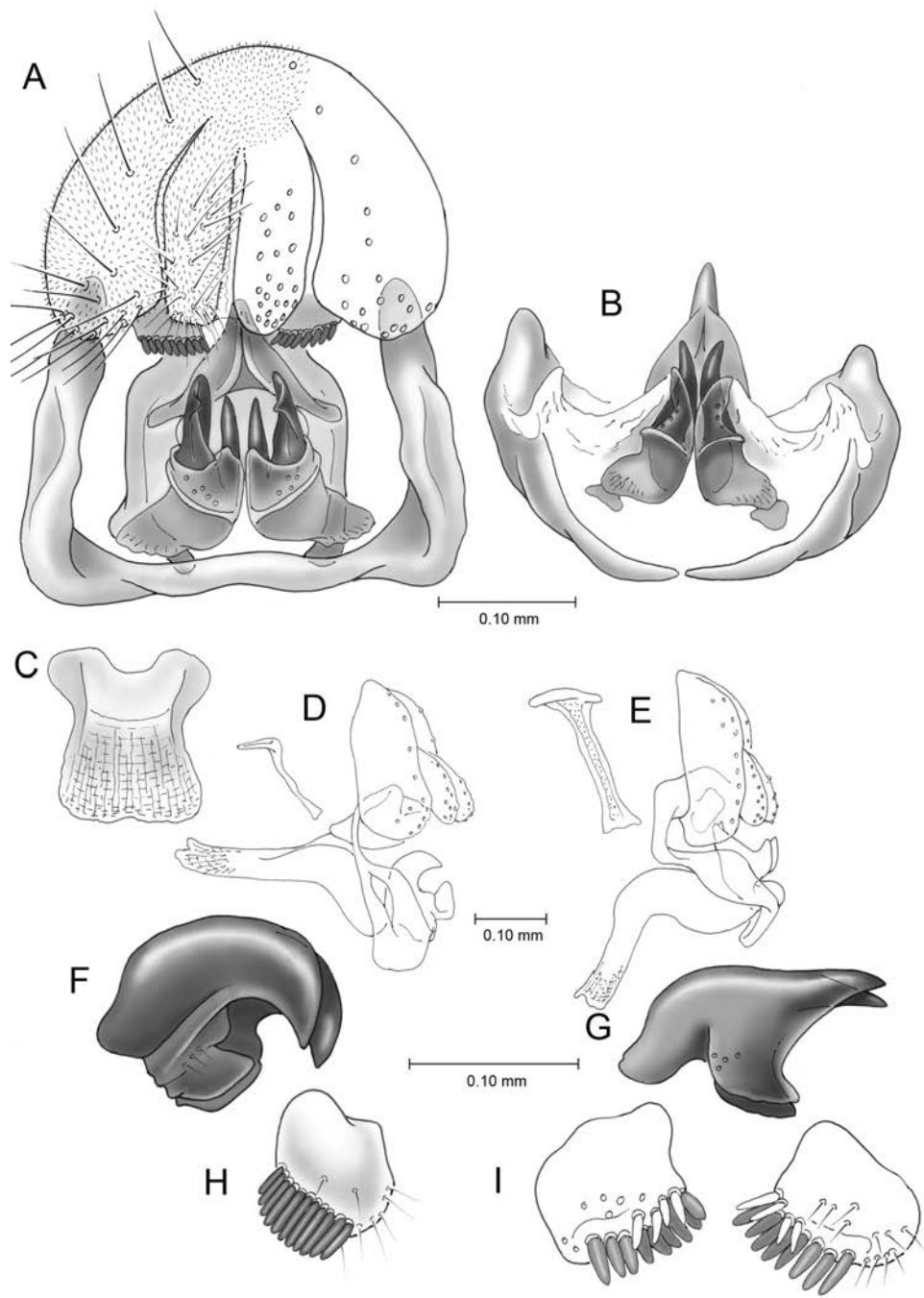


FIG. 38. Male terminalia, *A. onyx*. A, C–D, F, H. A. Posterior view. C. Aedeagal apodeme. D. Lateral view. F. Outer paraphysis, lateral. H. Surstylus. (*Am* 1505, holotype). Male terminalia, *A. avipes*. B, E, G, I. B. Posterior view of genitalia. E. Lateral view. G. Outer paraphysis, lateral. I. Surstyli. (*Am* 1453, holotype).

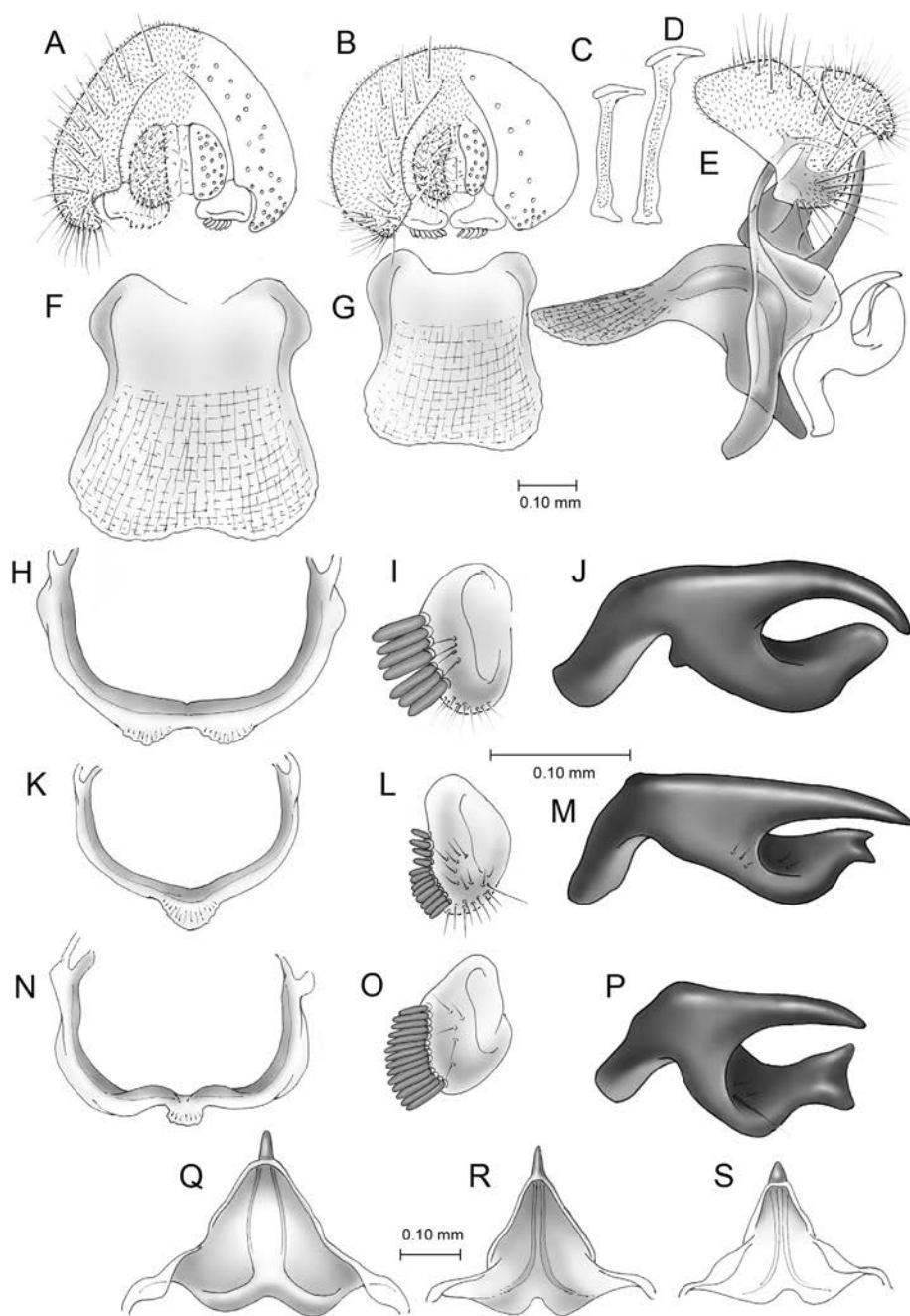


FIG. 39. Male terminalia, *A. biacuminis*. (D-E, H-J, Q: Am 1485, holotype); *A. forceps* (A, N-P, S: Am 1452, holotype); *A. uniacuminis* (B, C, G, K-M, R: Am 1511, holotype). A-B. Epandrium and cerci. C-D. Ejaculatory apodeme. E. Lateral view. F-G. Aedeagal apodeme. H, K, N. Hypandrium. I, L, O. Surstylus. J, M, P. Outer paraphysis. Q-S. Subepandrial sclerite.

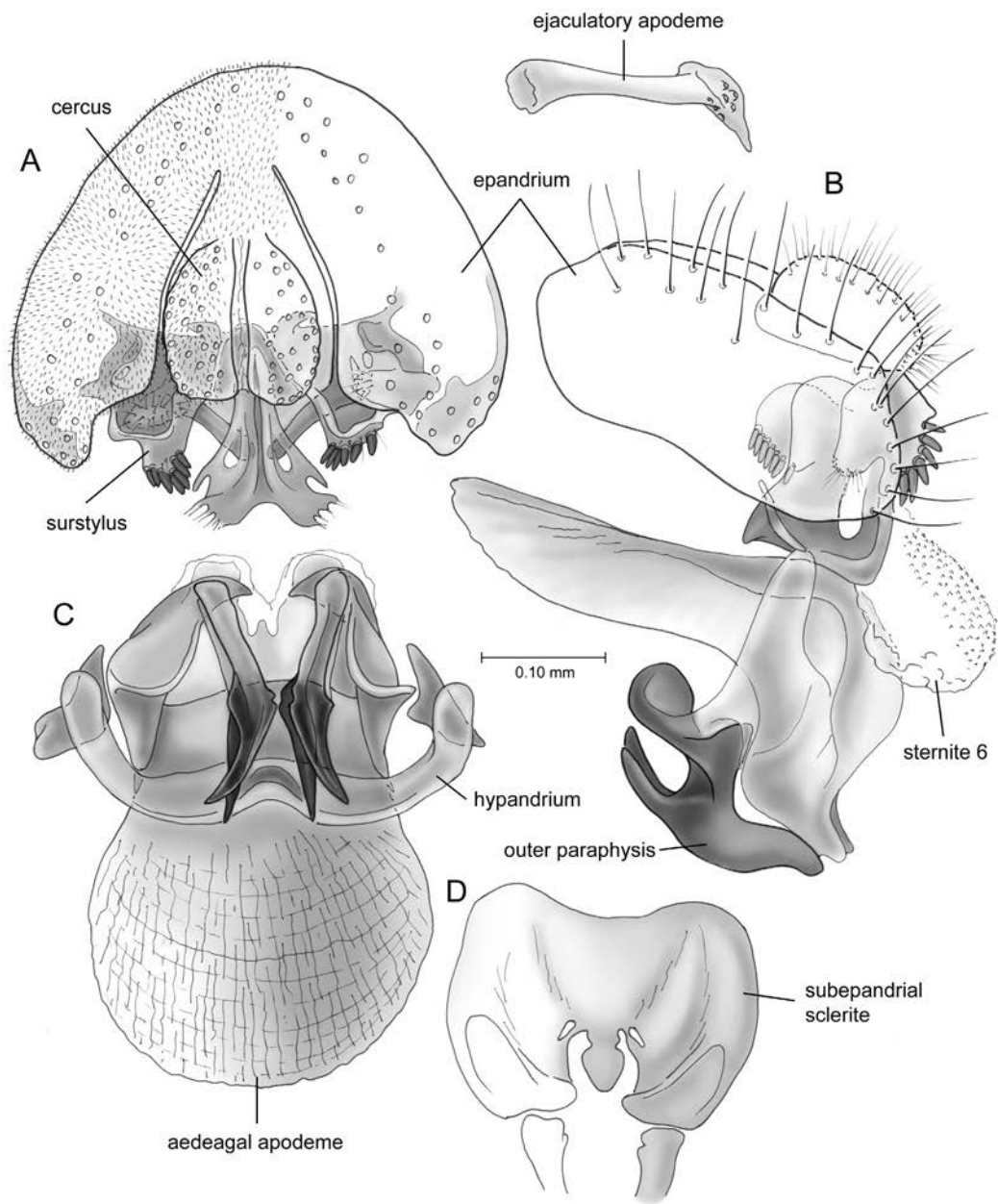


FIG. 40. Male terminalia, *A. minor* (Malloch). A. Epandrium and cerci. B. Lateral view. C. Posterior view. D. Subepandrial sclerite. (Am 233)

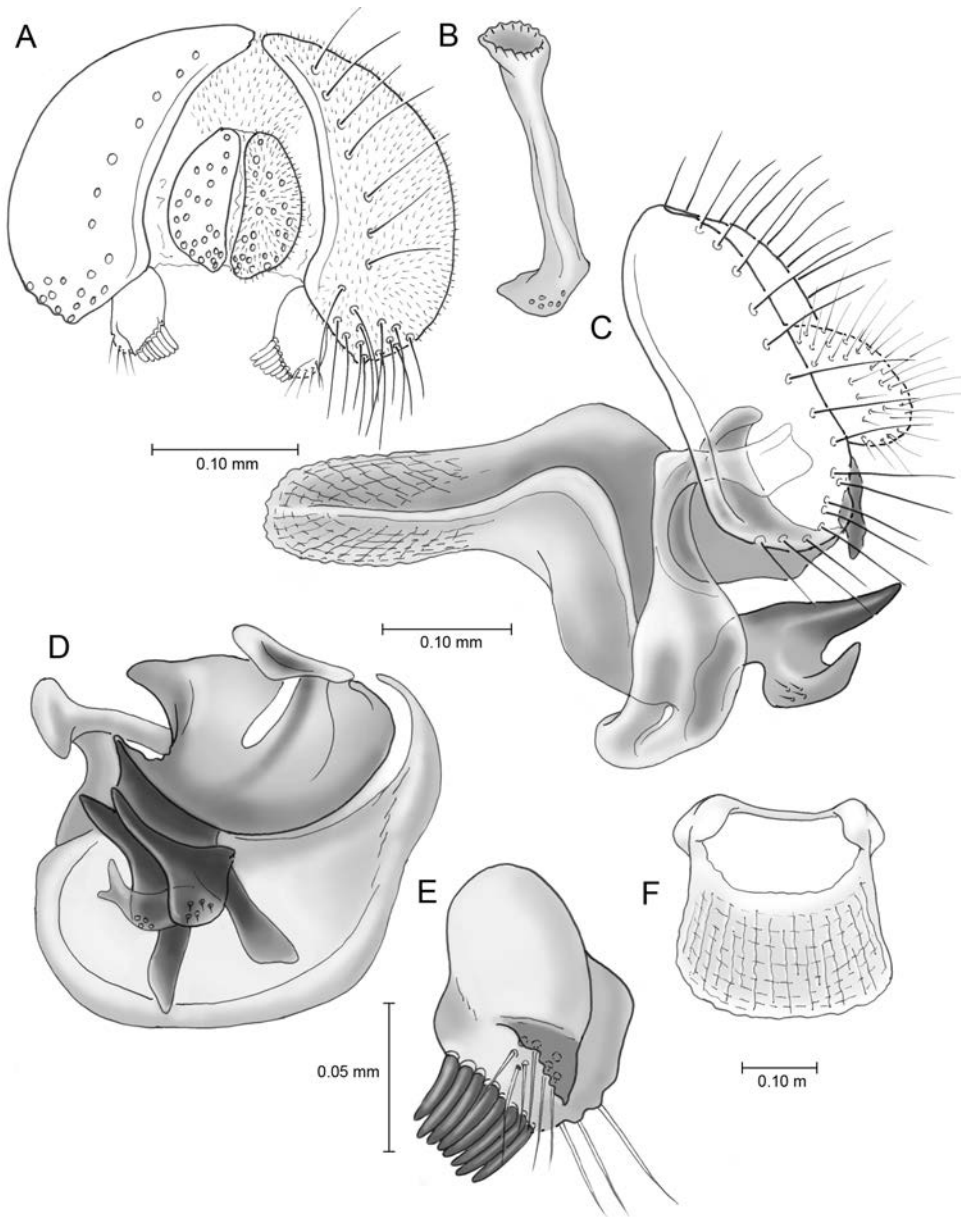


FIG. 41. Male terminalia, *A. pseudominor*. **A**. Epandrium and cerci. **B**. Ejaculatory apodeme. **C**. Lateral view. **D**. Subepandrial sclerite, outer paraphysis, hypandrium. **E**. Surstylus. **F**. Aedeagal apodeme. (Am 256, holotype).

with gonopod consisting of two lobes of unequal size, dorsalmost larger. Ejaculatory apodeme long, straight, and stout, 3/4 the length of epan-drium. Head and thorax measurements: (n = 3; Am 721, 1310, 1311) FL/FW 0.72 (0.60–0.76), EL/EW 1.39 (1.23–1.55), EL/CW 14.94 (11.3–19.33), FML/FMW 0.34 (0.27–0.38), PR/RR 0.57 (0.54–0.63), ThL 1.75 (1.61–1.92 mm).

**TYPE MATERIAL:** **Holotype:** male: “Mont Tremblant, QUE., [46.218957, -74.555477], 15.VII.1959, 3000', B.V. Peterson,” Am 1310, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC). **Para-type:** “Mont Tremblant, QUE., 15.VII.1959, 3000', B.V. Peterson,” 1♂ (Am 1311\*, CNC).

**OTHER MATERIAL EXAMINED:** **USA: Maine:** SE Guarete, 1948-07, M.R. Wheeler and T.C. Hsu, 1891.7 [genitalia on slide in AMNH], 1♂ (Am 304\*, AMNH). **Michigan:** Marquette Co., Huron Mtns., Huron Mtn. Club property vicinity, 46.874950, -87.891717, 2018-07, leg. T. Werner, 1♂ (Am 721\*, AMNH). **Tennessee:** Great Smoky Mt. N.P., 6.6 air mi. NNE Clingman Dome, 1987-06-16, leg. D.W. Webb, 1♂ (Am 1594\*, INHS).

**ETYMOLOGY:** Named for Tessa Steenwinkel, undergraduate researcher in the Werner laboratory of Michigan Technological University, on behalf of Thomas Werner.

**DISTRIBUTION:** Currently, this species is only known from locations near the 46th parallel including the upper peninsula of Michigan, Quebec, and Maine.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota* (T. Werner, personal commun.).

#### THE *SUBTUSRADIATA* SPECIES GROUP (NEW GROUP)

**DIAGNOSIS:** Large flies; thorax dark blackish brown, with typical white markings; arisal branches medium (*tibialis*) to very long (*byersi*); frons largely dull, anterior portion dark yellow in *A. byersi*, entirely dark in *A. tibialis*; mid and hind tibia with comb. Male genitalia distinctive:

Subepandrial sclerite with distinctive subepandrial appendage having toothed apex and lateral pair of striate membranous lobes.

**NEARCTIC SPECIES:** *Amiota byersi*, *A. subtusradiata* Duda, and *A. tibialis*.

**COMMENTS:** Chen and Toda (2001) erected the *alboguttata* species group, which accommodated *A. subtusradiata* Duda. Parsimony analysis of morphological data (fig. 3) suggests a rather distant relationship between Old World species of the *alboguttata* species group and what is now designated as the *subtusradiata* species group. While the *alboguttata* species group was originally defined exclusively by leg characters, the distinctiveness of the male genitalia warrants the separation of *A. subtusradiata* Duda, as well as other closely related Nearctic species, *A. byersi* and *A. tibialis*. These species seem infrequently collected, usually as individuals rather than series. It is unknown whether members of this species group are attracted to the eyes and face as in other *Amiota*, although specimens have been caught in banana traps or found on fungi (see Comments under various species).

#### *Amiota byersi*, sp. nov.

Figures 47A–B, 48A, 49, 90B

**DIAGNOSIS:** Large fly (ThL 1.49–1.70 mm); cheek wide (EL/CW 16–28); middle tibia with comb of ~15 setae; hind tibia with comb of ~10 setae; aedeagal apodeme deeply lobed with lateral concavities; subepandrial sclerite with elaborate subepandrial appendage having 1 dorsal and 2 broad, lateral processes; dorsal process bifurcated; lateral process bearing a serrated distal edge; similar to *A. subtusradiata* Duda and *Amiota tibialis*, but greatly differing in the appendage of the subepandrial sclerite.

**DESCRIPTION:** Large fly (ThL 1.49–1.70 mm), black, glossy; legs yellow. Ventral portion of frons and orbital plate tawny, dorsal half of frons black. Eye with anterior margin evenly convex; posterior margin flattened. Cheek wide (EL/CW 16–28), white posteriorly. Facial mark-

ing large, almost semicircular, depth  $0.5\times$  width. Middle tibia with comb composed of  $\sim 15$  setae (length of longest ones  $\sim 0.7\times$  tibia width). Hind tibia with comb composed of  $\sim 10$  setae (length of longest ones  $\sim 0.8\times$  width of tibia). Tergites 1 and 2 lightly colored. Arista: Very long, plumose; longest branch D2; A.R. 0.5; 5 long dorsal, 2 long ventral branches; branch D4 pointed laterad; arista trunk with medium length microtrichia along entire length. Male genitalia: Epandrium distinct, separated at midline, margins discrete (not grading into membrane). Cercus oval, margins discrete from surrounding membrane; most space surrounded by epandrium is dorsal to cerci. Surstylus roughly square; midregion with many scattered setulae; lateral fingerlike projection present, extending barely beyond prensisetae, long setulae continuing up lateral margin; 12 prensisetae, apices blunt, even lengths and spaces, comblike. Subepandrial sclerite with prominent subepandrial appendage; in lateral view with 1 dorsal process and 2 lateral processes; dorsal process laterally bifurcated, the most posterior bifurcation serrated; distal margin of lateral process with small, rounded teeth; posterior view of subepandrial appendage invaginated in appearance, surrounded by prominent striated membrane. Outer paraphyses long, symmetrical, sclerotized, bent  $90^\circ$  near base, oriented posteriorly, distal end tapered. Inner paraphyses smaller, sinuous, projecting anterolaterally. Aedeagal apodeme as long as wide, constricted on 4 sides; the base forming deep-pocketed lobes. Hypandrium nearly V-shaped, the anterior apex with a prominent convex point; lateral arms thickened with a wide, nearly triangular gonopod. Ejaculatory apodeme large, equal to length of epandrium. Head and thorax measurements: ( $n = 5$ ; Am 294, 295, 401, 434, 1349) FL/FW 0.75 (0.68–0.80), EL/EW 1.31 (1.22–1.38), EL/CW 22.27 (16–28), FML/FMW 0.38 (0.35–0.41), PR/RR 0.46 (0.33–0.57), ThL 1.61 (1.49–1.70 mm).

TYPE MATERIAL: **Holotype:** male: “Wayne” Co., Mich., [42.269878, -83.322396], “Aug. 8” 19

“59,” Geo. Steyskal, “#8,” Am 294, [pinned via minuten, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratype:** “Wayne” Co., Mich., “Aug. 16,” 19 “59,” Geo. Steyskal, “#8,” 1 ♂ (Am 295\*, AMNH).

OTHER MATERIAL EXAMINED: **USA: Illinois:** Iroquois Co., Iroquois Co. Cons. Area, 6.4 mi ENE Beaverville, 1990-09-02, leg. E.A. Lisowski, 1 ♂ (Am 1595\*, INHS). **North Carolina:** Highlands, Whitesides Cove, 2000', 1957-08-11, leg. J.G. Chillingworth, 1 ♂ (Am 1349\*, CNC). **Pennsylvania:** Swarthmore, 1907-08-25, leg. C.L. Fox, 1 ♂ (Am 401\*, CAS). **Virginia:** Floyd Co., #1, Mile 175.4 Blue Ridge Parkway, 1960-06-23, leg. G.W. Byers, 1 ♂ (Am 434\*, SEMC).

ETYMOLOGY: Named for George W. Byers (1923–2018), late professor of entomology at the University of Kansas who collected one of the specimens of this rare species; in recognition of his contributions to the study of Diptera and Mecoptera and, as one of us (D.A.G.) remembers him, a true, affable gentleman.

DISTRIBUTION: This species is found in the northern Midwest and Mid-Atlantic.

COMMENTS: It is unknown whether this species is attracted to the face and eyes as other *Amiota*.

#### *Amiota subtsuradiata* Duda, 1934

*Amiota alboguttata* var. *subtsuradiata* Duda, 1934: 32 (original description).

*Amiota subtsuradiata* Duda, 1934: Wheeler, 1965: 761 (Nearctic catalog); Máca, 1980: 336 (description, genitalia figured, lectotype designated); Chen and Toda, 2001: 1540 (description); Bächli et al., 2004: 43 (description, genitalia figured); Brake and Bächli, 2008: 256 (world catalog).

*Amiota quadrata* Takada and Toda, 1981: 2 (type locality: Canada, Northwest Territories, Inuvik; deposited in Hokkaido University, Sapporo, Japan, EIHU).

*Amiota subtsuradiata* subsp. *quadrata* Takada and Toda, 1981 (Toda et al. 1996; stat. nov., as subspecies of *A. subtsuradiata* Duda).

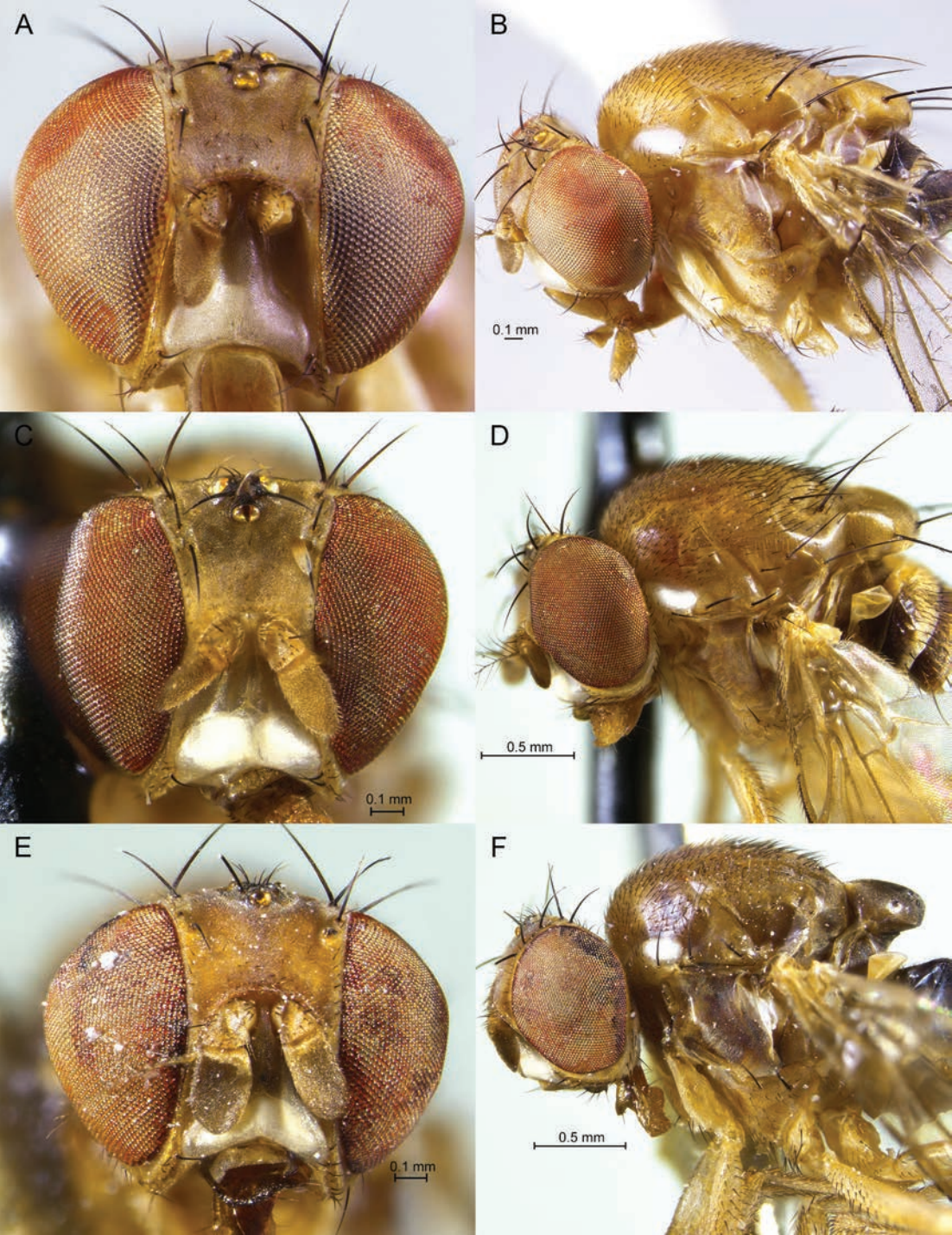


FIG. 42. Heads and lateral views, *A. rufescens* species group. A–B. *A. leucostoma* Loew (Am 399). C–D. *A. mcalpinei*, sp. nov. (Am 1315, holotype). E–F. *A. tessae*, sp. nov. (Am 1310, holotype).

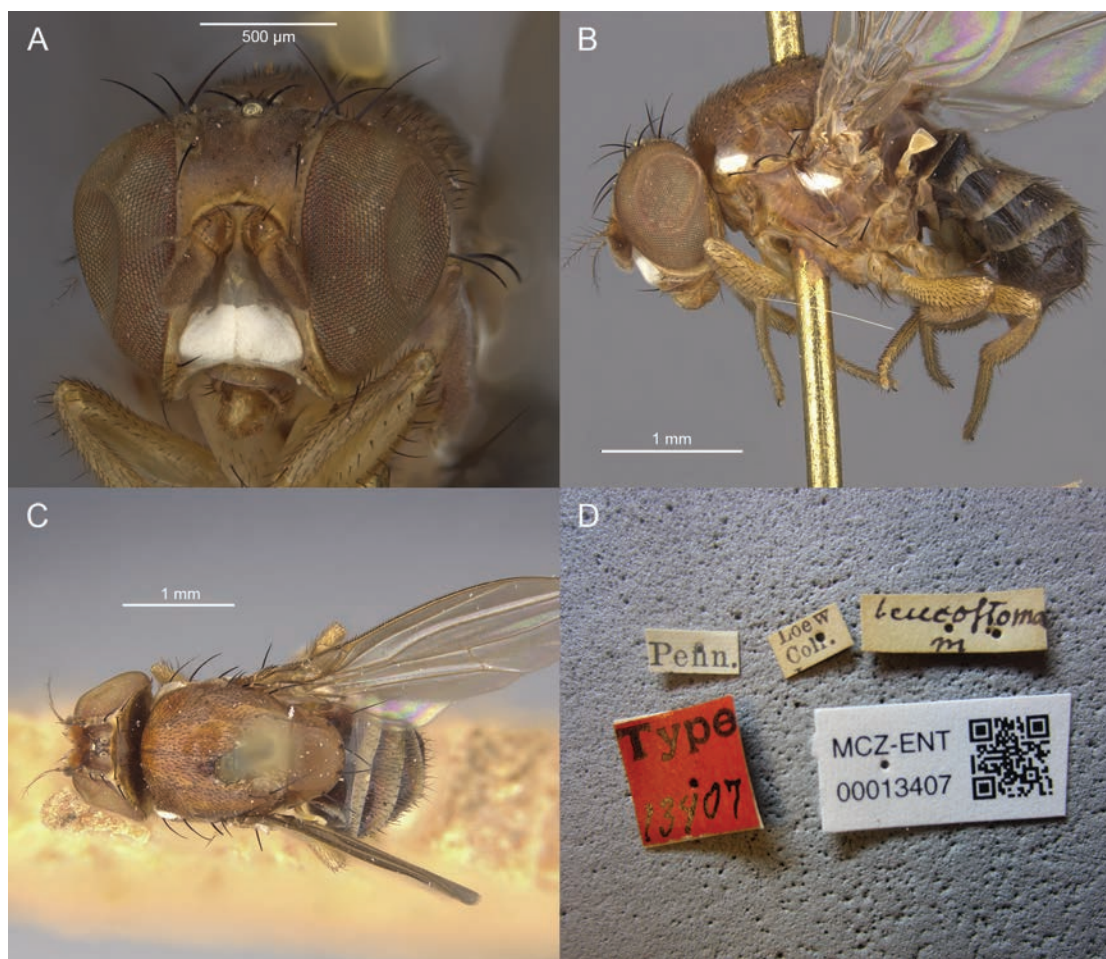


FIG. 43. Holotype of *A. leucostoma* Loew (MCZC), Museum of Comparative Zoology, Harvard University. Photographs by Charles Farnum. **A.** Head. **B.** Lateral view. **C.** Dorsal view. **D.** Specimen labels and barcode.

**TYPE MATERIAL:** Lectotype as designated by Máca (1980): "Finland: Tvärminne, without date, R. Frey lgt., Coll. Zool. Museum of the University Helsinki. This specimen, bearing a label with number 802, Duda's determination label and a red label with the inscriptions 'Holotypus' (printed) and 'unpublished' (written)." Deposited in the Finnish Museum of Natural History, Helsinki (MZH).

**DISTRIBUTION:** This species has a Holarctic distribution and is known from Europe, Far East Russia, Korea, Siberia, and Northwest Territories, Canada (Brake and Bächli, 2008).

Michigan is also cited as a locality (due to a series collected by G. Steyskal), but these specimens are of *A. byersi*.

**COMMENTS:** Takada and Toda (1981) described *A. quadrata* from specimens collected in the high arctic of Canada (Inuvik). This species was eventually considered to be a subspecies of *A. subtusradiata* (Toda et al., 1996). Regrettably, the entire type series was deposited in Hokkaido University rather than in the Canadian National Collection of Insects, Ottawa, which would have been a more convenient repository for restudy, and so remains unexamined for this

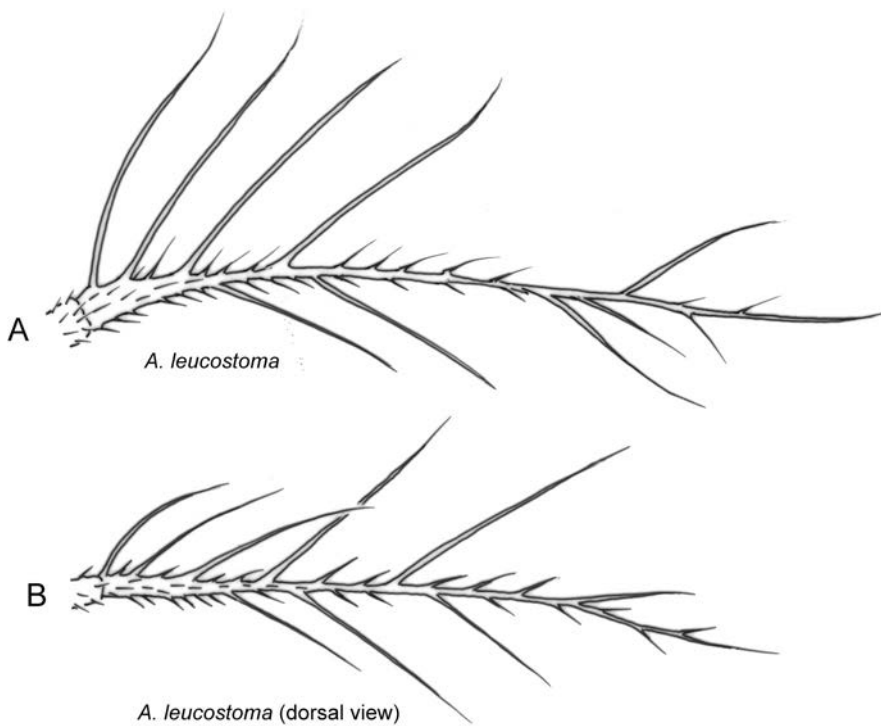


FIG. 44. Aristae. *A. leucostoma* Loew.

revision. The figures of the male genitalia (Takada and Toda, 1981) complicate the comparison to the two new Nearctic species, and Toda et al. (1996) did not redescribe or refigure *A. quadrata*.

We adopt the treatment of *A. subtusradiata* Duda from Bächli et al. (2004), which recognizes one broadly distributed, Holarctic *A. subtusradiata* (with no subspecies). Based on the description and figures from Bächli et al. (2004), we conclude that *A. byersi* and *A. tibialis* are different species from *A. subtusradiata*. Other synonyms of *A. subtusradiata* are reported by Bächli et al. (2004) in Eastern Asia. Eventually it would be useful to examine the type series of *A. quadrata*, along with European specimens of *A. subtusradiata*. It is very interesting that any species of *Amiota* is found so far north (Inuvik is ~ 68.331193, -133.610240), which is surrounded by tundra. The only nonconifers in which these *Amiota* could be breeding would be willows (*Salica-*

*ceae*). The holotype of *A. quadrata* was collected on traps baited with banana.

***Amiota tibialis*, sp. nov.**

Figures 47C–D, 48B, 50, 90C

**DIAGNOSIS:** Large fly (ThL 1.63–1.79 mm), black; cheek very deep; middle tibia with comb of ~12 setae; hind tibia with comb of ~8 setae; male genitalia distinctive, heavily sclerotized and complex; aedeagal apodeme deeply lobed with lateral pockets; subepandrial sclerite with large, curved appendage having 2 distal valves, each valve bearing a serrated distal edge with a proximal large spine; similar to *Amiota byersi* but significantly differing in the subepandrial appendage.

**DESCRIPTION:** Large fly (ThL 1.63–1.79 mm), black, legs yellowish. Frons dark, slightly lighter ventrally, pollinose. Cheek deep (EL/CW 0.07–0.09mm), whitish-gray. Middle tibia with comb

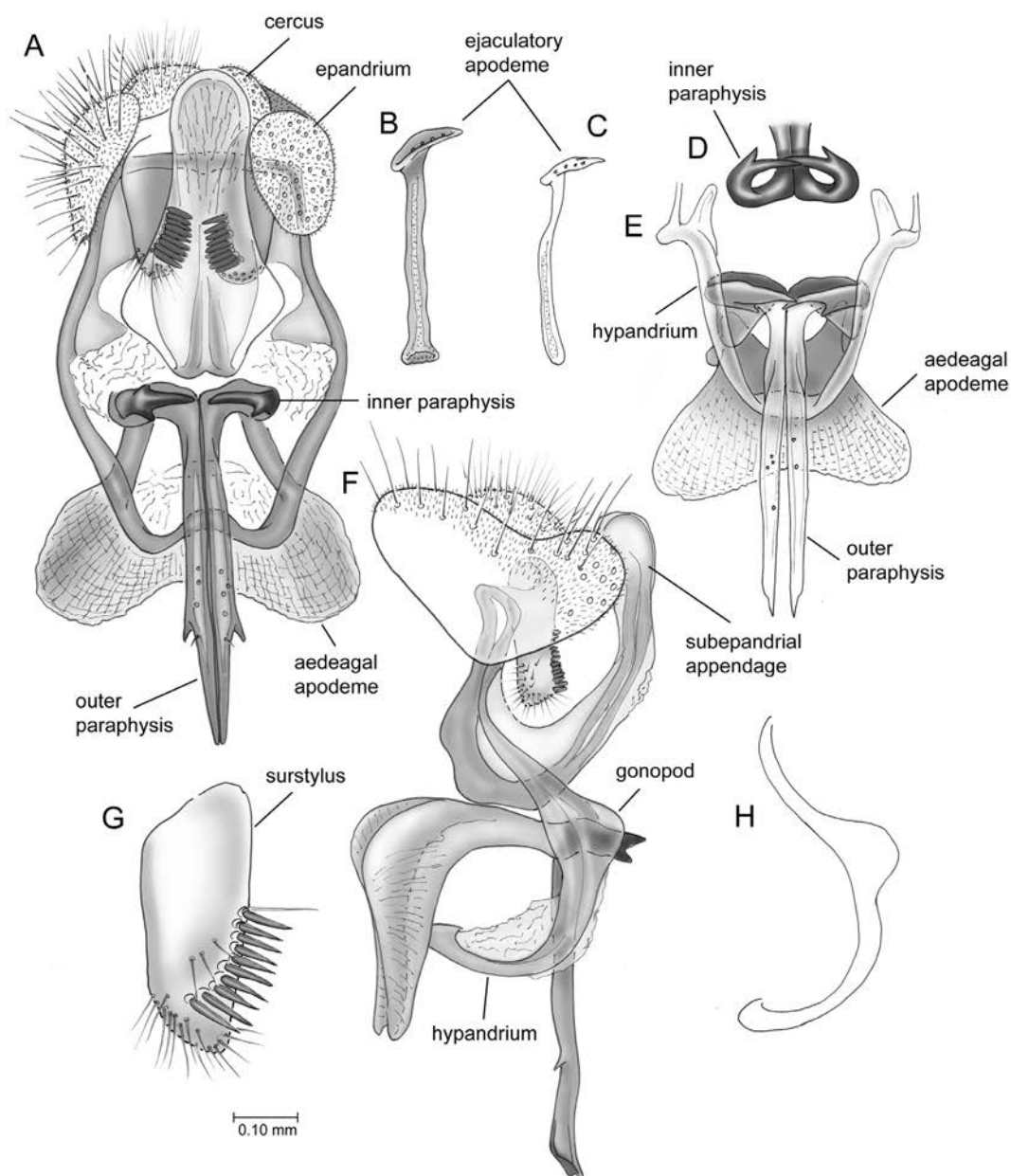


FIG. 45. Male terminalia, *A. leucostoma* Loew. A–B, F–G. A. Ventral view. B. Ejaculatory apodeme. F. Lateral view. G. Surstylus. (Am 379). Male terminalia, *A. mcalpinei*, sp. nov. C–E, H. C. Ejaculatory apodeme. D. Inner paraphyses. E. Ventral view. H. Hypandrium and gonopod, lateral. (Am 1315, holotype).

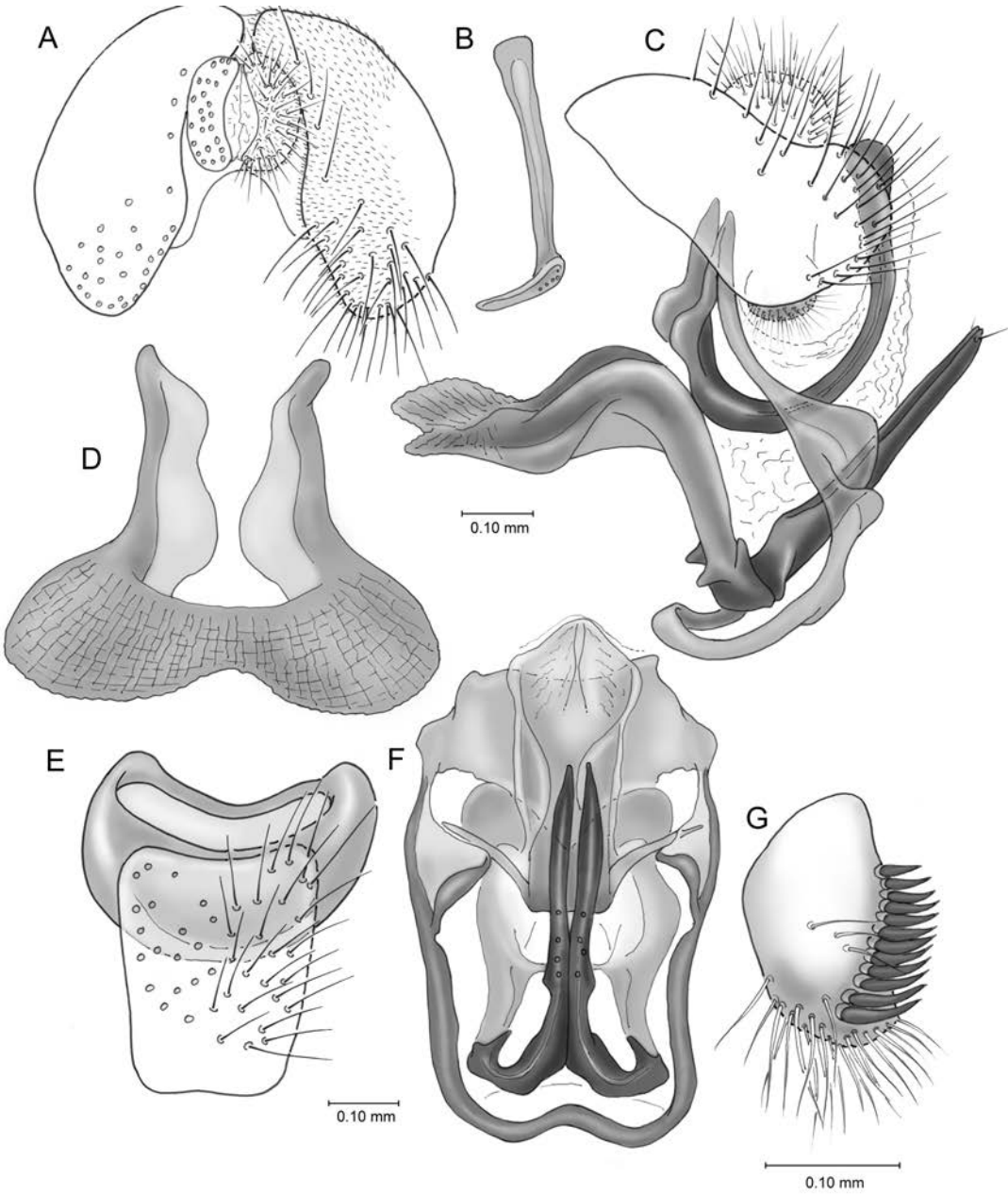


FIG. 46. Male terminalia, *A. tessae*. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Aedeagal apodeme. **E.** Sternite 6 (shaded) + 7. **F.** Ventral view. **G.** Surstylus. (Am 721).

composed of ~12 setae (length of longest setae ~0.7× width of tibia). Hind tibia with comb composed of ~8 setae (length of longest setae ~0.7× width of tibia). Tergites 1 and 2 lightly colored. Arista: Short, plumose; longest branch D3; A.R. 0.30; 5 long dorsal, 3 shorter ventral branches, none pointed medially/laterally; arista trunk with short microtrichia, bare on apical half. Male genitalia: Epandrium dorsally incomplete in middle. Cercus distinct from surrounding membrane, each crescentic. Surstylus with lateral thumblike projection, 9 prenisetae, apices blunt, comblike, becoming slightly smaller medially. Subepandrial sclerite complex, forming a semicircle, each half with ostium and 4 anteriorly facing lobes; an elaborate heavily sclerotized appendage present, heavily sclerotized, arching ventrally and the apex directed posteriorly; apex with pair of serrated valves, in lateral view with 2 prominent spines, flanked above and below with smaller serrations; each subepandrial appendage in ventral view flanked by a faintly striated membranous sac. Outer paraphysis long and acuminate, no visible sensilla, oriented posteroventrally, bent ~ 90° at base. Inner paraphysis slightly sinuous and pointed antero-laterally. Aedeagal apodeme very distinctive, length and width nearly equal, scalloped, deeply lobed and bent in lateral; prominent lateral lobes forming scoop, constricted on all 4 sides and concave in dorsal view; no obvious flanges. Hypandrium thick, heavily sclerotized; lateral arms thick coming to a very wide gonopod, nearly triangular; apex a strong mucronate point ventral to aedeagal apodeme. Ejaculatory apodeme long, length slightly shorter than depth of epandrium; bent near middle of shaft, heavily sclerotized. Head and thorax measurements: (n = 5; Am 7, 470, 482, 489, 556) FL/FW 0.65 (0.55–0.72), EL/EW 1.46 (1.37–1.54), EL/CW 10.30 (8.77–11.71), FML/FMW 0.39 (0.35–0.43), PR/RR 0.54 (0.50–0.72), ThL 1.73 (1.63–1.79 mm).

**TYPE MATERIAL:** **Holotype:** male: UTAH, Cache Co, Logan Cyn [canyon], Turner CG

[campground], [41.883204, -111.572736], 10–20 Jun 85, W.J. Hanson, Am 470, [reglued directly pin, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** UTAH, Cache Co, Logan Cyn [canyon], Turner CG [campground], 5–17 Jul 85, W.J. Hanson, 3 ♂ (Am 472, 481, 482\*, LACM); 20–27 Jun 85, W.J. Hanson, 1 ♀ (Am 483); 27 Jun–5 July 85, W.J. Hanson, 3 ♂ (Am 475, 478, 489\*, LACM).

**OTHER MATERIAL EXAMINED:** **Canada:** **Ontario:** Low Bush, Lake Abitibi, 1925-08-08, leg. N.K. Bigelow, 3 ♂ (Am 1352\*, 1353, 1354\*, CNC); Petawawa Reservation, 1935-06-26, leg. D. Gray, 1 ♂ (Am 556\*, DEBU). **Saskatchewan:** Mankota, 1952-01-30, [collector unknown], Prob ex. Tort. In apple fungus (*Daldinia grandis*), 1 ♂ and 1 ♀ (Am 1350, 1351\*, CNC). **USA:** **Utah:** Cache Co., W. Hodges Canyon, 1978-08-15 through 1978-08-21, leg. Knowlton and W.J. Hanson, 1 ♂ (Am 495\*, LACM); 1985-07-18 through 1985-07-23, leg. W.J. Hanson, 2 ♂ (Am 485\*, 486, LACM); 1985-07-23 through 1985-08-03, leg. W.J. Hanson, 1 ♂ (Am 488, LACM); 1985-08-16 through 1985-08-30, leg. W.J. Hanson, 1 ♂ (Am 473, LACM); 12 mi W Long Junction, Dixie N. For. Ut., 1953-08-18, leg. W.B. Heed, 1 ♂ and 1 ♀ (Am 1\*, 6\*, AMNH); 1953-08, leg. W.B. Heed and F.A. Cowan, 2356.4, 1 ♂ (Am 7\*, AMNH).

**ETYMOLOGY:** From *tibia*, Latin for “leg,” in reference to the tibial comb on the hind leg.

**DISTRIBUTION:** *Amiota tibialis* is known from Utah, specifically the Wasatch and Uinta Montane Forests which stretch from north to south in the state, as well as eastern and central Canada.

**COMMENTS:** Of note are the two specimens from Saskatchewan (CNC) found to be associated with apple fungus, *Daldinia grandis* Child. *Amiota alboguttata* (Wahlberg) has been reared from *Daldinia concentrica* (Bolton) Ces. and De Not. in the United Kingdom (Buxton, 1960; Hingley, 1971).

#### THE NEBOJSA SPECIES GROUP (NEW GROUP)

**DIAGNOSIS:** Large to very large flies; thorax dark blackish brown, body with typical white

markings; frons dark, mostly dull, anterior portion with faint bluish-silvery pollinosity; facial marking quite large; cheek deep; arisal branches short to medium length, confined to base in some species. Male genitalia: Uniform; epandrium with lateral projection on anterior margin; surstylus with lateral fingerlike lobe; subepandrial sclerite large, recurved; subepandrial appendage prominent, rather heart-shaped in posterior view; outer paraphyses heavily sclerotized, with 1–3 dorsal spines and preapical dorsal hook; inner paraphysis lost; hypandrium with large, bulging gonopod on lateral arm; ejaculatory apodeme large, nearly equal to or larger than depth of epandrium in most species.

NEARCTIC SPECIES: *Amiota amputata*, sp. nov., *A. latilabrum*, sp. nov., *A. nebojsa* Máca, *A. occidentalis*, sp. nov., *A. oviraptor*, sp. nov., and *A. subnebojsa*, sp. nov.

COMMENTS: This distinctive group is found in the western United States, British Columbia, and throughout Mexico. Members of this species group are difficult to identify through external morphology. Several species can be caught in a single series. Dissection of the male genitalia is critical for identification to the species level, with emphasis on lateral view of the outer paraphysis (fig. 60).

***Amiota amputata*, sp. nov.**

Figures 51A–B, 53A, 54, 60D, 91A

DIAGNOSIS: Large fly (ThL 1.51–1.71 mm), dark brown, legs yellow; outer paraphysis laterally flattened, with hook on distal end, 2 short, blunt spines along middle portion of dorsal margin, base minutely serrate; inner paraphysis lost.

DESCRIPTION: Large fly (ThL 1.51–1.71 mm), dark brown, legs yellow. Frons light brown on ventral half, dorsal half of head darker. Facial marking large (FML/FMW 0.29–0.38). Cheek deep (EL/CW 7–13.66), posterior milky white. Marking under wing base prominent, large, milky white, margins clearly defined. Haltere yellow. Tergites 1 and 2 lightly colored. Arista:

Short, plumose; longest branches D1 and D2; A.R. 0.28; 3 long dorsal, 2 short ventral branches; branch D3 pointed medially; arista trunk with short-medium length microtrichia along most of its length. Male genitalia: Epandrium separated at midline with a large gap, margins distinct from surrounding membrane; long lobe ventrally, densely haired, single line of setae ascending dorsally; anterolateral projection small, oriented anteriorly. Cercus semicircular, margins entirely distinct from surrounding membrane. Surstylus approximately rectangular, ventral half covered in scattered setulae; 12 short, peglike prenisetae, apices blunt; small fingerlike lateral lobe, not extending beyond prenisetae. Subepandrial sclerite C-shaped in lateral view, with appendage heart shaped in posterior view, invaginated medially. Outer paraphysis laterally flattened with hook on distal end; 2 short, blunt spines along middle portion in lateral view; small proximal “wing” at base, minutely serrate. Inner paraphysis lost. Aedeagal apodeme as wide as long; curved 90° in lateral view, curved segment forming deep pockets; distal end slightly flared with a deep central emargination. Hypandrium thin, apex with gap; triangular in anterior, accommodating paraphysis; lateral arm with prominent gonopod, triangular, ventrally pointed. Ejaculatory apodeme long, 0.8× length of epandrium. Head and thorax measurements: (n = 5; Am 4, 457, 753, 1483, ×1504) FL/FW 0.73 (0.66–0.81), EL/EW 1.30 (1.21–1.43), EL/CW 9.34 (7–13.66), FML/FMW 0.34 (0.29–0.38), PR/RR 0.60 (0.46–0.77), ThL 1.63 (1.51–1.71 mm).

TYPE MATERIAL: **Holotype:** male: Oak Cr. Canyon, Ariz., [34.912694, -111.726958], VII-9-41, R.H. Beamer, Am 457, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** 14 mi. SW. El Salto, Dgo. [Durango] MEX, [23.786449, -105.597725], 8000', June “26” 1964, J.F. McAlpine, 4♂ (Am 1448\*, 1482\*, 1483\*, 1556\*, CNC)

OTHER MATERIAL EXAMINED: **Mexico: Chiapas:** 5 mi NE San Cristobal, 1969-05-21, leg. B.V. Peterson, 1♂ (Am 1504\*, CNC); 5 mi. W San Cristobal, 7500', 1969-05-06, leg. H.J. Teskey, 1♂ (Am

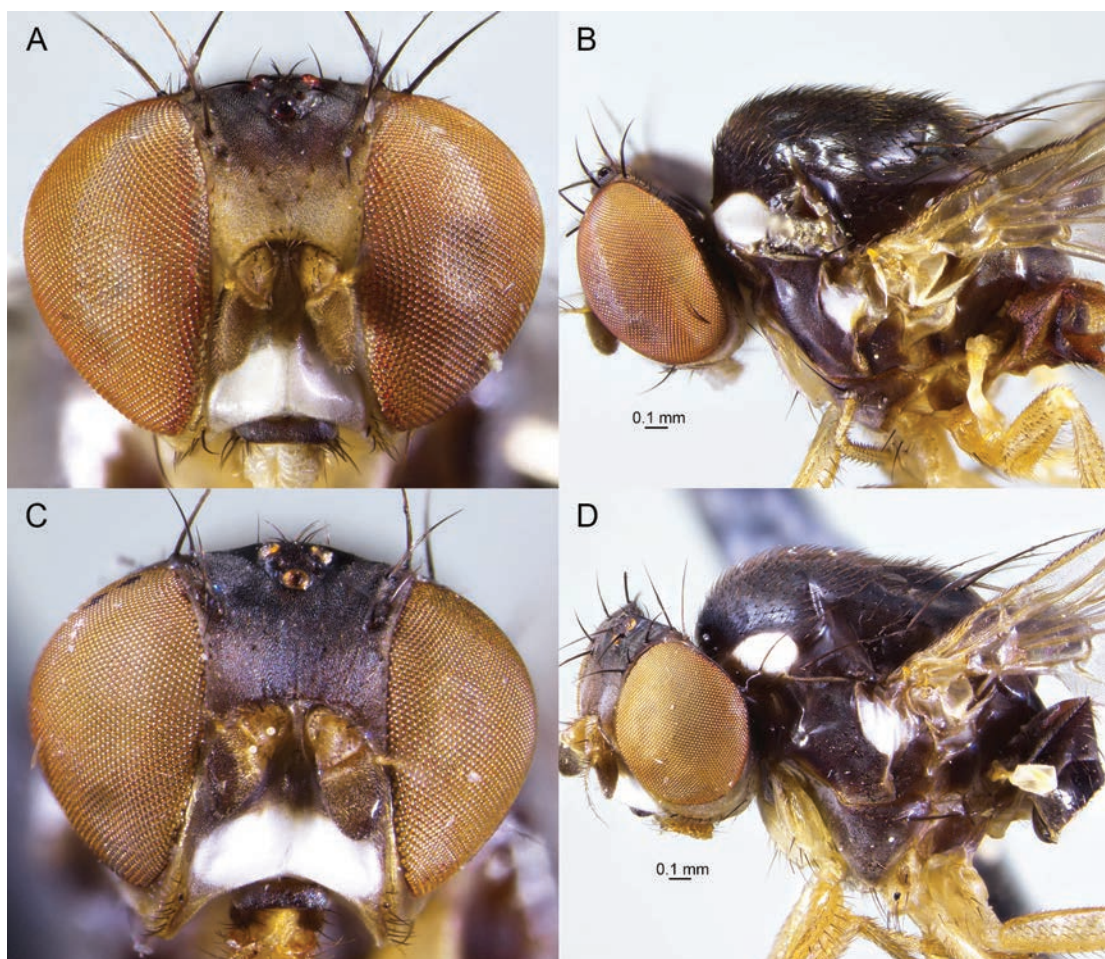


FIG. 47. Heads and lateral views, A. *subtusradiata* species group. A–B. *A. byersi*, sp. nov. (Am 295, paratype, lateral image flipped). C–D. *A. tibialis*, sp. nov. (Am 495).

1427\*, CNC). **Durango:** 24 mi W La Ciudad, 7000', 1964-07-11, leg. J.F. McAlpine, 1♂ (Am 1553\*, CNC). **Puebla:** 9 mi SE Huachinango, 1952-06, leg. M. Wasserman and W.B. Heed, 2260.13, 1♂ (Am 4\*, AMNH). **USA: Arizona:** Cochise Co., Ramsay Canyon, Mile High Trail. Near Sierra Vista, 1984-07-24, leg. L.B. Carlson, sweep, 1♂ (Am 753\*, DEBU); Oak Creek Canyon, 1941-07-09, leg. R.H. Beamer, 1♂ (Am 457\*, SEMC).

**ETYMOLOGY:** From the Latin *amputata*, feminine past participle, for “pruned” or “amputated,” in reference to the stublike nature of the prongs on the outer paraphyses, which are much longer in other closely related species.

**DISTRIBUTION:** This species has a large distribution from Chiapas State in Mexico north through central Arizona.

**COMMENTS:** The paratype described in Máca (2003) as an “aberrant individual” from the type series of *A. nebojsa* Máca belongs is *Amiota amputata*. See Comments under that species.

***Amiota latilabrum*, sp. nov.**

Figures 51C–D, 53B, 55, 60A, 91B

**DIAGNOSIS:** Large fly (ThL 1.75–1.84 mm), dark brown and glossy; outer paraphysis heavily

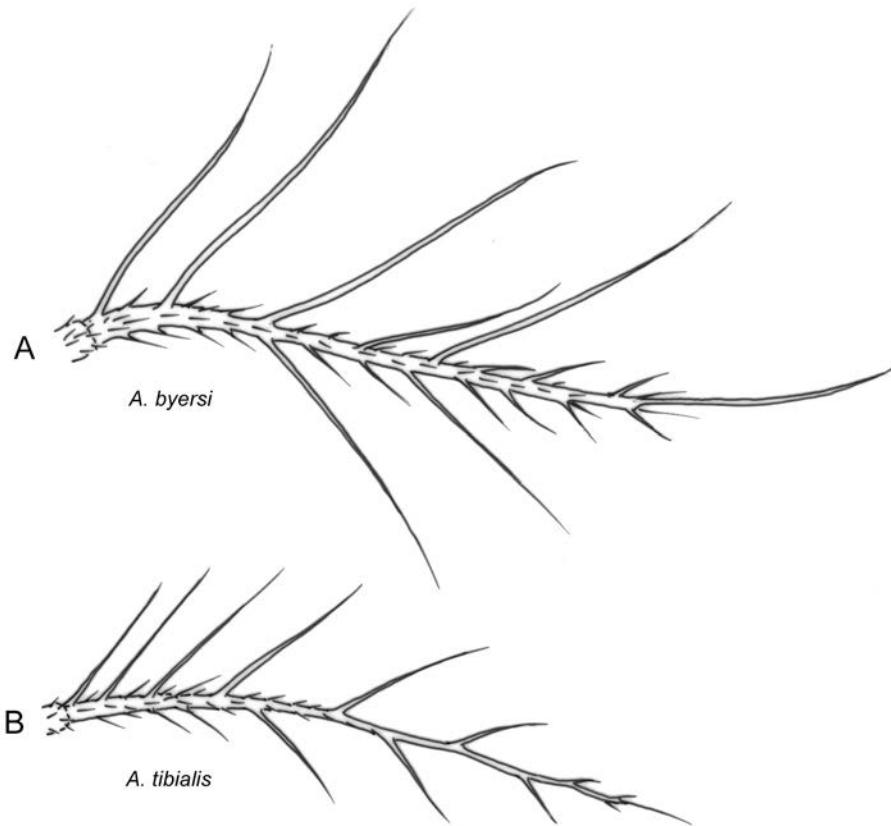


FIG. 48. Aristae, *A. subtusradiata* species group. A. *A. byersi*. B. *A. tibialis*, sp. nov. Not to the same scale.

sclerotized, apex with hook, in lateral view with 2 long spines on posterodorsal margin, proximal spine longer, usually curving inward medially, nearly touching opposing appendage; base forming a tapered wing, curving medially in ventral; very similar to *Amiota subnebojsa*, but differs as follows: cercus smaller; surstylus less crescentic, apical lobe slightly longer (vs. shorter) than prensisetae; aedeagal apodeme shorter relative to its width; subepandrial sclerite appendage shape less cordate; basal paraphysis spine without small apical notch; ejaculatory apodeme slightly longer (vs. shorter) than depth of epandrium.

**DESCRIPTION:** Large fly (ThL 1.75–1.84 mm), dark brown, uniformly so, glossy; legs yellow. Facial marking large, semicircular. Cheek wide (EL/CW 8.50–11.57), milky white posteriorly. Palp dark brown. Tergites 1 and 2 lightly colored.

**Arista:** Short, plumose; longest branch D3; A.R. 0.28; graded series 7–8 dorsal branches shortening distad, 1 short ventral branch; none pointed mediad/laterad; arista trunk with medium-length microtrichia along entire length. **Male genitalia:** Epandrium nearly split medially, not grading with surrounding membrane; dense cluster of setae ventrally, ascending in a single line toward apex; small lobe projecting on anterolateral margin. Cercus oval shaped, distinct from surrounding membrane; barely protruding beyond distal margin of epandrium in lateral view. Surstylus roughly triangular, ventral half with scattered setulae; 13 peglike prensisetae, apices blunt, comblike; distal-lateral fingerlike lobe present, length equal to that of prensisetae. Subepandrial sclerite large, broad, trapezoidal, lateral margins thickened; C-shaped in lateral view; subepandrial appendage well

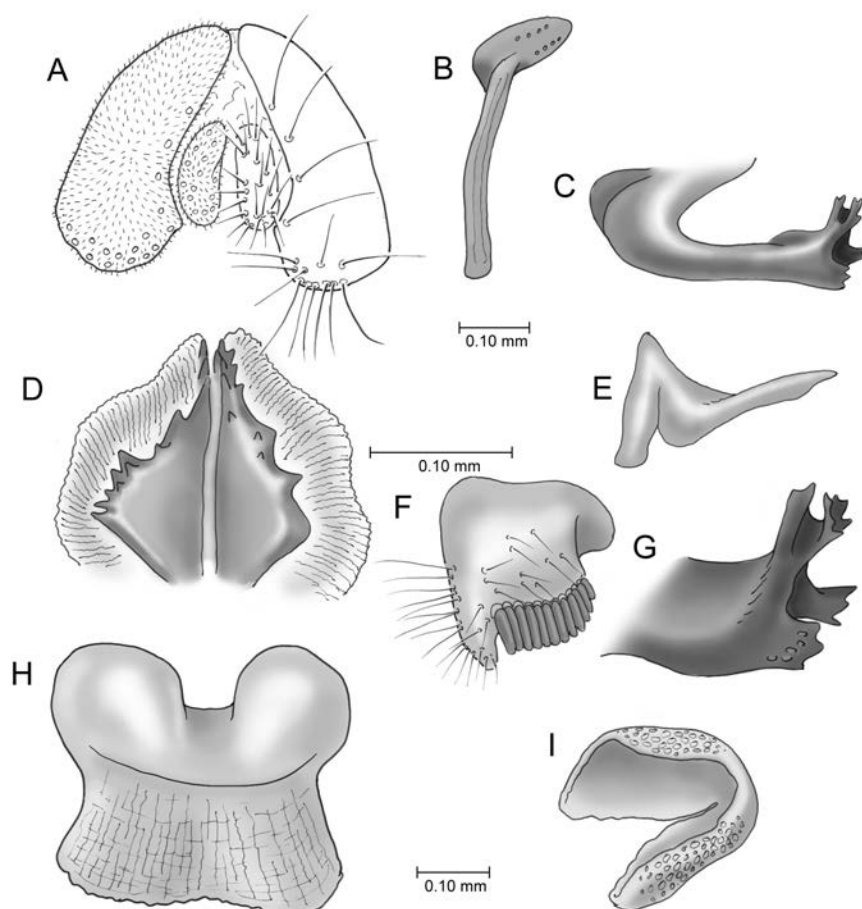


FIG. 49. Male terminalia, *A. byersi*. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C–D.** Subepandrial appendage. **C.** Entire. **D.** Detail of apex, ventral view. **E.** Outer paraphysis, lateral. **F.** Surstylus. **G.** Subepandrial appendage, detail of apex. **H.** Aedeagal apodeme. **I.** Sternite 6 sac. (Am 294, holotype).

developed, apex with thin, mucronate point (in lateral view), subcordate in posterior view. Outer paraphysis heavily sclerotized, formed of 2 lobes, split deeply medially, apex laterally flattened; distal end with sharply curved hook in lateral view, ventrally with preapical lobe; dorsal margin with 2 long spines, distal spine shorter, basal spine curving medially in some specimens; lobes at base in ventral view. Inner paraphysis lost. Aedeagal apodeme nearly wide as long, curved in lateral view; distal end widely flared with a broad emargination. Hypandrium U-shaped, thickness consistent; apex notched, accommodating outer paraphyses; lateral arm with gonopod, oriented

posteroventrally. Ejaculatory apodeme very large, equal to or slightly longer than length/depth of epandrium. Head and thorax measurements: ( $n = 5$ ; Am 2, 3, 5, 1426, 1525) FL/FW 0.72 (0.66–0.77), EL/EW 1.32 (1.22–1.42), EL/CW 10.09 (8.50–11.57), FML/FMW 0.41 (0.34–0.54), PR/RR 0.57 (0.54–0.70), ThL 1.79 (1.75–1.84 mm).

**TYPE MATERIAL:** **Holotype:** male: “9 mi. SE.” Huachinango, Puebla MEX., [20.062775, -97.962064], M Wasserman, WB Heed, “June 1952,” 2260:13, Am 2, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** “9 mi. SE.” Huachinango, Puebla MEX.,

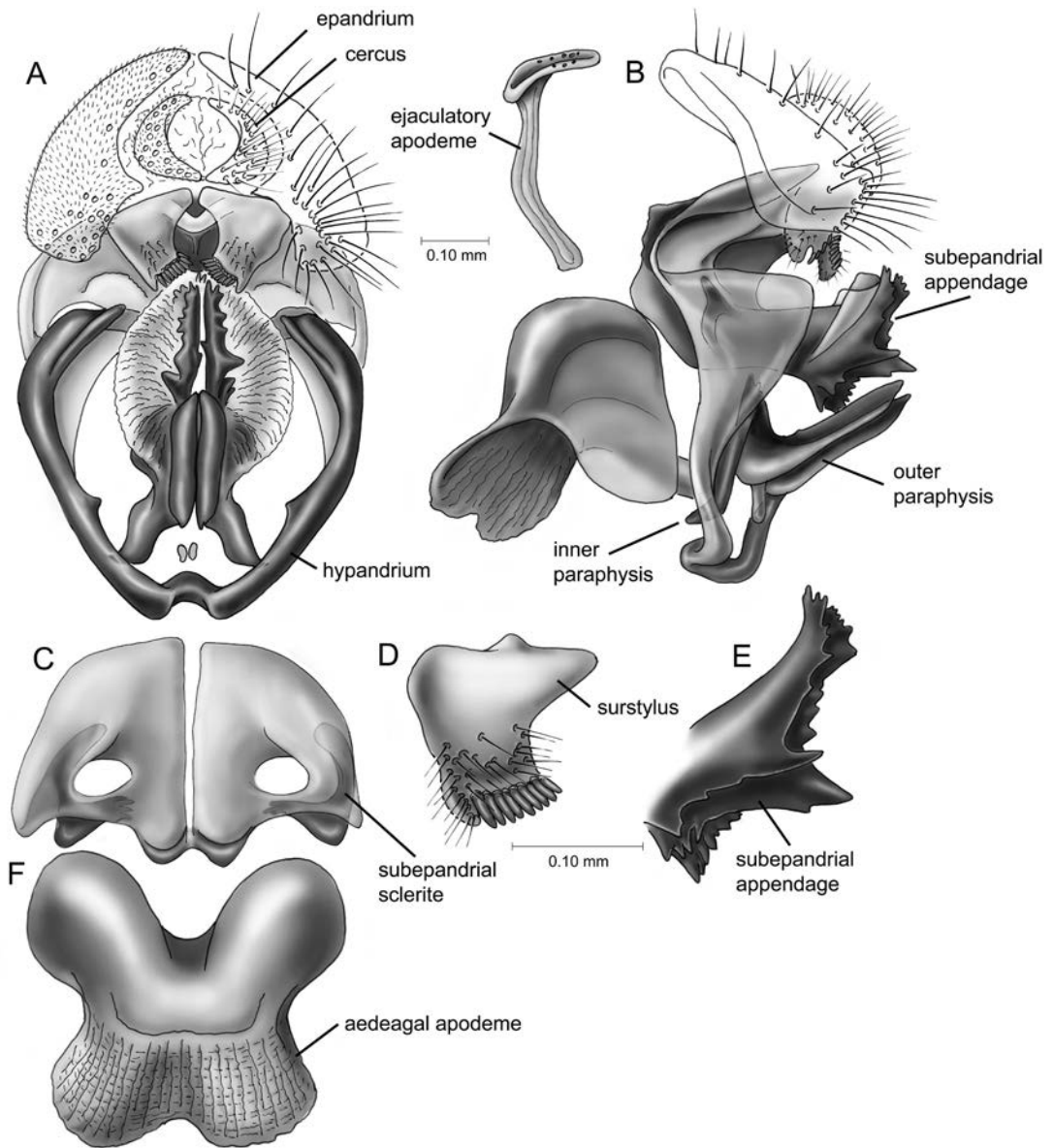


FIG. 50. Male terminalia, *A. tibialis*. **A.** Ventral view. **B.** Lateral view, with ejaculatory apodeme. **C.** Subepandrial sclerite. **D.** Surstylus. **E.** Subepandrial appendage, apex lateral view. **F.** Aedeagal apodeme. (Am 470, holotype).

M Wasserman, WB Heed, "June 1952," 2260:13, 2♂ (Am 3\*, 5\*, AMNH).

OTHER MATERIAL EXAMINED: **Mexico: Chiapas:** 5 mi. W San Cristobal, 7500', 1969-05-06, leg. H.J. Teskey, 1♂ (Am 1426\*, CNC); 20 mi N. Bochil, Yerba Buena, 6500', 1969-06-09 through

1969-06-10, leg. W.R.M. Mason, 1♂ (Am 1264\*, CNC). **Durango:** 14 mi. SW El Salto, 8000', 1964-06-26, leg. J.F. McAlpine, attracted to man, 1♂ (Am 1525\*, CNC). **Sinaloa:** El Palmito, 6400', 1964-07-02, leg. J.F. McAlpine, 1♂ (Am 1518\*, CNC).

**ETYMOLOGY:** From Latin *latus* for “wide” and *labrum* for “lip.” Used as a noun in apposition. In reference to the characteristic wide facial marking of this species.

**DISTRIBUTION:** *Amiota latilabrum* occurs widely throughout Mexico including the states of Chiapas, Durango, Sinaloa, and Puebla.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota nebojsa* Máca, 2003

Figures 51E–F, 53C–D, 56, 60E, 91C

*Amiota nebojsa* Máca, 2003: 269 (original description); Brake and Bächli, 2008: 254 (world catalog).

**DIAGNOSIS:** Large fly (ThL 1.73–1.92 mm), dark brown and glossy; outer paraphysis in lateral view forming distinctive structure: laterally flattened with a distal hook, proximal end with 2 long, nearly parallel spines very near each other, basal spine shorter; inner paraphysis lost.

**DESCRIPTION:** Large fly (ThL 1.73–1.92 mm), dark brown and glossy, legs yellow. Frons shiny; dark brown dorsally, light brown ventrally. Cheek deep, variable in size (EL/CW 6.76–22.66), milky white posteriorly. Facial marking large (FML/FMW 0.35–0.42). Palp brown. Haltere yellow. Tergites 1 and 2 lightly colored. Arista: Short, plumose; longest branch D4; A.R. 0.28–35; 4–5 long dorsal, 0 long ventral branches; D4 pointed laterad; arista trunk with very long microtrichia along entire length. Male genitalia: Epandrium separated at midline, distinct from membrane surrounding cerci; middle section without long setae; small anterolateral projection. Cercus oval shaped, distinct from surrounding membrane. Surstylus wide, almost square; ventral half with 18–20 long, scattered setulae; 11–13 peglike prensisetae, apices blunt, comblike; small lateral lobe present, oriented anteriorly. Subepandrial sclerite well sclerotized, C-shaped in lateral view;

subepandrial appendage extending posteriorly; apex heart shaped in posterior view. Outer paraphysis long, laterally flattened, heavily sclerotized; hook on distal end; proximal end with 2 long spines in lateral view, nearly parallel to each other, distal spine slightly shorter; sternite 6 modified into large membranous sac, lightly sclerotized, basal portion microtrichose, cobbled distally. Inner paraphysis lost. Aedeagal apodeme as long as wide, strongly curved in lateral view; proximal region inflated, forming pockets; distal end widely flared with deep concave depression. Hypandrium thin, apex notched, accommodating outer paraphysis; lateral arm with a large gonopod, rectangular, oriented posteriorly. Ejaculatory apodeme very large, nearly as long as epandrium. Head and thorax measurements: (n = 5; Am 10, 11, 458, 637, 741) FL/FW 0.66 (0.61–0.73), EL/EW 1.38 (1.35–1.41), EL/CW 12.54 (6.76–22.66), FML/FMW 0.38 (0.35–0.42), PR/RR 0.56 (0.42–0.70), ThL 1.80 (1.73–1.92 mm).

**TYPE MATERIAL:** **Holotype:** As reported by Máca (2003): “♂: USA, Arizona Cochise Co., Huachuca Mts., Pinary Cyn., 5100 ft., 9.8.1991, leg. Y.F. Hsu, [not examined]. Coll. Jan Máca, intended for National Museum, Prague (NMPC). **Paratypes:** As reported by Máca (2003): “same locality, 4 ♂ and 1 ♀”. Coll. Jan Máca, intended for National Museum, Prague (NMPC).

**OTHER MATERIAL EXAMINED:** **Mexico:** **Durango:** 3 mi E. El Salto, 8200', 1964-07-04, leg. J.F. McAlpine, 1 ♂ (Am 1432\*, CNC); 1965-06-20, leg. J.F. McAlpine, 1 ♂ (Am 1542\*, CNC); 3 mi W. El Salto, 8000', 1964-06-19, leg. J.F. McAlpine, attracted to man, 1 ♂ (Am 1487\*, CNC); 10 mi W. El Salto, 9000', 1964-08-03, leg. J.F. McAlpine, 10 ♂ (Am 1410\*, 1543–1551\*, CNC); 1964-06-30, leg. W.R.M. Mason, 2 ♂ (Am 1424\*, 1500\*, CNC); 14 mi SW. El Salto, 8000', 1964-06-26, leg. J.F. McAlpine, attracted to man, 17 ♂ (Am 1411\*, 1413\*, 1445\*, 1446\*, 1451\*, 1454\*, 1491–1493\*, 1497\*, 1507\*, 1508\*, 1510\*, 1516\*, 1517\*, 1519\*, 1521\*, CNC); 1964-07-17, leg. W.R.M. Mason, 2 ♂ (Am 1210\*, 1430\*, 1431\*, CNC). **Guerrero:** Gro 12 km S of Xochipala, 1992-07-15, leg. D.M. Wood, 1 ♂ (Am 1386\*, CNC). **USA:** **Arizona:** Cochise Co., Ramsay Canyon, Mile High

Trail. Near Sierra Vista, 1984-08-24, leg. L.B. Carlson, sweep, 3♂ (Am 637\*, 639\*, 741\*, DEBU); Graham Mtns., Wet Canyon, 32 39 1 N, 109 48.8 W, 6050', 2011-08-14, leg. J.E. O'Hara, 1♂ (Am 1225\*, CNC); Oak Creek Canyon, 1947-07-15, leg. R.H. Beamer, 1♂ (Am 458\*, SEMC). **New Mexico:** Gila National Forest, Iron Creek Picnic ground near Emory Pass, 2007-08-16, leg. J.H. Skevington, CNC787037, 1♂ (Am 1222\*, CNC); Gila National Forest, Cherry Creek campground, 32.914167 S, 108.22500 W, 2103 m, 2007-08-14, leg. S. Kelso, CNC Diptera #58844, 1♂ (Am 1289\*, CNC); Gila National Forest, Meadow Creek campground, 32 57 18 S, 108 10 17 W, 2025 m, 2007-08-14, leg. S. Kelso, CNC Diptera #57715, 1♂ (Am 1287\*, CNC); Grant Co., 14 mi north Silver City, Cherry Creek Campground, 32 54 8 N, 108 13 6 W, 7400', 2007-08-23, leg. J.E. O'Hara, 1♂ (Am 1200\*, CNC); Grant Co., 14 mi north Silver City, Cherry Creek Campground, 32 54.8 N 108 13.6 W, 6850', 2010-10-13, leg. J.E. O'Hara, 1♂ (Am 1241\*, CNC); 12 mi N of Silver City, 1950-08, leg. M.R. Wheeler, 2051, [paratypes of *A. buccata* Wheeler, see Discussion under that species] 2♂ and 1♀ (Am 9, 10\*, 11\*, AMNH); 1950-08, leg. M.R. Wheeler, 2074, [paratype of *A. buccata* Wheeler, see Discussion under that species] 1♀ (Am 8, AMNH).

**DISTRIBUTION:** This species is found in the mountainous regions throughout Arizona and New Mexico, as well as Guerrero State in southern Mexico.

**COMMENTS:** When Máca described *A. nebojsa* (2003), he cited a paratype in the type series as an "aberrant individual." This paratype is a different species, *Amiota amputata*. *Amiota nebojsa* and *Amiota amputata* have overlapping distributions and specimens in DEBU of the two species were also collected in the same series. This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota occidentalis*, sp. nov.

Figures 52A–B, 53E, 57, 60C, 92A

**DIAGNOSIS:** Very large fly (ThL 1.93–2.09 mm), dark brown to black; outer paraphysis with 2 long dorsal spines in lateral view, nearly paral-

lel, equal length, proximal one blunt; apical hook bifid; basalmost spine long, apex with small notch; inner paraphysis lost.

**DESCRIPTION:** Very large fly (ThL 1.93–2.09 mm), dark brown to black, uniformly so, glossy; legs dark yellow. Frons dark, nearly black; with lighter brown central band, running laterally. Facial marking large (FML/FMW 0.30–0.43), semicircular. Cheek very wide (EL/CW 6.29–11.62), white posteriorly. Palp brown. Marking under wing base somewhat faded. Haltere light yellow. Tergites 1 and 2 lightly colored. Arista: Very short, plumose; longest branch D2; A.R. 0.25; 5 dorsal, 0 ventral branches, none pointed mediad/laterad; arista trunk with long microtrichia along entire length. Male genitalia: Epandrium separated at midline, ventral margin of dorsal arch distinct from surrounding membrane; ventral portion densely hairy, with a line of single setae ascending ventrally; small anterolateral projection. Cercus thin, crescentic; distinct from surrounding membrane. Surstylus approximately rectangular, middle portion and ventrolateral edge with setulae; 7–9 short, peglike prenisetae, apices blunt; small lateral lobe present, not extending beyond prenisetae. Subepandrial sclerite C-shaped in lateral view, well sclerotized; with subepandrial appendage that is heart shaped in posterior view, apex broad and round. Outer paraphysis laterally flattened, slightly hooked at apex; 3 long spines in lateral view; 2 along middle portion at angle, nearly parallel to each other, distal spine blunt; proximal spine with pointed apex and small preapical tooth; basalmost spine long, apex with small notch. Male sternite 6 moderately sclerotized, developed into sac with faintly cobbled surface. Inner paraphysis lost. Aedeagal apodeme longer than wide, width 0.75× length; curved 90° in lateral view, curved portion forming inflated pockets; distal end with a deep emargination. Hypandrium thickened; apex notched, accommodating outer paraphysis; lateral arm with gonopod, bulging, oriented pos-

teriorly. Ejaculatory apodeme of moderate length,  $0.7 \times$  length of epandrium. Head and thorax measurements: ( $n = 5$ ; Am 375, 406, 409, 625, 666) FL/FW 0.62 (0.57–0.66), EL/EW 1.44 (1.32–1.72), EL/CW 8.33 (6.29–11.62), FML/FMW 0.37 (0.30–0.43), PR/RR 0.57 (0.40–0.70), ThL 1.99 (1.93–2.09 mm).

**TYPE MATERIAL:** **Holotype:** male: UTAH, Cache Co, Logan Cyn [canyon], Turner CG [campground], [41.883204, -111.572736], 27 Jun-5 Jul 85, W.J. Hanson, Am 476, [glued directly to pin, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** UTAH, Cache Co, Logan Cyn [canyon], Turner CG [campground], 27 Jun–5 Jul 85, W.J. Hanson, 4♂ (Am 474\*, 477\*, 479, 480, LACM).

**OTHER MATERIAL EXAMINED:** **Canada: British Columbia:** Ainsworth, 1980-07-31, leg. S.A. Marshall, sweep, 1♂ (Am 625\*, DEBU); Six Mile [Point?], 1959-07-28, leg. H.R. Foxlee, 1♂ (Am 1399\*, CNC). **USA: California:** L.A. Co., Angeles Nat. For., 34.389176, -117.716479, 02017-06-05, leg. C.M. Cohen, 1♂ (Am 524\*, AMNH); Siskiyou Co., McBride Springs, 1524 m, 1976-08-08, leg. P.H. Arnaud Jr., 1♂ (Am 374\*, CAS); Trinity Co., Swift Cr. 3900 ft., 1972-07-06, leg. T. Griswold, 1♂ (Am 375\*, CAS). **Montana:** Missoula Co., Lubrecht Experimental Forest, 46 53.61 N, 113 27.08 W, 1250 m, 2017-06-28, leg. J.E. O'Hara, malaise, CNC821145, 1♂ (Am 1282\*, CNC). **Oregon:** Baker Co., U. Goose Vrk., 34 mi. SE Union, 4160 ft., 1977-06-19 through 1977-06-22, leg. E.J. Davis, malaise baited with CO<sub>2</sub>, 1♂ (Am 409\*, WSU). **Utah:** Box Elder Co., 1 mi N Mantu, 1969-07-21 through 1969-07-27, leg. W.J. Hanson, malaise trap, 1♂ (Am 672, LACM); Cache Co., Green Canyon, Cache Co., Green Canyon, 1985-06-12 through 1985-06-15, leg. N.N. Youssef, 1♂ (Am 469\*, LACM); 1985-06-15 through 1985-06-19, leg. N.N. Youssef, 1♂ (Am 468\*, LACM); Cache Co., Logan Canyon, Turner C.G., 1985-06-10 through 1985-06-20, leg. W.J. Hanson, 1♂ (Am 471, LACM); 1985-06-20 through 1985-06-27, leg. W.J. Hanson, 1♂ (Am 484\*, LACM); Cache Co., Logan Canyon, Twin Creek, 1988-07-08 through 1988-07-15, leg. W.J. Hanson, 1♂ (Am 667\*, LACM); Cache Co., Mendon Cold Spg., 1977-06-20 through 1977-07-04, [collector unknown], malaise trap, 1♀ (Am 496, LACM); 1977-07-12 through 1977-07-19, [collector unknown], malaise trap, 1♂ (Am 494\*,

LACM); Cache Co. Sardine Canyon, 1969-06-18, leg. W.J. Hanson, malaise trap, 1♂ (Am 666\*, LACM); Cache Co., Tony Grove Jct., 1983-07-27 through 1983-08-02, [collector unknown], malaise trap, 1♂ (Am 492\*, LACM); 1984-07-03 through 1984-07-11, [collector unknown], malaise trap, 1♂ (Am 490, LACM); 1984-07-11 through 1984-07-25, [collector unknown], malaise trap, 2♂ (Am 487, 491\*, LACM). **Washington:** Okan Co., 4 mi E. Twisp, Rt. 20, 1972-07-19, leg. W.J. Turner and W.B. Garnett, malaise trap dry ice, 1♂ (Am 408\*, WSU); Skagit Co., 6.5 mi. E Marblemount, 48 31 57 N, 121 19 17 W, 1052 ft, 2018-06-08 through 2018-06-17, leg. J.M. Cumming and S.E. Brooks, MT across crk, CNC1109319, 1♂ (Am 1227\*, CNC); Skykomish, 1954-07-05, leg. R. Moree, 1♂ (Am 406\*, WSU).

**ETYMOLOGY:** From Latin *occidens* for “west” in reference to the distribution of this species, which is throughout western North America.

**DISTRIBUTION:** *Amiota occidentalis* is found widely throughout western North America from southern California to British Columbia and east to Utah and Montana. It extends more easterly in the northern parts of its range.

**COMMENTS:** It is unknown whether *Amiota occidentalis* is attracted to the face and eyes. According to specimen data, it has apparently been collected only by general sweeping and malaise traps, sometimes baited with dry ice (CO<sub>2</sub>), a method used to collect tabanids, mosquitoes and other blood-feeding flies. Attraction to CO<sub>2</sub> suggests it is attracted to humans, and that *Amiota* may use cues other than visual (e.g., mammal eyes) or perspiration scent.

### *Amiota oviraptor*, sp. nov.

Figures 52C–D, 53F–G, 58, 92B

**DIAGNOSIS:** Large fly (ThL 1.56–1.66 mm), dark brown to black; outer paraphysis heavily sclerotized, in lateral view strongly sinuate, anterior portion curving dorsally, posterodorsal portion with 2 posterior facing spines, posteroventral region forming a strong laterally flattened “wing” (posteriorly pointed), the apex with a minute hook; inner paraphysis lost.

**DESCRIPTION:** Large fly (ThL 1.56–1.66 mm), dark brown to black, legs yellow. Frons golden, pruinose. Facial marking large, depth  $0.5\times$  width. Cheek wide (EL/CW 11.14–12.5), milky white posteriorly. Palp dark brown. Haltere white. Tergites 1 and 2 lightly colored. Arista: Short, plumose; longest branch D3; A.R. 0.26; 4 longer dorsal, 2–3 short ventral branches; branch D4 pointed mediad; arista trunk with long microtrichia to apex. Male genitalia: Epandrium split medially, middle gap large, membranous; lower third with long setae; small projection anterolaterally. Cercus cylindrical, not grading into surrounding membrane; large membranous region dorsally. Surstylus squarish, ventral half densely covered with setulae; 13–14 short, peglike prenisetae, apices blunt; laterally with barely a lobe. Subepandrial sclerite sclerotized, C-shaped in lateral view, its broad section with muscle attachment scars; subepandrial appendage well developed, vaguely heart shaped in posterior view, apex with minute irregular serrations. Outer paraphysis heavily sclerotized; in lateral view strongly sinuate, anterior portion curving dorsally; posterodorsal portion with 2 posterior-facing spines; posteroventral region forming a strong, laterally flattened “wing,” posteriorly pointed; apex with a very small, downward pointed hook. Inner paraphysis lost. Aedeagal apodeme roughly trapezoidal, curved nearly  $90^\circ$  in lateral view, width  $1.25\times$  length; posterior portion deeply constricted; distal end widely flared, with deep concave depression/emargination. Hypandrium U-shaped; lateral arms thick, wing-like ventrally; lateral arm with a strong gonopod, posteriorly pointed. Ejaculatory apodeme relatively small, well sclerotized,  $0.6\times$  length of epandrium; flattened end nearly in line with stalk. Head and thorax measurements: ( $n = 2$ ; Am 1506, 1529): FL/FW 0.69 (0.68–0.70), EL/EW 1.20 (1.18–1.22), EL/CW 11.82 (11.14–12.5), FML/FMW 0.36 (0.34–0.38), PR/RR 0.62 (0.54–0.70), ThL 1.61 (1.56–1.66 mm).

**TYPE MATERIAL:** **Holotype:** male: 14 mi. SW. El Salto, Dgo. [Durango] MEX., [23.786449, -105.597725], 8000', June “9” 1964, J.F. McAlp-

ine, Am 1529, [glued to pin, dissected]. Deposited in the Canadian National Collection (CNC).

**Paratype:** 14 mi. SW. El Salto, Dgo. MEX., 8000', June “26” 1964, J.F. McAlpine, attracted to man, [dissection lost], 1 ♂ (Am 1506\*, CNC).

**OTHER MATERIAL EXAMINED:** Known only from the type series.

**ETYMOLOGY:** In reference to the lateral view of the fused paraphyses which resemble the “winglike” arm and head of an oviraptorid dinosaur and other birdlike dinosaurs.

**DISTRIBUTION:** *Amiota oviraptor* is currently known only from the vicinity of the city of El Salto within Durango State in Mexico.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

### *Amiota subnebojsa*, sp. nov.

Figures 52E–F, 53H, 59, 60B, 92C

**DIAGNOSIS:** Large fly (ThL 1.67–1.79 mm), glossy black with a black head; outer paraphysis heavily sclerotized; apex with short spine, barely hooked; lateral view with 2 long spines on dorsal margin; in ventral view base forming a tapered wing curving medially; inner paraphysis lost; very similar to *A. latilabrum*, differing as given in diagnosis for that species.

**DESCRIPTION:** Large fly (ThL 1.67–1.79 mm), dark brown, glossy, grading lighter ventrally; legs yellow. Facial marking very large, semicircular. Cheek wide (EL/CW 8.33–12.28), posteriorly milky white. Frons dark, nearly black dorsally, ventral portion light brown. Palp dark brown. Arista: Very short, plumose; longest branch D2; A.R. 0.29; 3 dorsal, 0 ventral branches, none pointed mediad/laterad; arista trunk with long microtrichia along entire length. Male genitalia: Epandrium nearly split medially, not grading with surrounding membrane; dense cluster of setae ventrally, ascending in a single line toward apex; small lobe projecting on anterolateral margin. Cercus oval shaped, distinct from surrounding mem-

brane. Surstylus rather semicircular, scattered setulae on ventral third; 15 peglike prensisetae, apices blunt, comblike; lateral fingerlike lobe present, not extending beyond prensisetae. Subepandrial sclerite C-shaped in lateral view, moderately sclerotized; subepandrial appendage long, oriented posteriorly, heart shaped in posterior view, tapering to a blunt point, invaginated medially. Outer paraphyses heavily sclerotized, formed of 2 lobes, split deeply medially; apex blunt with sharp hook in lateral view, laterally flattened; posterior margin forming a wing; anterior/dorsal margin with 2 long spines, distal spine oriented dorsally, proximal spine longer and with small subapical tooth, oriented anteriorly; basal portion modified into tapering wing; in ventral view 2 clawed appendages; proximal appendage, stubby; basal tapering wing, long, curving medially. Inner paraphysis lost. Aedeagal apodeme length equal to width; base with a deep cleft, distal end widely flared with medium emargination. Hypandrium deeply notched, accommodating outer paraphyses; lateral arm with gonopod, projecting postero-ventrally. Pair of membranous lobes present, connected to space within hypandrium. Ejaculatory apodeme not studied. Head and thorax measurements: ( $n = 5$ ; Am 442, 443, 447, 448, 1527) FL/FW 0.74 (0.72–0.78), EL/EW 1.30 (1.22–1.48), EL/CW 9.93 (8.33–12.28), FML/FMW 0.43 (0.40–0.44), PR/RR 0.53 (0.38–0.80), ThL 1.73 (1.67–1.79 mm).

**TYPE MATERIAL:** **Holotype:** male: MEXICO, Morelos #7, 14 mi N. Cuernavaca, [19.188745, -99.228691], 7300', 29 July 1963, George W. Byers, Am 443, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** MEXICO, Morelos #7, 14 mi N. Cuernavaca, 7300', 29 July 1963, George W. Byers, 6♂ (Am 442\*, 445, 446, 447\*, 448\*, 449, SEMC).

**OTHER MATERIAL EXAMINED:** **Mexico:** **Durango:** 14 mi. SW El Salto, 8000', 1964-06-26, leg. J.F. McAlpine, attracted to man, 1♂ (Am 1527\*, CNC).

**ETYMOLOGY:** Formed from *sub*, Latin for "under or below," and *nebojsa*, a previously described species in the genus which it is presumably closely related.

**DISTRIBUTION:** *Amiota subnebojsa* is currently known only from the state of Morelos in Mexico.

**COMMENTS:** This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

#### THE NIGRESCENS SPECIES GROUP (NEW GROUP)

**DIAGNOSIS:** Small to medium-sized flies; thorax dark blackish brown, with typical white markings; femora light brown (except some Arizona individuals of *A. nigrescens*), tibiae and tarsi yellow; arisal branch lengths short to very short, branches confined to basal half; frons dark, dull. Male genitalia: Relatively simple; surstylus slender, armlike, with few prensisetae; outer paraphyses with one or no spines, asymmetrical in size; inner paraphyses lost.

**NEARCTIC SPECIES:** *Amiota fulvitibia*, *A. nanonigrescens*, sp. nov., and *A. nigrescens* Wheeler.

**COMMENTS:** It is unknown whether any of the species in this group exhibit the common behavior among *Amiota* of being attracted to humans. All taxa seem commonly caught in Malaise, pan, and emergence traps.

#### *Amiota fulvitibia*, sp. nov.

Figures 61A–B, 62A, 63, 93A

**DIAGNOSIS:** Small to medium-sized fly (ThL 1.12–1.29 mm), dark brown and glossy, ventral half of head medium brown, dorsal half of frons black; femora medium brown, tibiae and tarsi yellow; outer paraphysis composed of two, asymmetric lobes: left lobe long, linear, tapered to a point, with a middorsal, perpendicular spine; right lobe shorter, strongly curved, with 2 upward-curving spines; inner paraphysis lost.

**DESCRIPTION:** Small to medium-sized fly (ThL 1.12–1.29 mm), dark brown, uniformly so, glossy. Femora medium brown, tibiae and tarsi light yellow. Ventral half of frons medium brown, dorsal half black. Cheek dark brown. Palp dark brown. Arista: Very short, plumose; longest branch D2; A.R. 0.17; 3 short dorsal, 0 ventral branches; none pointed mediad/laterad; arista trunk with medium-length microtrichia along entire length. Male genitalia: Epandrium fused at midline, margins distinct from surrounding membrane; ventral lobes densely hairy, middle portion without long setae. Cercus long, pendulous; not grading into surrounding membrane. Surstylus long, armlike; ventral half with setulae; 3 long prensisetae, apices blunt; 2 long setae on interior margin of apex, pointed medially. Subepandrial sclerite moderately sclerotized, C-shaped in lateral view; with broad, squarish inner portion; subepandrial appendage well developed, heart shaped in posterior view, wide at base, tapering to long, narrow point. Outer paraphysis asymmetrical, composed of 2 lobes; left one long, tapering to a point; small, dorsal spine perpendicular to axis; right lobe smaller, rounded, curved; 2 dorsal spines, each pointed upright and curving slightly medially. Inner paraphysis lost. Aedeagal apodeme nearly equal in length and width; curved 90° in lateral; distal end widely flared, with a very shallow emargination. Hypandrium deeply notched at apex, nearly level with base of hypandrium, accommodating outer paraphyses; lateral arm with prominent winglike gonopod, pointing ventrally. Ejaculatory apodeme 0.6× length of epandrium. Head and thorax measurements: (n = 5; Am 537, 577, 589, 599, 600) FL/FW 0.72 (0.63–0.82), EL/EW 1.26 (1.21–1.34), EL/CW 13.72 (11.80–15.25), FML/FMW 0.23 (0.20–0.29), PR/RR 0.43 (0.33–0.60), ThL 1.21 (1.12–1.29 mm).

**TYPE MATERIAL:** **Holotype:** male: ONT [Ontario]: Algonquin Prov. Pk. Swan Lk. Stn., Scott Lk Survey, [45.489399, -78.715496], shore C1 Mal. [malaise], 01-07.vi.94, [no collector stated, presumably E. Barr and S. Marshall], Am 587, [glued to paper point, dissected]. Deposited in the University of Guelph (DEBU). **Paratypes:**

ONT [Ontario]: Algonquin Prov. Pk. Swan Lk. Stn., Scott Lk Survey, shore, C1 Mal. [Malaise], 01-07.vi.94, E. Barr/S.M., 1 ♂ (Am 599\*, DEBU); ONT [Ontario]: Algonquin Prov. Pk. Swan Lk. Stn., Scott Lk Survey, C1 shore, Maltp. [Malaise trap], 01-07.vi.1994, [no collector stated, presumably E. Barr and S. Marshall], 1 ♂ (Am 596\*, DEBU).

**OTHER MATERIAL EXAMINED: Canada:**

**Ontario:** Algonquin Park, Swan Lake Station, Scott Lake, 1993-05-08 through 1993-05-19, leg. Larson, Marshall and Barr, malaise A1 lakeshore, 2 ♂ (Am 534\*, 535\*, DEBU); 1993-05-19 through 1993-05-31, leg. Larson, Marshall and Barr, malaise A1 lakeshore, 2 ♂ (Am 531\*, 537\*, DEBU); 1994-05-19 through 1994-05-26, [collector unknown], C1 Shore malaise trap, 1 ♂ (Am 588\*, DEBU); 1994-05-19 through 1994-06-26, leg. E. Barr and S.A. Marshall, A3 Malaise, Sphagnum, 1 ♂ (Am 600\*, DEBU); 1994-05-19 through 1994-06-26, leg. E. Barr and S.A. Marshall, C1 Malaise, shore, 1 ♂ (Am 598\*, DEBU); 1994-05-19 through 1994-05-27, [collector unknown], C1 shore, malaise trap, 1 ♂ (Am 589\*, DEBU); 1995-05-29 through 1995-06-16, leg. S.A. Marshall, D1 shorepans, 1 ♂ (580, DEBU); 1995-05-29 through 1995-06-16, leg. S.A. Marshall, fresh stump emergence, [dissection lost] 1 ♂ (Am 577\*, DEBU). **Tennessee:** Sevier Co., Great Smoky Mtns. N.P., Roaring Fork Creek and Trillium Gap Trails, 1999-05-28, leg. J.M. Cumming, ex. Blossoms Chrysanthemum, 1 ♂ (Am 1301\*, CNC).

**ETYMOLOGY:** Formed from Latin *fulvus* for “brown” and *tibia* for “leg,” in reference to the brown femur on the legs of this species.

**DISTRIBUTION:** This species is primarily known from Ontario, although one specimen has been collected from Great Smoky Mountains in Tennessee, suggesting a much wider distribution. Southern extensions of the distribution may be along higher altitudes.

**COMMENTS:** *Amiota fulvitibia* is very superficially similar to *A. albilabris* (Roth) in Bächli et al. (2004) in regard to the brown femora as well as genitalic structure (in lateral view), however, close inspection shows that the “three-pointed structure” in each is composed of very different structures (paraphyses in *Amiota fulvitibia* vs. the hypandrium and dorsal arch of *A. albilabris*).

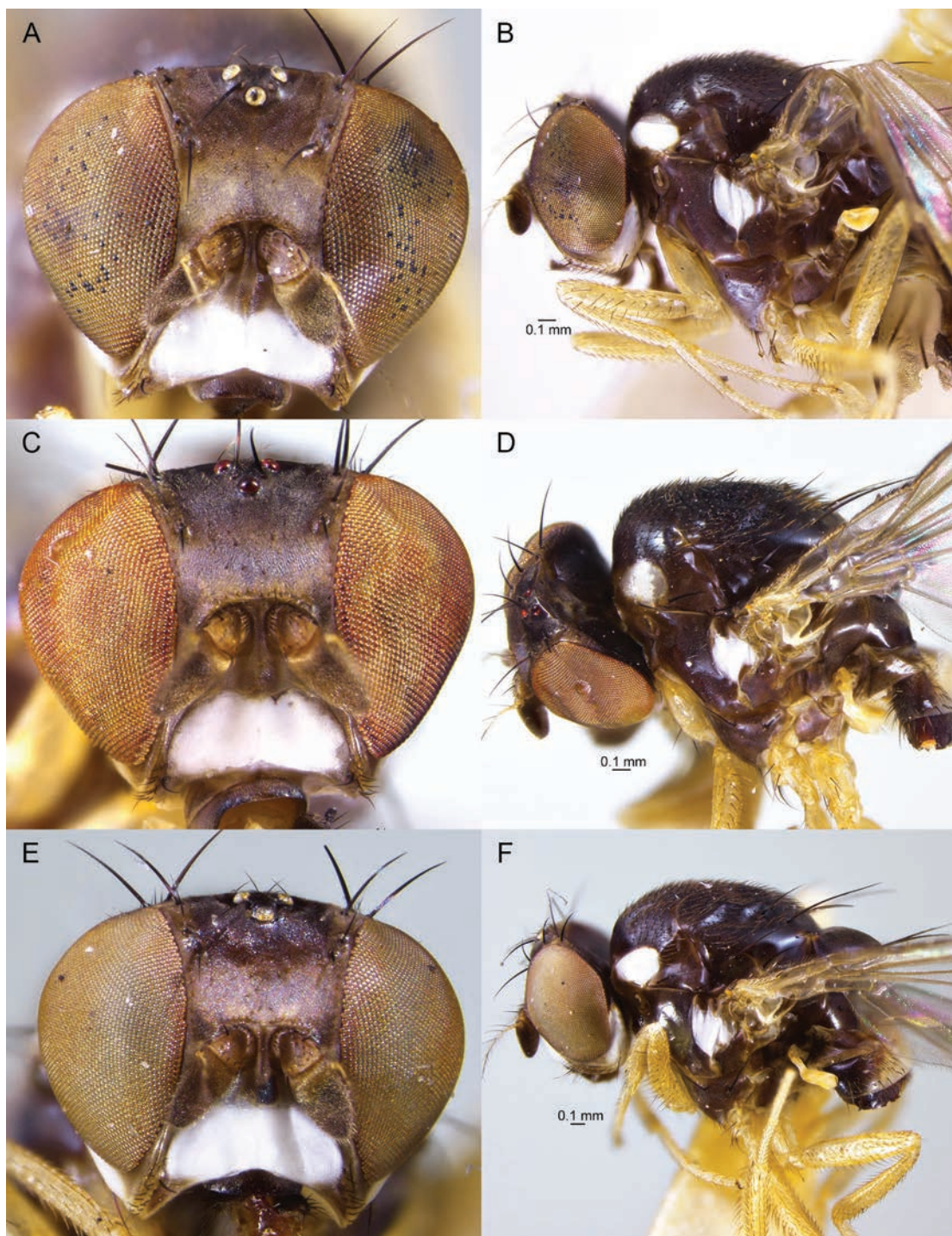


FIG. 51. Heads and lateral views, *A. nebojsa* species group. A–B. *A. amputata*, sp. nov. (Am 4, lateral image flipped). C–D. *A. latilabrum*, sp. nov. (Am 2, holotype, lateral image flipped). E–F. *A. nebojsa* Máca (Am 10, lateral image flipped).

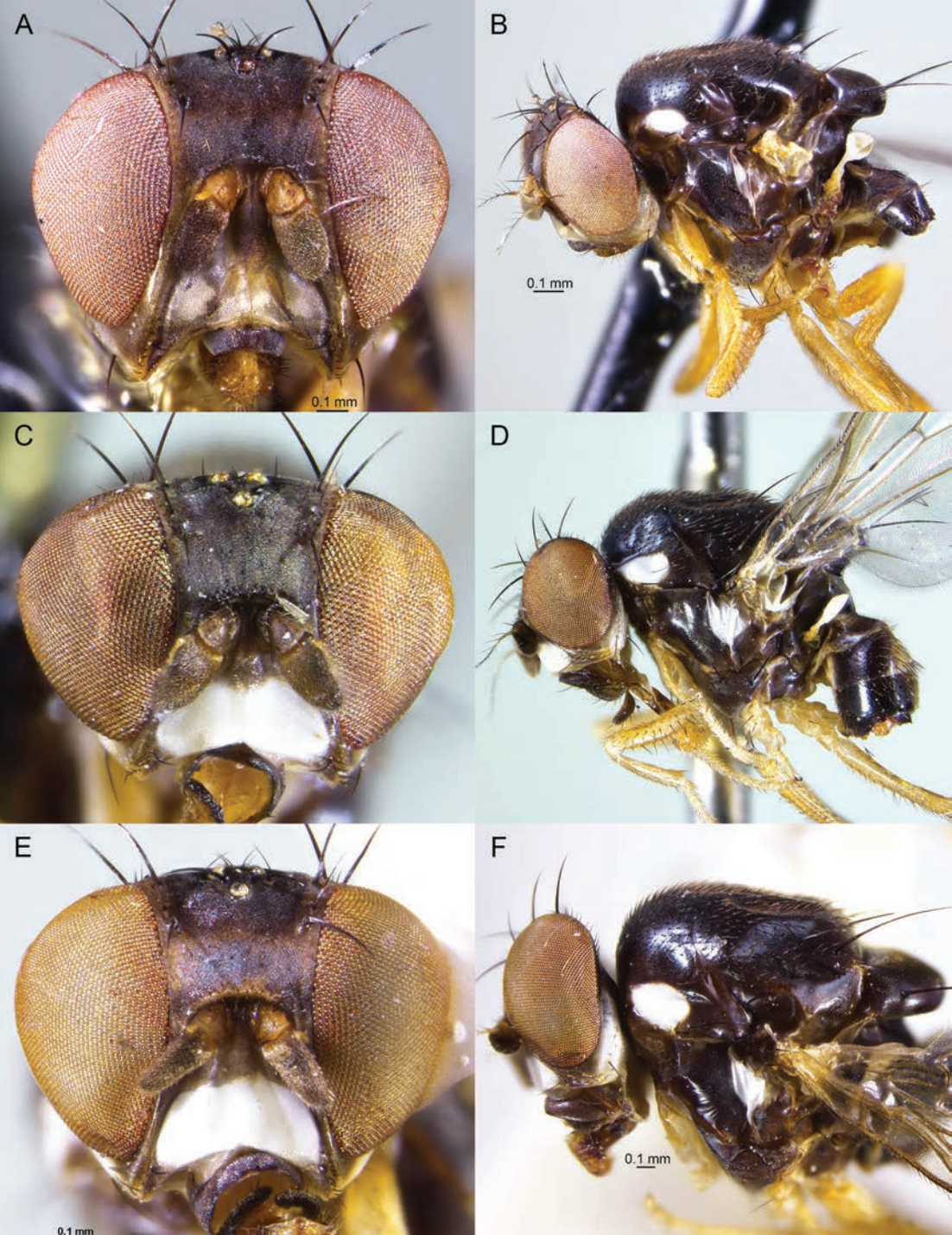


FIG. 52. Heads and lateral views, *A. nebojsa* species group. A–B. *A. occidentalis*, sp. nov. (Am 408). C–D. *A. oviraptor*, sp. nov. (Am 1506, paratype). E–F. *A. subnebojsa*, sp. nov. (Am 442, paratype, lateral image flipped).

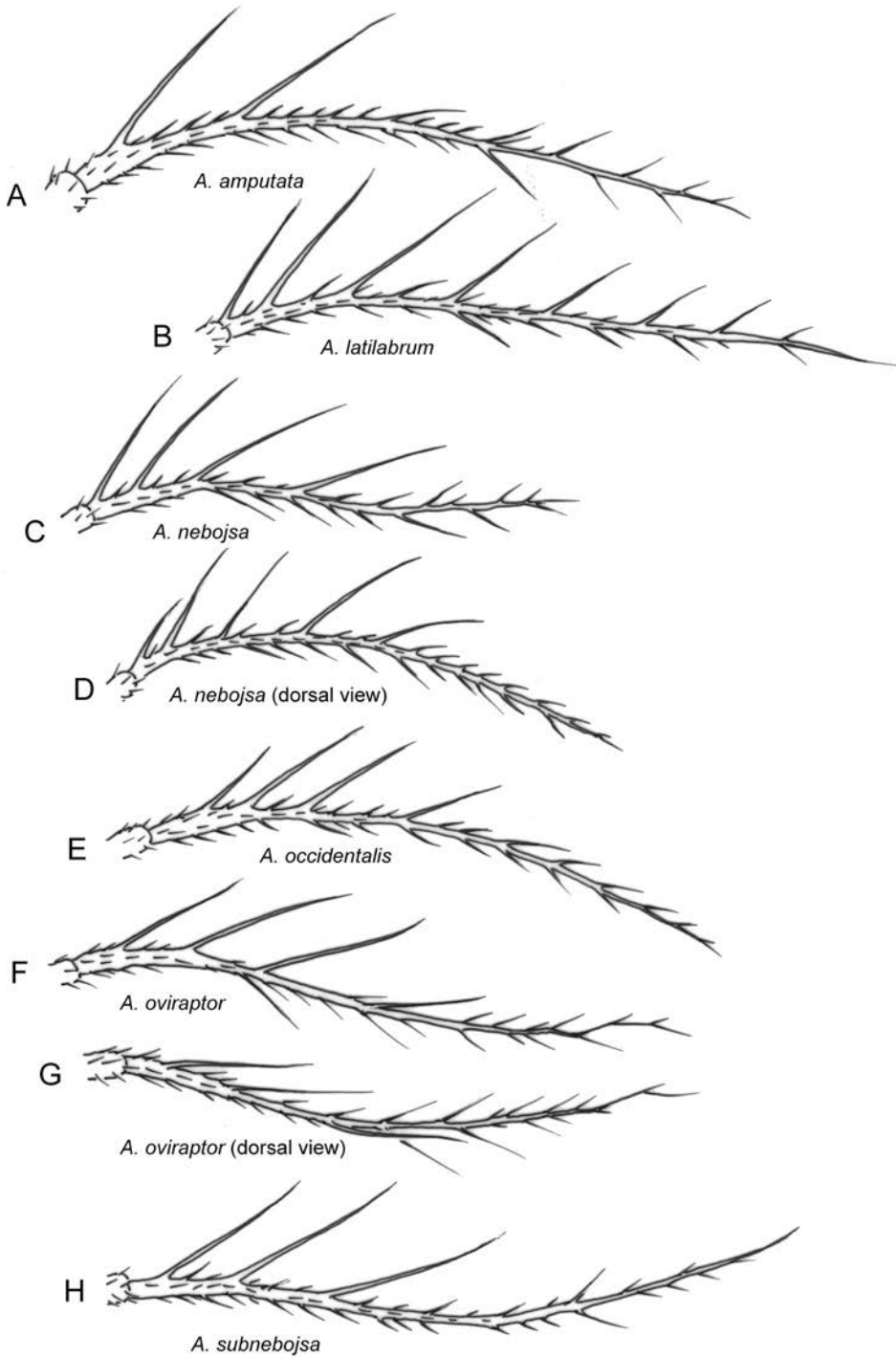


FIG. 53. Aristae, *A. nebojsa* species group. A. *A. amputata*, sp. nov. B. *A. latilabrum*, sp. nov. C–D. *A. nebojsa* Máca. E. *A. occidentalis*, sp. nov. F–G. *A. oviraptor*, sp. nov. H. *A. subnebojsa*, sp. nov. Not to the same scale.

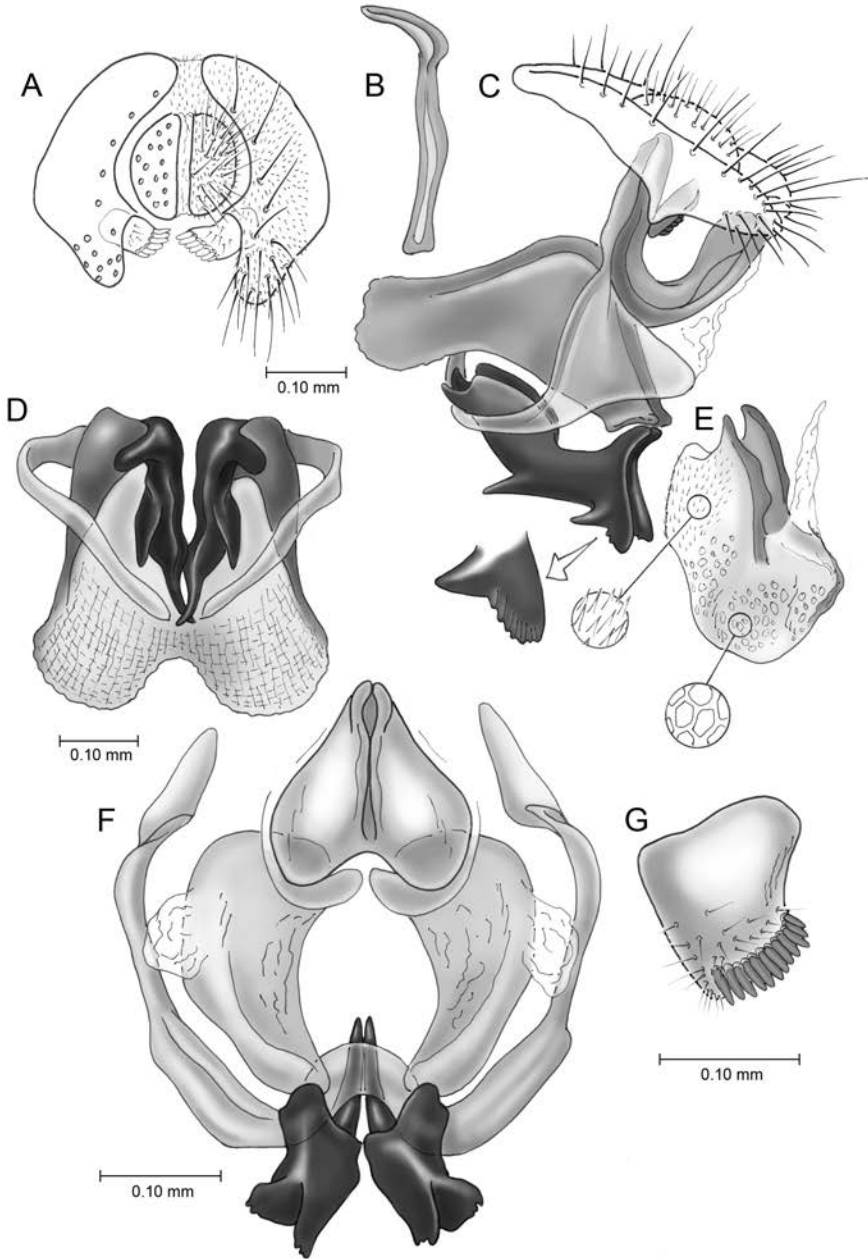


FIG. 54. Male terminalia, *A. amputata*. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Aedeagal apodeme, paraphyses, hypandrium, lateral view. **D.** Posterior view. **E.** Sternite 6 sac, with surface detail. **F.** Ventral view (apex of subepandrial appendage at top). **G.** Surstylus. (Am 753).

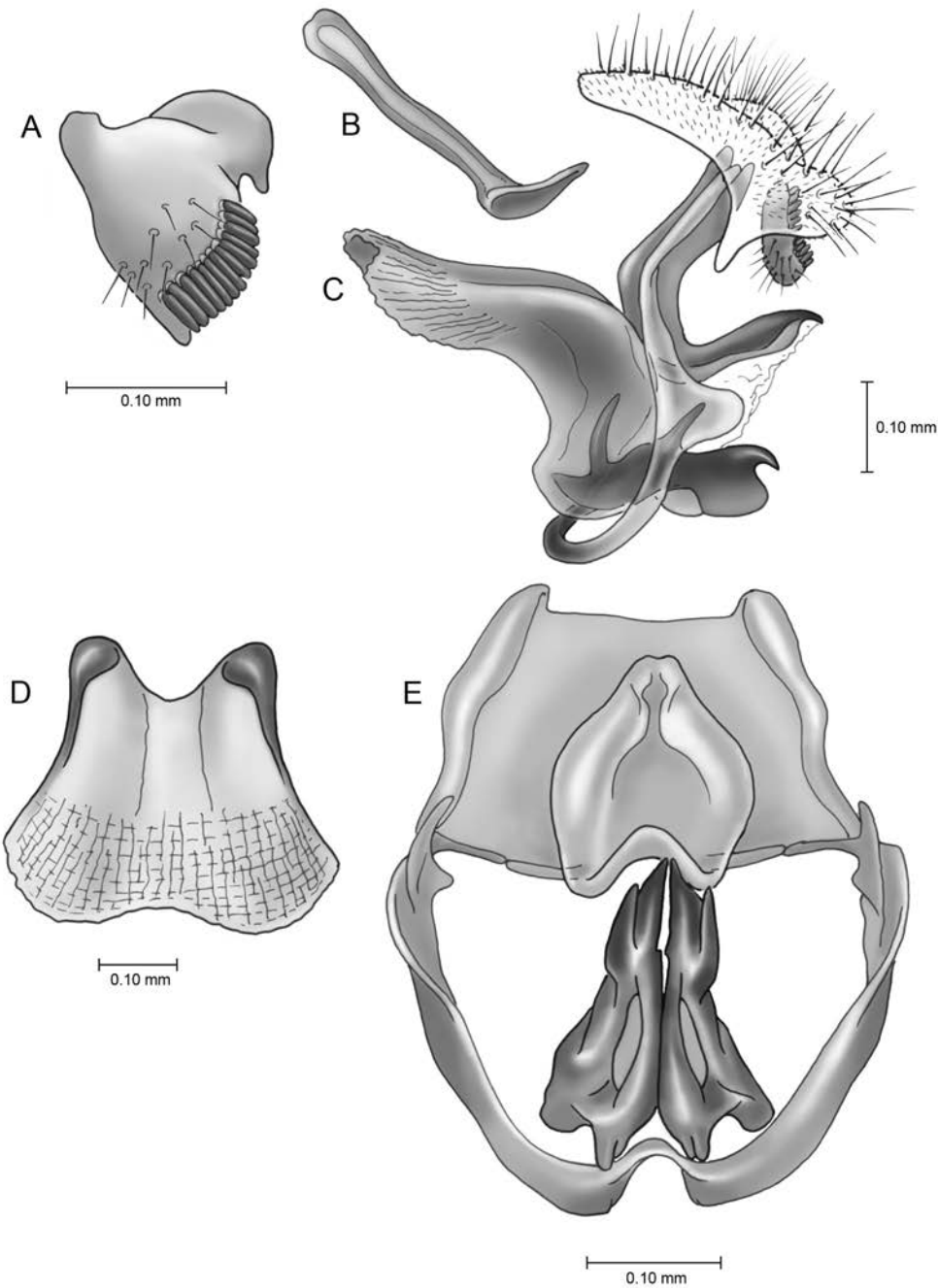


FIG. 55. Male terminalia, *A. latilabrum*. A. Surstylus. B. Ejaculatory apodeme. C. Lateral view. D. Aedeagal apodeme. E. Subepandrial sclerite and appendage, paraphyses, hypandrium, ventral view. (Am 2, holotype).

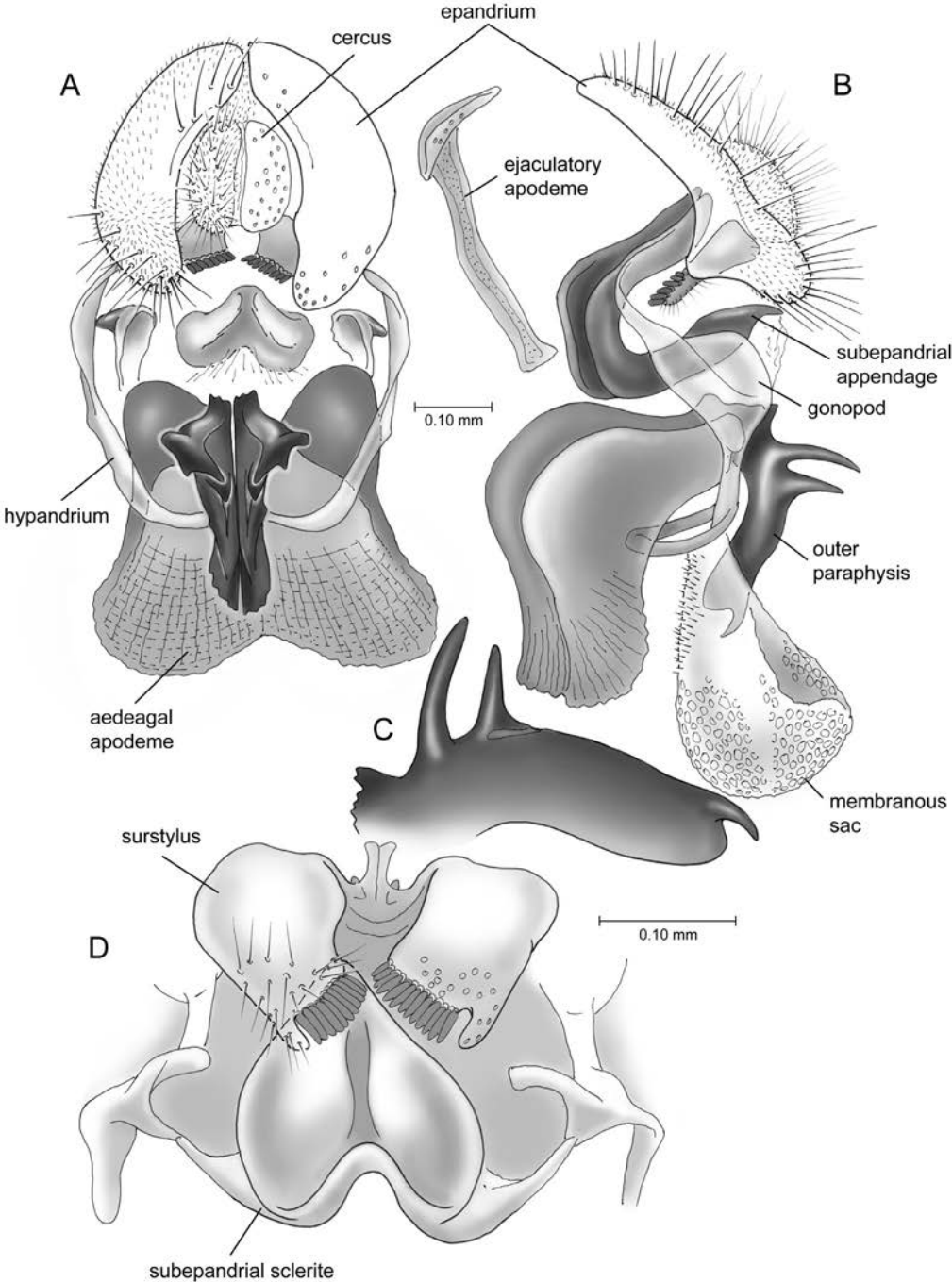


FIG. 56. Male terminalia, *A. nebojsa* Máca. **A.** Posteroventral view. **B.** Lateral view, with ejaculatory apodeme. **C.** Outer paraphysis, lateral view. **D.** Surstyli and subepandrial sclerite, ventral view. (Am 11).

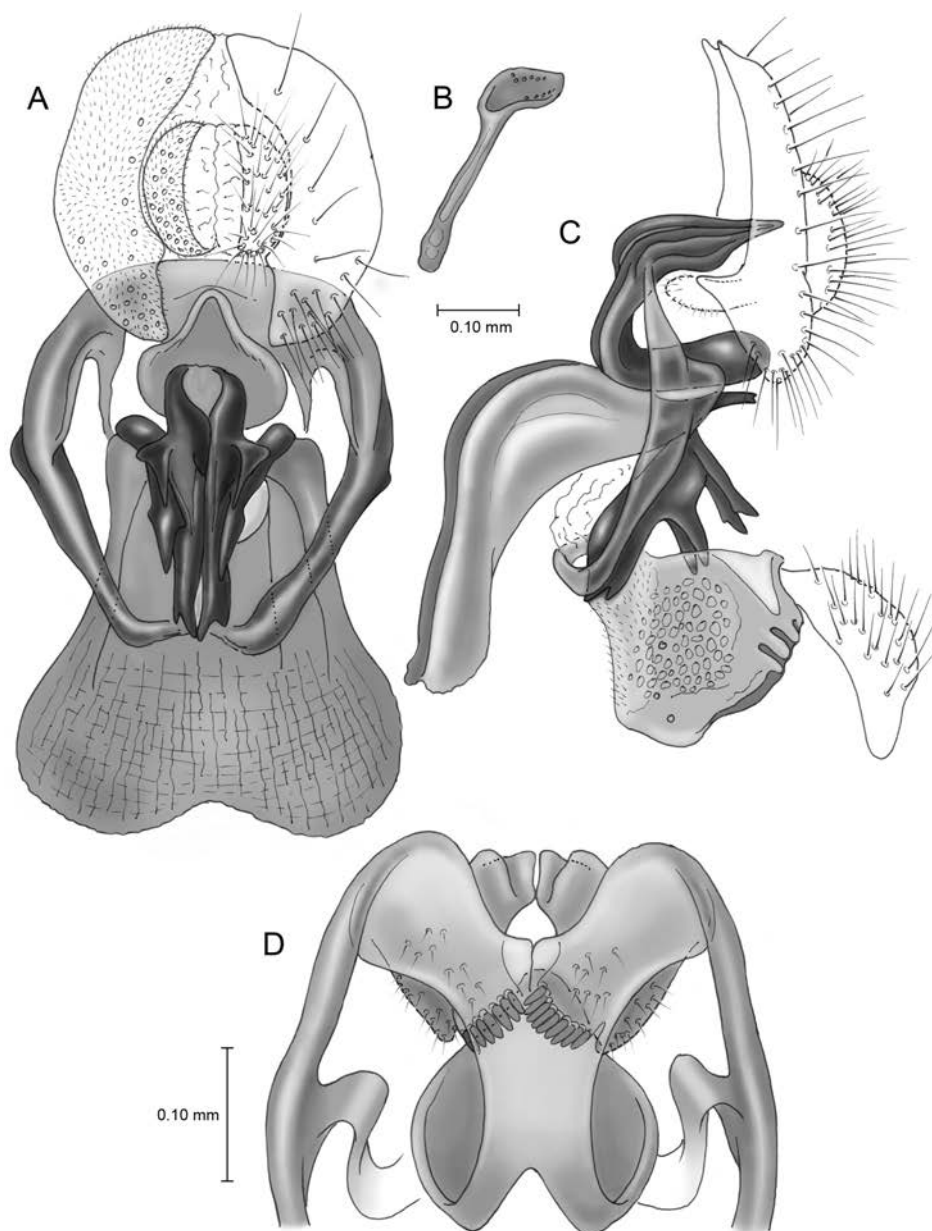


FIG. 57. Male terminalia, *A. occidentalis*. **A.** Posteroventral view. **B.** Ejaculatory apodeme. **C.** Lateral view, including sternite 6 sac (shaded). **D.** Surstyli, hypandrium, subepandrial sclerite, anterior view. (Am 524).

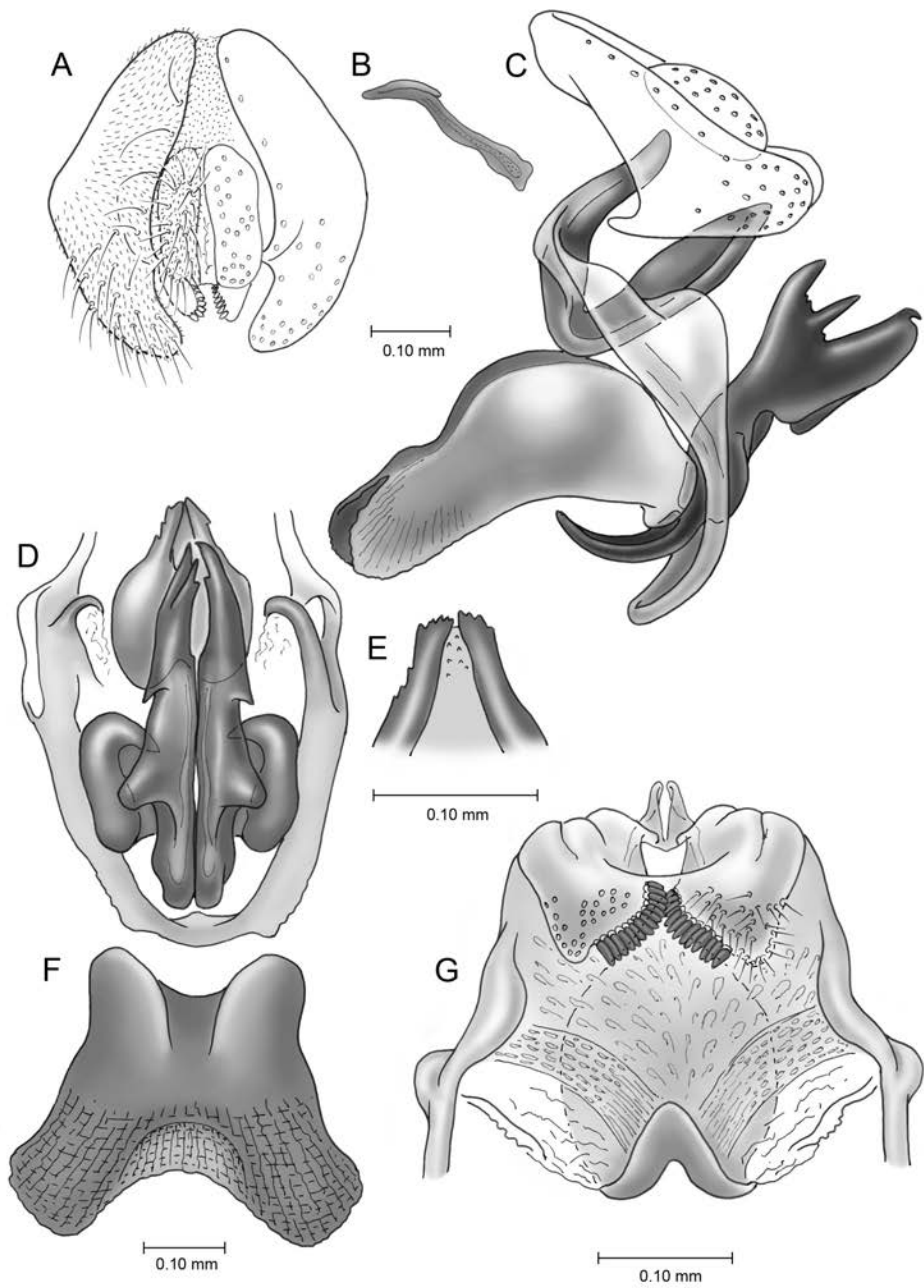


FIG. 58. Male terminalia, *A. oviraptor*. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Paraphyses, hypandrium, apex of subepandrial appendage, ventral view. **E.** Detail of subepandrial appendage. **F.** Aedeagal apodeme. **G.** Surstyli and subepandrial sclerite (with muscle scars), ventral view. (*Am* 1506, paratype).

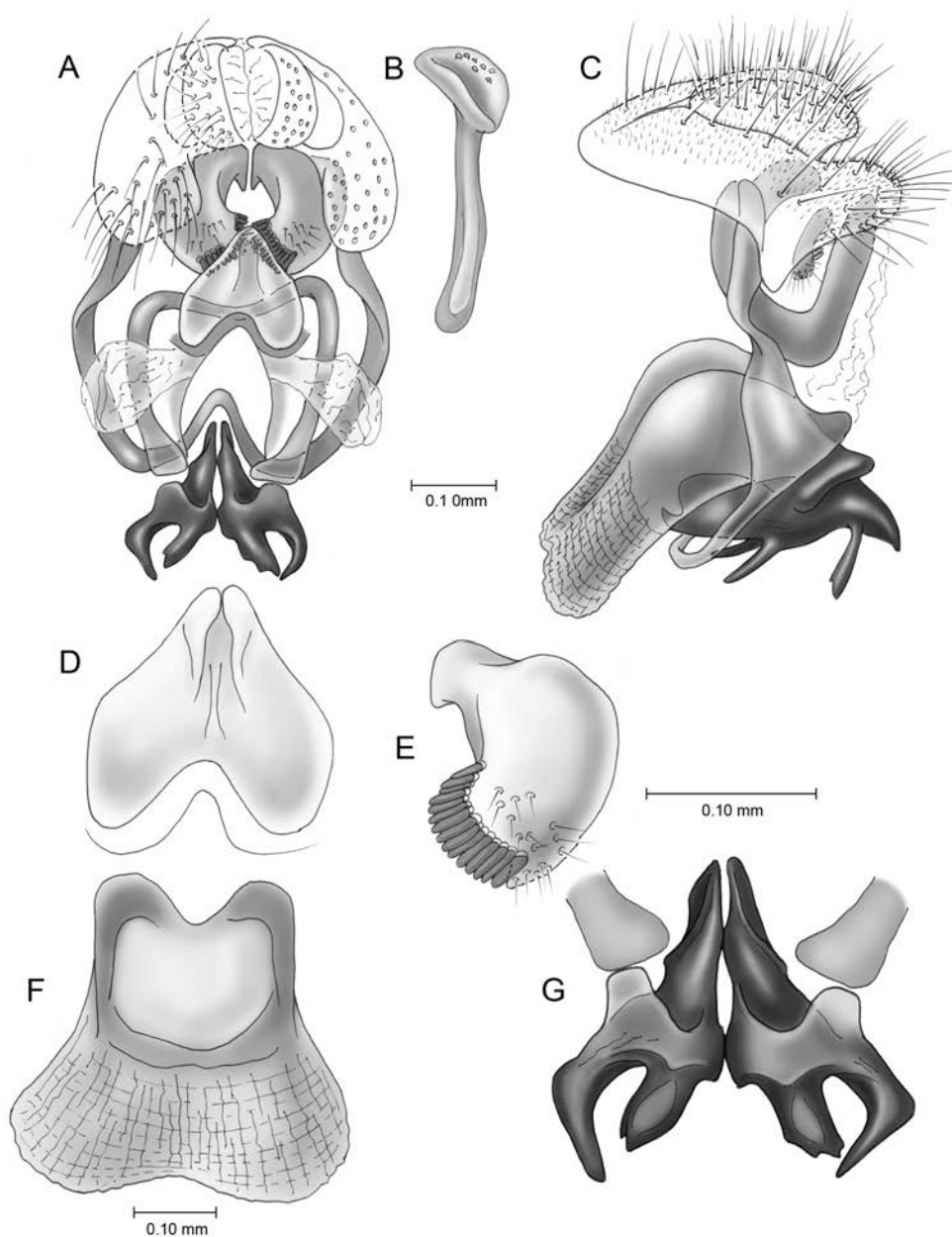


FIG. 59. Male terminalia, *A. subnebojsa*. A. Posteroventral view. B. Ejaculatory apodeme. C. Lateral view. D. Subepandrial sclerite, ventral view of apex. E. Surstylus. F. Aedeagal apodeme. G. Paraphyses, ventral view. (Am 443, holotype).

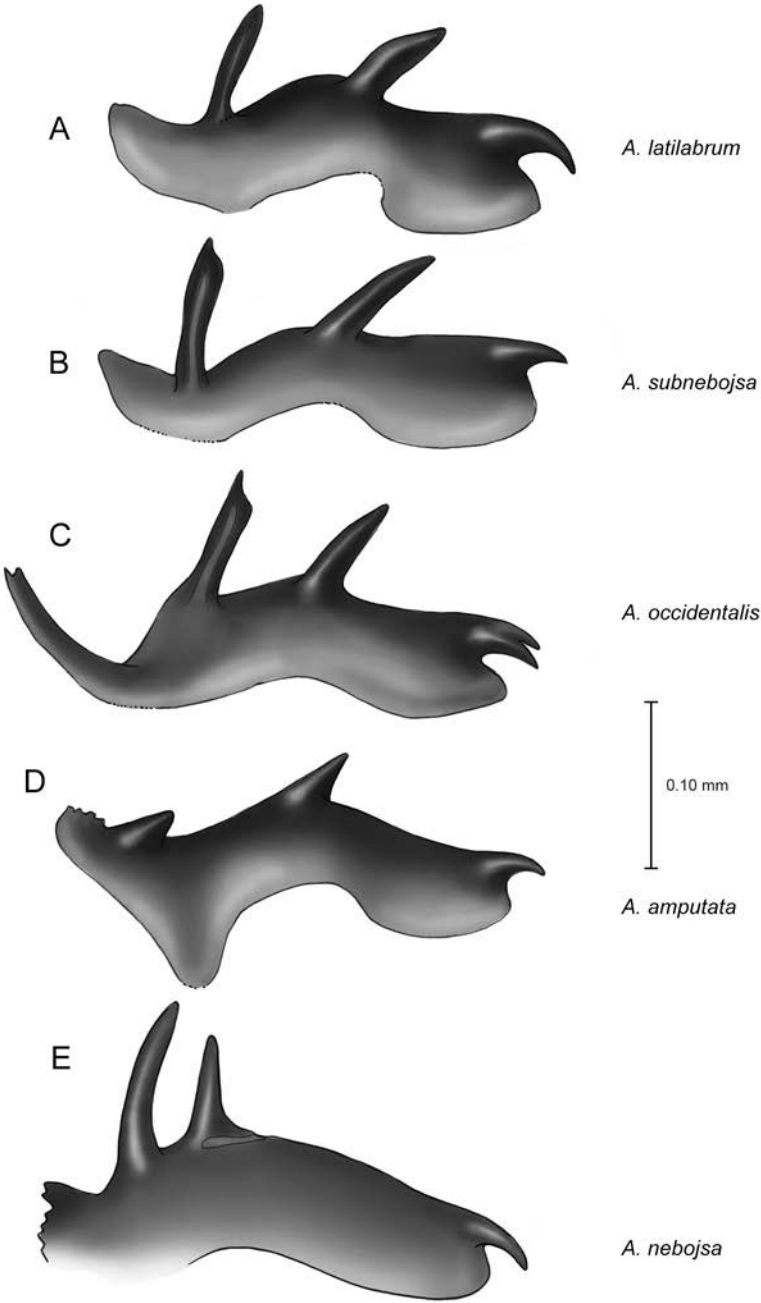


FIG. 60. Outer paraphyses of the *nebojsa* species group, lateral view. A. *A. latilabrum*. B. *A. subnebojsa*. C. *A. occidentalis*. D. *A. amputata*. E. *A. nebojsa* Máca. All to same scale.

All known specimens of this species have been collected via pans, malaise, and emergence traps. It is unknown whether it is attracted to the face and eyes as is common in other *Amiota*.

*Amiota nanonigrescens*, sp. nov.

Figures 61C–D, 62B, 64, 93B

**DIAGNOSIS:** Medium-sized fly (ThL 1.22 mm), body black grading dark brown ventrally, femora light brown, tibiae and tarsi light yellow; male terminalia entirely faint (except for tips of outer paraphyses, which are sclerotized), lightly sclerotized; outer paraphysis swollen, distal end tapered to small, slightly curved, blunt point; inner paraphysis lost; similar to *A. nigrescens* Wheeler, but differing in the faint sclerotization; deep-pocketed lobes of the aedeagal apodeme; surstylus with distal end narrow and 4 prensisetae, the most medial one pointed and 2× length of the others.

**DESCRIPTION:** Medium-sized fly (ThL 1.22 mm), black grading dark brown ventrally. Femora brown, tibiae and tarsi light yellow. Frons black except orbital plates. Cheek brown. Palp dark brown. Arista: Short, plumose; longest branch D3; A.R. 0.32; 3 long dorsal, 0 long ventral branches, none pointed mediad/laterad; arista trunk with long microtrichia along entire length. Male genitalia: Epandrium dorsal complete, faintly sclerotized. Cercus large, occupying most of the space surrounded by the epandrium, distinct from surrounding membrane. Surstylus armlike, ventral portion narrowed, covered with setulae, dorsal portion glabrous; 4 prensisetae, apices blunt, medialmost one long and pointed, twice the length of the other prensisetae, widely spaced and at sharp angle; lateral prensisetae small, closely spaced. Subepandrial sclerite small. Outer paraphysis on long stalk; distal portion swollen in middle, the distal end with small, blunt, tapered point. Inner paraphysis lost. Aedeagal apodeme flared widely at anterior end, distal margin not emarginate; base deeply constricted; curved in lateral view, with deep lobes. Hypandrium simple, apex notched; lateral arm wide, with prominent posterior

gonopod. Ejaculatory apodeme not studied. Head and thorax measurements: (n = 1, Am 540) FL/FW 0.78, EL/EW 1.50, EL/CW 14.25, FML/FMW 0.23, PR/RR 0.66, ThL 1.22 mm.

**TYPE MATERIAL: Holotype:** male: CANADA: Algonquin Pk., Swan Lake Stn., Scott Lake Survey, 45°29'15"N, 78°43'20"W, [45.489399, -78.715496], malaise A1, lakeshore, 3-14.vi.1993, Larson/Marshall/Barr, Am 540, [specimen glued to paper point, dissected]. Deposited in the University of Guelph (DEBU).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** Formed from *nanos*, Greek for "dwarf," and *nigrescens*, a previously named species in the genus, in reference to a smaller version of *A. nigrescens* Wheeler, a species to which it is closely related.

**DISTRIBUTION:** This species is only known from Ontario, Canada.

**COMMENTS:** It is unknown whether this species is attracted to the face and eyes as is common in other species of *Amiota*. The holotype of *Amiota nanonigrescens* was caught in a Malaise trap, a very common method for catching species in this species group.

*Amiota nigrescens* Wheeler, 1952

Figures 61E–F, 62C, 65, 93C

*Amiota nigrescens* Wheeler, 1952: 170 (original description); Wheeler, 1965: 761 (Nearctic catalog); Brake and Bächli, 2008: 254 (world catalog).

**DIAGNOSIS:** Small to medium-sized fly (ThL 0.99–1.27 mm), dark brown nearly black; legs yellow (femora light brown in some individuals); surstylus slender, armlike, 4 prensisetae, 2 most lateral larger and 2× length of the others; subepandrial sclerite process behind surstylus, like a fifth prensiseta; paraphyses fully sclerotized; outer paraphysis on right side slightly sinuous; apex tapered, base swollen; left outer paraphysis shorter, apex also tapered, base swollen; inner paraphysis lost.

**DESCRIPTION:** Small to medium-sized fly (ThL 0.99–1.27 mm), dark brown nearly black. Legs dark yellow (femora dark brown in some individuals). Frons dark brown (nearly black in Ontario populations). Cheek dirty yellow to brown. Facial marking small, width  $0.5\times$  length (depth smaller in Ontario populations). Palp brown. Arista: Short, plumose; longest branch D3; A.R. 0.31; 4 long dorsal, 1 long ventral branches; D4 pointed laterad; arista trunk with medium microtrichia for most of its length. Male genitalia: Epandrium fused at midline, indistinct; ventral lobes with dense cluster of setae, lower third of epandrium devoid of long setae. Cercus long, pendulous, distinct from surrounding membrane, ventral portion overlapping bases of surstyli. Surstylus armlike, bent at midpoint, entirely glabrous; 4 prensisetae, apices blunt, closely spaced, lateral 2 prensisetae  $2\times$  length of the 2 medial; heavily sclerotized subepandrial sclerite process anterior to surstylus, resembling a fifth prensiseta. Subepandrial sclerite consisting of 3 lobes in posterior view, 2 lateral lobes and central lobe; lateral lobe large, rounded, faintly sclerotized, central flange running to margin, thick, flange apex flared distally; central lobe heavily sclerotized, bulbous, apex tapering, incomplete flange reaching outer margin; central lobe with squarelike extension anterior to surstylus, the central portion with process. Outer paraphyses slightly asymmetrical, both heavily sclerotized; left one slightly longer and slightly sinuous, distal end tapered to a point; base bulbous, flaring outward; right outer paraphysis parallel to left one with apex tapered, base bulbous with a small notch. Inner paraphysis lost. Aedeagal apodeme bent  $90^\circ$  at midpoint, of equal length and width; widely flared distally, with deep concave emargination; 2 strong lateral flanges at base. Hypandrium simple, thickness consistent across length; apex simple, V-shaped; lateral arm with small posteriorly pointing gonopod. Ejaculatory apodeme slightly bent at base,  $0.7\times$  length of epandrium. Head and thorax measurements: ( $n = 5$ ; Am 129, 138, 146, 583, 585) FL/FW 0.70 (0.63–0.86), EL/EW 1.41 (1.34–

1.52), EL/CW 11.32 (10.2–12.6), FML/FMW 0.33 (0.28–0.48), PR/RR 0.39 (0.33–0.44), ThL 1.16 (0.99–1.27 mm).

**TYPE MATERIAL:** **Holotype:** As reported by Wheeler (1952): “♂, 2164.7, from Slide Rock Campground, Oak Creek Canyon, Coconino National Forest, south of Flagstaff, Arizona, collected June, 1951 by the writer” [not examined]. Deposited in National Museum of Natural History, Washington D.C. (USNM). **Paratypes:** Localities and numbers of paratype specimens in AMNH differ slightly from Wheeler (1952) in some cases: “4, same data as holotype” [ARIZONA: Oak Creek Canyon, Coconino Nat. For., 15 mi. S. Flagstaff, VI/21–VI/22/51, 2164.7, W.B. Heed and M.R. Wheeler, paratype], [34.907104, -111.727342], 1♂ and 3♀ (Am 138–141\*, AMNH); “Tonto Creek near Payson (11, one on slide),” [Tonto Creek Camp, Arizona, June 1951, MR Wheeler and WB Heed, 2168.3, paratype], [34.320806, -111.084756], 5♂ and 4♀ (Am 129–135\*, 142\*, AMNH); “Long Valley near Pine (2),” [ARIZONA: Clover Springs, Coconino Nat'l. Forest, 50 mi S Flagstaff, VI/22–VI/23/51, W.B. Heed and M.R. Wheeler, 2165.12, paratype], [34.506258, -111.362842], 1♂ (Am 144, AMNH); “NEW MEXICO: Cherry Creek Camp, near Silver City (5)” [New Mexico: “Cherry Creek” Campground, Gila Nat. For., N. Silver City, VI/7–VI/8/51, W.B. Heed and M.R. Wheeler, 2151.4, paratype], [32.914274, -108.225999], 1♂ and 3♀ (Am 145–148\*, AMNH).

**OTHER MATERIAL EXAMINED: Canada:**

**Ontario:** Algonquin Park, Swan Lake Station, Scott Lake Station, 1993-05-19 through 1993-05-31, leg. Larson/Marshall/Barr, malaise A1 lakeshore, 1♂ (Am 536\* [dissection missing], DEBU); 1993-06-03 through 1993-06-14, leg. Larson/Marshall/Barr, malaise A1 lakeshore, 2♂ (Am 542\*, 543\*, DEBU); 1993-06-03 through 1993-06-17, leg. Larson/Marshall/Barr, Pan A3, clubmoss/hemlock, 1♂ (Am 539\*, DEBU); 1993-06-17 through 1993-06-19, leg. Larson/Marshall/Barr, 1♂ (Am 545\*, DEBU); 1993-07-16 through 1993-07-28, leg. Larson/Marshall/Barr, malaise A1 lakeshore, 1♂ (Am 544\*, DEBU); Algonquin Park, Swan Lake Station, Scott Lake Survey, 1994-06-07 through 1994-06-14, [collector

unknown], C1 shore malaise trap, 2♂ (Am 583\*, 591\*, DEBU); 1994-06-23 through 1994-06-30, [collector unknown], C1 shore malaise trap, 1♂ (Am 594\*, DEBU); 1994-07-10 through 1994-07-17, [collector unknown], C1 Shore malaise trap, 1♂ (Am 597, DEBU); 1994-07-18 through 1994-07-31, [collector unknown], C1 shore malaise trap, 1♂ (Am 557\*, DEBU); 1995-05-29 through 1995-06-16, leg. S.A. Marshall, fresh stump emergence, 2♂ (Am 582\*, 584\*, DEBU); 1995-05-29 through 1995-06-17, leg. S.A. Marshall, D2 Hemlock pans, 1♂ (Am 585\*, DEBU); Algonquin Provincial Park, W.R.S. G (B2), 1995-06-11, leg. R. Bonduriansky, moose antler, 1♂ (Am 611\*, DEBU); Fathom Five National Park, Bear Rumpis, 1996-06-23 through 1996-07-26, leg. T. Woodcock and S. Marshall, Dry Alvar Pan Trap #4, debu00078364, 1♂ (Am 527, DEBU); Nipissing Distr., Algonquin Park., Swan Lake Station, Scott Lake. Shore site A1., 1995-07-04, [no collector], debu00104926, pan traps, 1♂ (Am 634\*, DEBU); Ottawa, 1991-08-01, leg. J.R. Vockeroth, damp growth Acer-Betula wood, 1♂ (Am 1253\*, CNC); 1993-06-22, leg. J.R. Vockeroth, damp growth Acer-Betula wood, 1♂ (Am 1228\*, CNC); Ottawa, Chapel Hill, NW Wood, 2002-07-01, leg. J.R. Vockeroth, CNC Diptera #193451, 1♂ (Am 1197\*, CNC). **Quebec:** Knowlton Lodge, 1968-07-18, leg. J.R. Vockeroth, 1♂ (Am 1580\*, CNC). **USA: Arizona:** Oak Creek Canyon, 1951-06-21, [collector unknown], [possible paratypes?] 2♂ (Am 136\*, 137\*, AMNH).

**DISTRIBUTION:** *Amiota nigrescens* has disjunct populations from central Arizona and southwestern New Mexico as well as Ontario, Canada. No intervening populations between these extremes are known.

**COMMENTS:** It is unknown whether this species is attracted to the eyes and face like other *Amiota*. Populations of *Amiota nigrescens* in Ontario are commonly caught in Malaise and pan traps. This species is a documented saproxylic, one specimen (DEBU) having been reared from a tree stump emergence trap. The species is variable for the brown femora and cheek seen in the other species of the group. Four of 19 specimens in the Southwest had the light brown femora, 12 of 21 Great Lakes specimens had light brown femora, while 2 had dark brown femora. The facial marking in Ontario populations is also much smaller in

depth. No discernable differences are found in the male genitalia of both populations. It would be very useful to compare DNA barcodes of specimens in the two localities.

#### THE NAGATAI SPECIES GROUP

**DIAGNOSIS:** Vein C with row of small, dark spinules between apices of  $R_{2+3}$  and  $R_{4+5}$ . Male genitalia: Reduced and basic; subepandrial sclerite well developed but not extended past posterior margin of epandrium; outer paraphyses small, simple (no spines); inner paraphysis present, but small, simple.

**NEARCTIC SPECIES:** *Amiota raripennis*, sp. nov.

**COMMENTS:** Chen and Toda (2001) erected this species group to accommodate three Old-World species. This group may also include *A. steganoptera* Malloch, known from Costa Rica, plus several undescribed Neotropical species, all of which possess costal spinules. These species will be treated in a future study. *Amiota raripennis* differs from the Old World species by several apomorphic features of the epandrium: setae very sparse, very short; with pair of distinct, setulose ventral epandrial lobes. Plesiomorphically this species differs from the Old World species by lacking the lobe on the hind trochanter in the male. He et al. (2009) provided a treatment of the Old World species. Thus, there appears to be two lineages, an Old and New World one.

#### *Amiota raripennis*, sp. nov.

Figures 66A–B, 67, 94A

Wheeler, 1957: 110 (distribution, as *A. steganoptera*); Wheeler, 1965: 761 (Nearctic catalog, as *A. steganoptera*).

**DIAGNOSIS:** Medium-sized fly (ThL 1.16 mm), dark brown to black; wartlike spines on third costal division between  $R_{2+3}$  and  $R_{4+5}$ ; male terminalia very faintly sclerotized, relatively reduced; dorsal portion of epandrium very smooth, no

microtrichia, but with microtrichose ventral lobes, setae on posterior and ventral margins very short; aedeagal apodeme small, faint, and poorly developed; outer paraphysis forming a fork with rounded apices, moderately sclerotized, curving anteriorly; inner paraphysis a small lobe, appendage oriented dorsally.

**DESCRIPTION:** Medium-sized fly (ThL 1.16 mm), black, fading to dark brown ventrally, legs light yellow. Katepisternum lighter in color than remaining pleuron. Frons dark, nearly black. Black band just dorsal to facial marking. Cheek small (EL/CW 22), white. Palp yellow. Wartlike spines on third costal division between  $R_{2+3}$  and  $R_{4+5}$ . Tergite 1 lightly colored. Arista: Very long, plumose; longest branch D2; AR 0.70; 4 long dorsal (1 short preapical), 2 long ventral (1 short preapical); arisal trunk with medium-length microtrichia on basal half. Male genitalia: Complex barely sclerotized and very faint, with exceptions of distal end of outer paraphysis and prensisetae. Epandrium dorsally complete; dorsal 3/4 glabrous, no microtrichia; ventral 1/4 with small lobe, with dense microtrichia; very short setae on posterior and ventral margins of epandrium, ventral setae with large sockets. Cercus distinct, not grading with surrounding membrane; with small ventral lobe (best seen in lateral view). Surstylus large relative to genitalia complex, armlike (length greater than width), constricted in middle; 10 long prensisetae, apices blunt, closely spaced, becoming smaller medially. Subepandrial sclerite broad and large, amphitheater shaped. Outer paraphysis bifurcated; each appendage slender, heavily sclerotized, the distal end rounded, curved strongly anteriorly. Inner paraphysis a small, wrinkled, lateral lobe; giving rise to small, dorsally projecting appendage. Aedeagal apodeme small, underdeveloped; consisting of stalk, distal end a striated pad. Hypandrium simple, of uniform thickness, strongly S-shaped in lateral view; apex strongly curled anteriorly. Ejaculatory apodeme  $0.8\times$  length of epandrium. Head and thorax measurements: ( $n = 1$ , Am

298) FL/FW 0.84, EL/EW 1.46, EL/CW 22, FML/FMW 0.35, PR/RR, 0.63, ThL 1.16 mm.

**TYPE MATERIAL:** **Holotype:** male: USA: VIRGINIA: Blacksburg, [37.188955, -80.431634], IX/9/53, M. Levitan, Am 298, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratype:** "Kushla, Ala." [Alabama], [30.814854, -88.162265], "Je.22.52" [June 22, 1952], [collector unknown, likely Alfred H. Sturtevant]; ALABAMA: Kushla, ?/22/52, [collector unknown, likely Sturtevant], 1 ♀ (Am 191\*, AMNH).

**OTHER MATERIAL EXAMINED: USA: Mississippi:** Saucier, 1954-09-03, leg. M.R. Wheeler, "Steganoptera female" [specimen presumably female, dissection not seen], 1 ♀ (Am 196\*, AMNH).

**ETYMOLOGY:** Formed from Latin *rari* for "rare" and *pennis* for "wing" in reference to the unique wing character among species in the Nearctic and its rarity in collections.

**DISTRIBUTION:** This species is found in the American South and the Mid-Atlantic. Steyskal, in his notes kept at the AMNH, cites a specimen of this new species from Gainesville, Florida, likely in the collections of the USNM. This unverified record would be a significant range expansion for this species and would suggest a distribution that is subtropical and primarily in the Gulf Coastal Plains.

**COMMENTS:** *Amiota raripennis* is rarely collected. Malloch's description of *A. steganoptera* from Costa Rica noted the presence of wartlike spines on the wings, similar to two genera in Steganinae, *Leucophenga* and *Stegana* (1926). Wheeler (1957) reported *A. steganoptera* Malloch from the United States, primarily from the southeastern United States. Detailed comparison of the male terminalia of the American species to specimens throughout Central America with the costal warts indicates that the American species is new. There are many undescribed species with this wing character in Central America in the collections of the AMNH (L.E.J., personal obs.), and

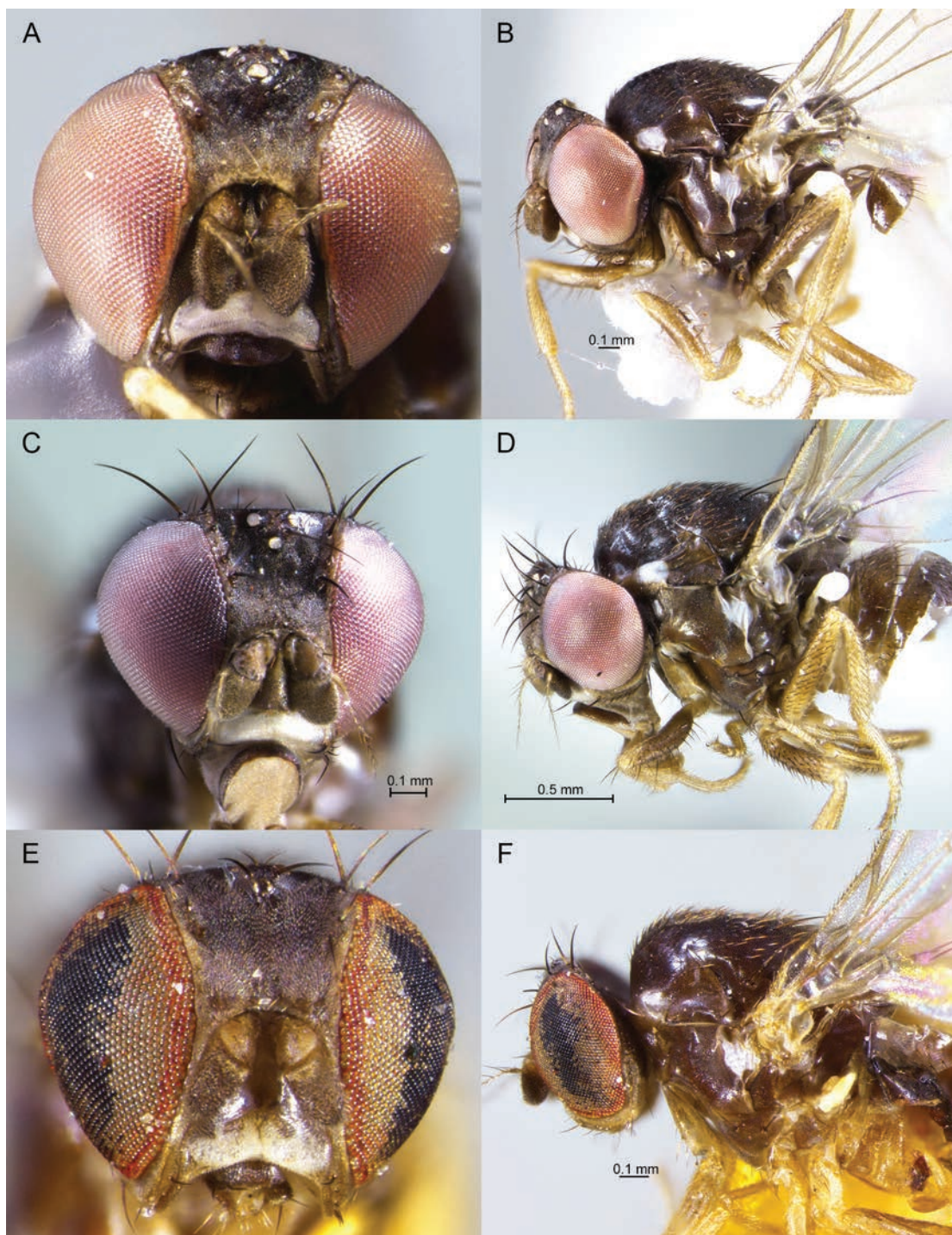


FIG. 61. Heads and lateral views, *A. nigrescens* species group. A–B. *A. fulvitibia*, sp. nov. (Am 577). C–D. *A. nanonigrescens*, sp. nov. (Am 540, holotype). E–F. *A. nigrescens* Wheeler (Am 146, paratype, lateral image flipped).

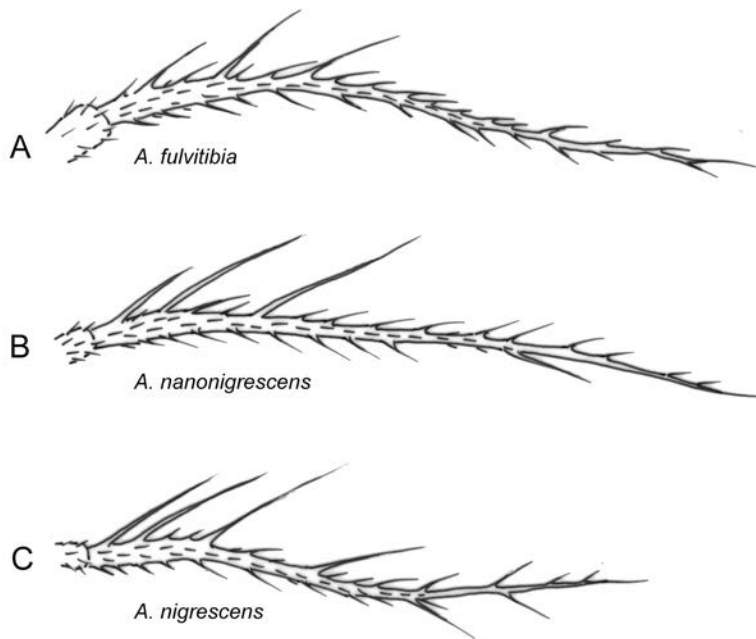


FIG. 62. Aristae, *A. nigrescens* species group. *A. fulvitibia*. **B.** *A. nanonigrescens*. **C.** *A. nigrescens* Wheeler. Not to the same scale.

Wheeler (1957) indicated several undescribed species with this wing character in Brazil as well. Prior records of *A. steganoptera* in the United States are likely of this new species. Members of this species group in the Neotropics will be the subject of a future study.

#### UNGROUPED SPECIES

*Amiota barretti* (Johnson, 1921)

Figures 68A–B, 72A, 73, 94B

*Stegana barretti* Johnson, 1921: 59 (original description).

*Amiota barretti* (Johnson): Wheeler, 1952: 172 (comb. nov. by Wheeler); Brake and Bächli, 2008: 250 (world catalog).

**DIAGNOSIS:** Very large fly (ThL 1.87–2.26 mm); shiny black with bluish highlights; frons entirely dark, dull; facial marking wide, 0.75× length; cheek very deep (EL/CW 7.08–90), medium to light brown; arista with very short

plumosity; femora and tibiae dark brown, tarsi yellow; epandrium heavily sclerotized; outer paraphysis heavily sclerotized, long, linear, bowing outward at midpoint in dorsal/ventral views, with apical hook; left outer paraphysis with spine near midpoint arising medially; inner paraphyses heavily sclerotized, small, right one with 2 and left with 3 spines.

**DESCRIPTION:** Very large fly (ThL 1.87–2.26 mm), black, bluish from certain angles; thorax and abdomen very glossy. Femora and tibiae dark brown, tarsi dark yellow. Frons broad, nearly black. Facial marking wide, width 0.75× length. Cheek very deep (EL/CW 7.08–90), medium to light brown. Palp brown. Arista: Very short, plumose; longest branch D2; A.R. 0.17; 3 dorsal, 0 ventral branches; no branch pointed mediad or laterad; arista trunk with short microtrichia to apex. Male genitalia: Epandrium heavily sclerotized; crescentic in posterior view, narrow in lateral view; margins discrete (not graded into membrane), dorsal incomplete. Cercus distinct from surrounding membrane, fairly

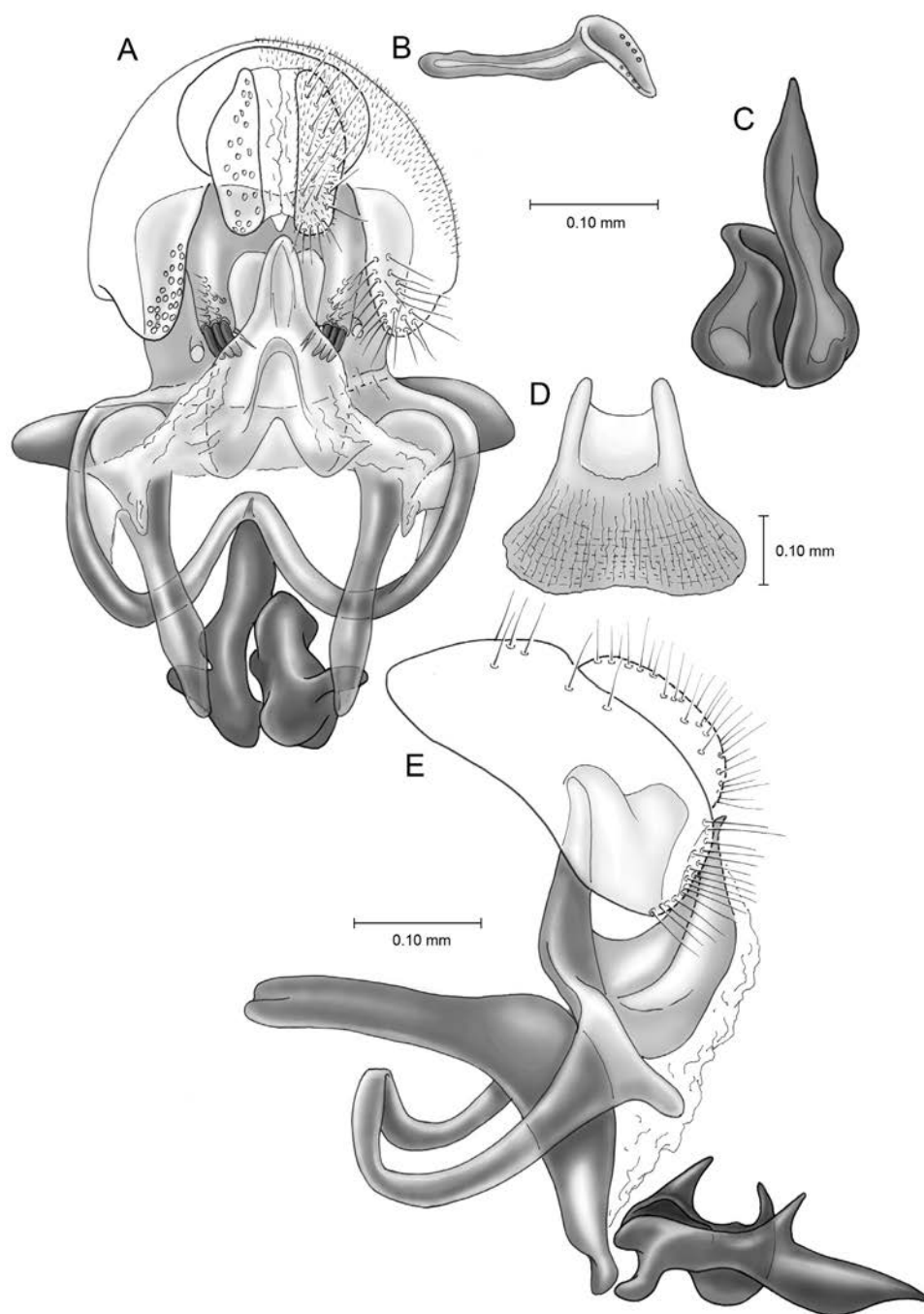


FIG. 63. Male terminalia, *A. fulvitibia*. A. Posteroventral view. B. Ejaculatory apodeme. C. Outer paraphyses. D. Aedeagal apodeme. E. Lateral view. (Am 587, holotype)

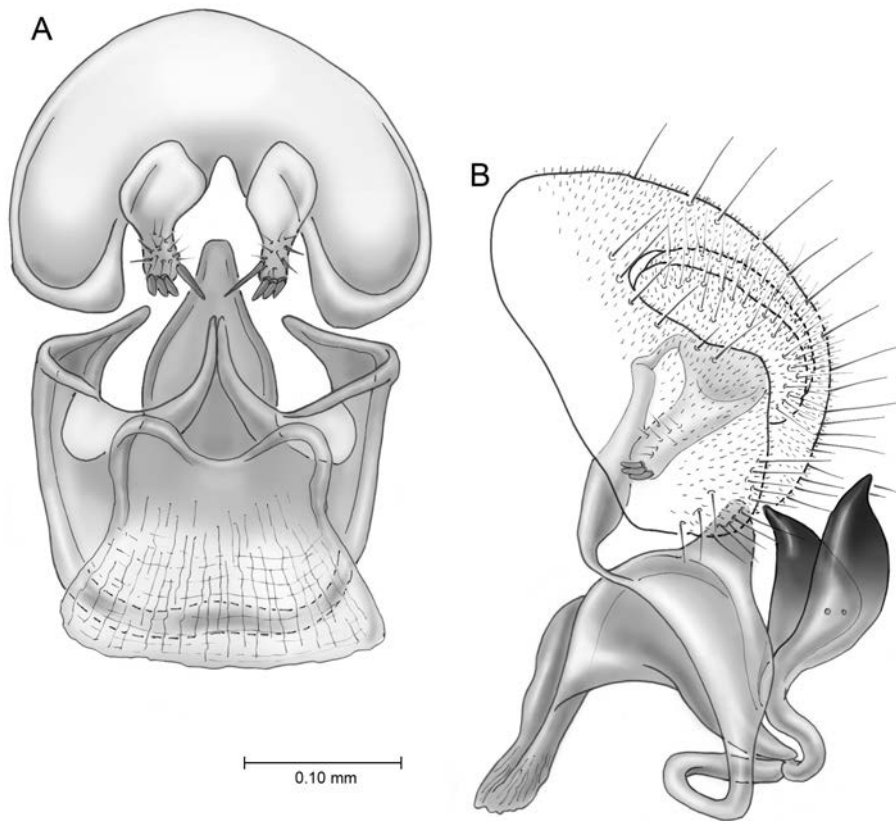


FIG. 64. Male terminalia, *A. nanonigrescens*. **A.** Interior view of epandrium, surstyli, aedeagal apodeme, and subepandrial sclerite. **B.** Lateral view. (Am 540, holotype).

long; ventral setae distinctly longer than others. Surstylus with only a small cluster of setae along mostly the distal margin; 11 long prensisetae, tips slightly narrowed, closely spaced, comblike. Subepandrial sclerite well developed and sclerotized; C-shaped in lateral view; subepandrial appendage not extending past epandrium, heart shaped in full ventral view. Outer paraphysis long, linear, well sclerotized, bowing outward past midpoint (as seen in full ventral view); distal end with apical claw; left outer paraphysis with spine near midpoint that arises on medial surface. Inner paraphyses small, heavily sclerotized, projecting dorsally, half the length of the outer paraphysis, terminating in 2 and 3 spines. Aedeagal apodeme bent nearly 90°, roughly heart shaped, with a shallow emargination; base and

surrounding margins heavily sclerotized, dark. Hypandrium thin at apex; with small lateral, slightly wrinkled wings flanking apex; lateral arms greatly thickening, with large posteriorly pointing gonopod. Ejaculatory apodeme 0.60× length of epandrium, slightly curved. Head and thorax measurements: (n = 4; Am 432, 1423, 1489, 1499) FL/FW 0.60 (0.56–0.63), EL/EW 1.33 (1.20–1.49), EL/CW 8.24 (7.08–9), FML/FMW 0.43 (0.37–0.47), PR/RR 0.57 (0.40–0.66), ThL 2.20 (1.87–2.26 mm).

**TYPE MATERIAL: Holotype:** Amecameca, “IX” 190”0” [year partially handwritten], Mex., Collected by O.W. Barrett, HOLOTYPE No., Type “7855,” Collection C.W. Johnson, “Phortica,” “S. barretti Johns” [cited as female], [barcode] MCZ-ENT 00007855, [not examined,

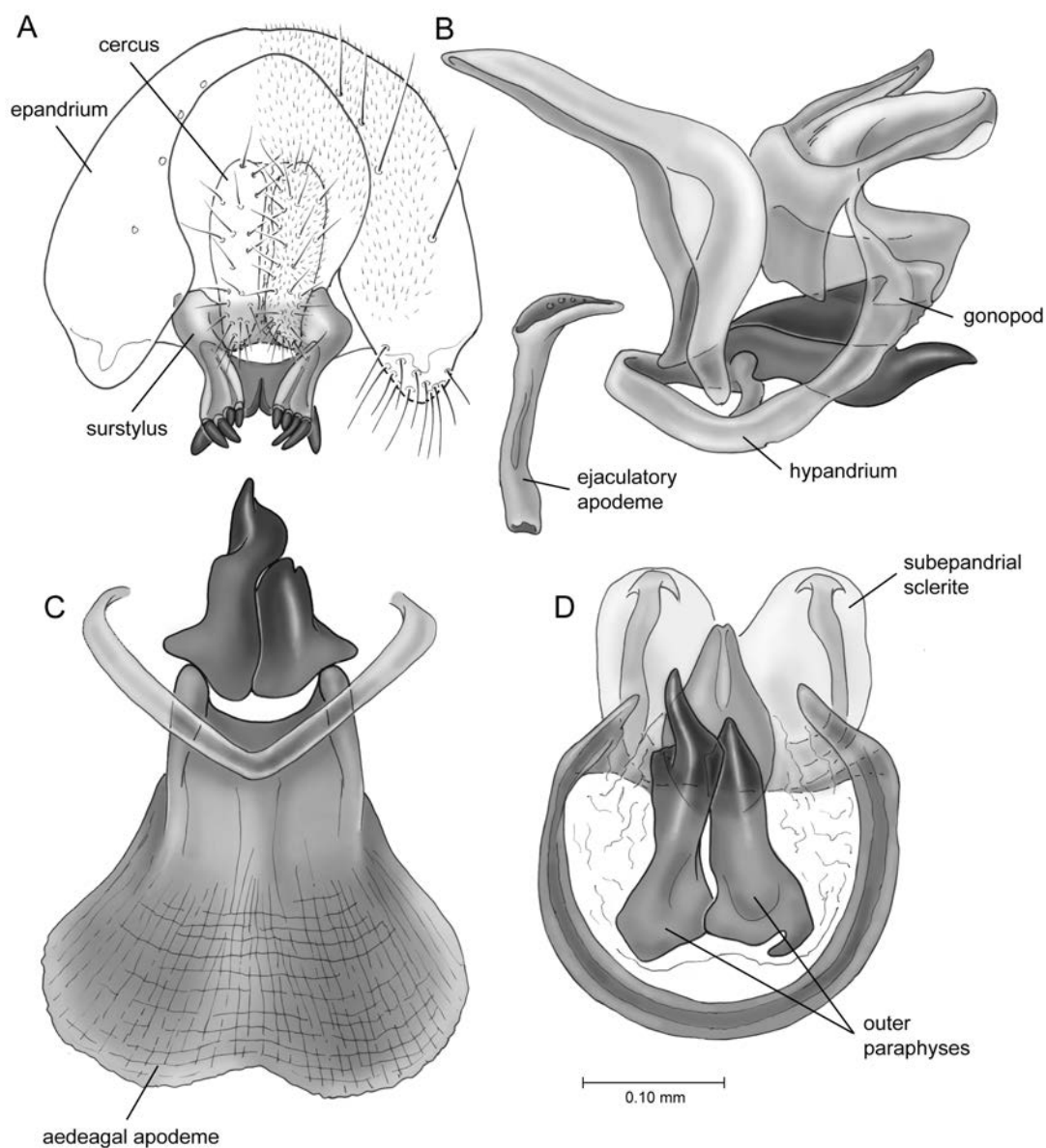


FIG. 65. Male terminalia, *A. nigrescens* Wheeler. **A.** Epandrium and cerci. Surstyli and subepandrial sclerite shaded. **B.** Lateral view, with ejaculatory apodeme. **C.** Ventral view. **D.** Dorsal view. (Am 137).

only photomicrographs reviewed]. Deposited in the Harvard Museum of Comparative Zoology, Cambridge (MCZC).

**OTHER MATERIAL EXAMINED:** **Mexico: Chiapas:** El Triunfo (49 km S. Jaltenango), 1985-05-13 through 1985-05-15, 2000 m, leg. A. Freidberg, 1♂ (Am 432\*, AMNH); 10 mi. NE San Cristobal,

7500', 1969-05-05, leg. H.J. Teskey, 1♂ (Am 1423\*, CNC). **Durango:** Buenos Aires, 10 mi W La Ciudad, 9000', 1964-06-16, leg. J.F. McAlpine, 1♂ (Am 1499\*, CNC); 3 mi. W El Salto, 9000', 1964-06-19, leg. J.F. McAlpine, 1♀ (Am 1490, CNC); 14 mi. SW El Salto, 8000', 1964-06-09, leg. J.F. McAlpine, attracted to man, 1♂ (Am 1489\*, CNC); 1964-06-

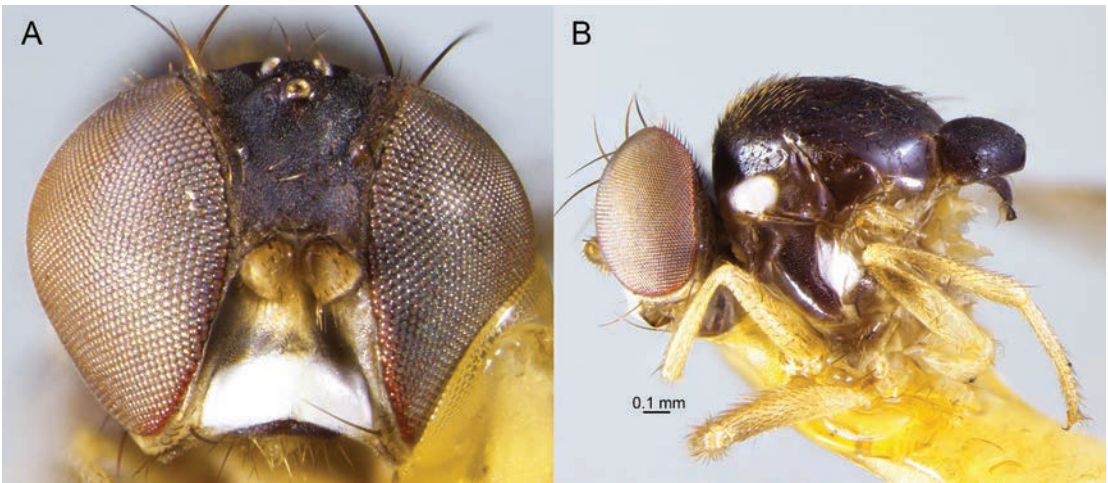


FIG. 66. **A.** Head and **B.** lateral view, *A. nagatai* species group. *A. raripennis*, sp. nov. (Am 298, holotype, lateral image flipped).

26 leg. J.F. McAlpine, attracted to man 1 ♀ (Am 1531, CNC).

**DISTRIBUTION:** The holotype of *A. barretti* was collected just outside of Mexico City in the southern highlands of the country, but newly identified material from the AMNH and CNC shows a wider distribution into Durango and Chiapas.

**COMMENTS:** This distinctive species has not been mentioned since Johnson's description in 1921. Males are now known for this species, originally described from a female. *Amiota barretti* is immediately identifiable by its very large size, deep cheek, dark brown femora and tibiae, and short plumosity on the arista. While found within the boundaries of the Nearctic, this species was left out of Wheeler's catalog of Nearctic Drosophilidae (1965) since it covered species occurring north of Mexico. This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota buccata* Wheeler, 1952

Figures 68C–D, 72B, 74, 94C

*Amiota buccata* Wheeler, 1952: 171 (original description); Wheeler, 1965: 761 (Nearctic catalog); Brake and Bächli, 2008: 250 (world catalog).

**DIAGNOSIS:** Large fly (ThL 1.54–1.71 mm), dark brown, nearly black; cheek very deep (EL/CW 5.46–6.18), white posteriorly; frons brown, dull, arista with few, short branches; epandrium dorsally complete; surstylus slender, foot-shaped; subepandrial sclerite with spindle-shaped central appendage; aedeagal apodeme large, shieldlike, quadrate in dorsal view; outer paraphysis a broad complex in lateral view, posterior portion laterally flattened and short with small preapical dorsal hook, base with large spine facing ventrally; inner paraphyses a simple pair of narrow lobes.

**DESCRIPTION:** Large fly (ThL 1.54–1.71 mm), dark brown, almost black, legs yellow. Cheek very deep (EL/CW 5.46–6.18), white posteriorly. Frons entirely dark golden-rust. Facial marking large, semicircular, width 0.5× length. Palp golden, tip brown. Tergite 1 lightly colored. Arista: Very short, plumose; longest branch D2; A.R. 0.26; 4 dorsal, 0 ventral branches, none pointed mediad/laterad; arista trunk with medium microtrichia along entire length. Male genitalia: Epandrium fused at midline, not distinct, barely grading with membrane surrounding cercus. Cercus small, oval, distinct from membrane. Surstylus armlike, slender, bent distally with scattered setulae; 7 prensisetae, apices blunt, closely spaced, of increasing size laterally.

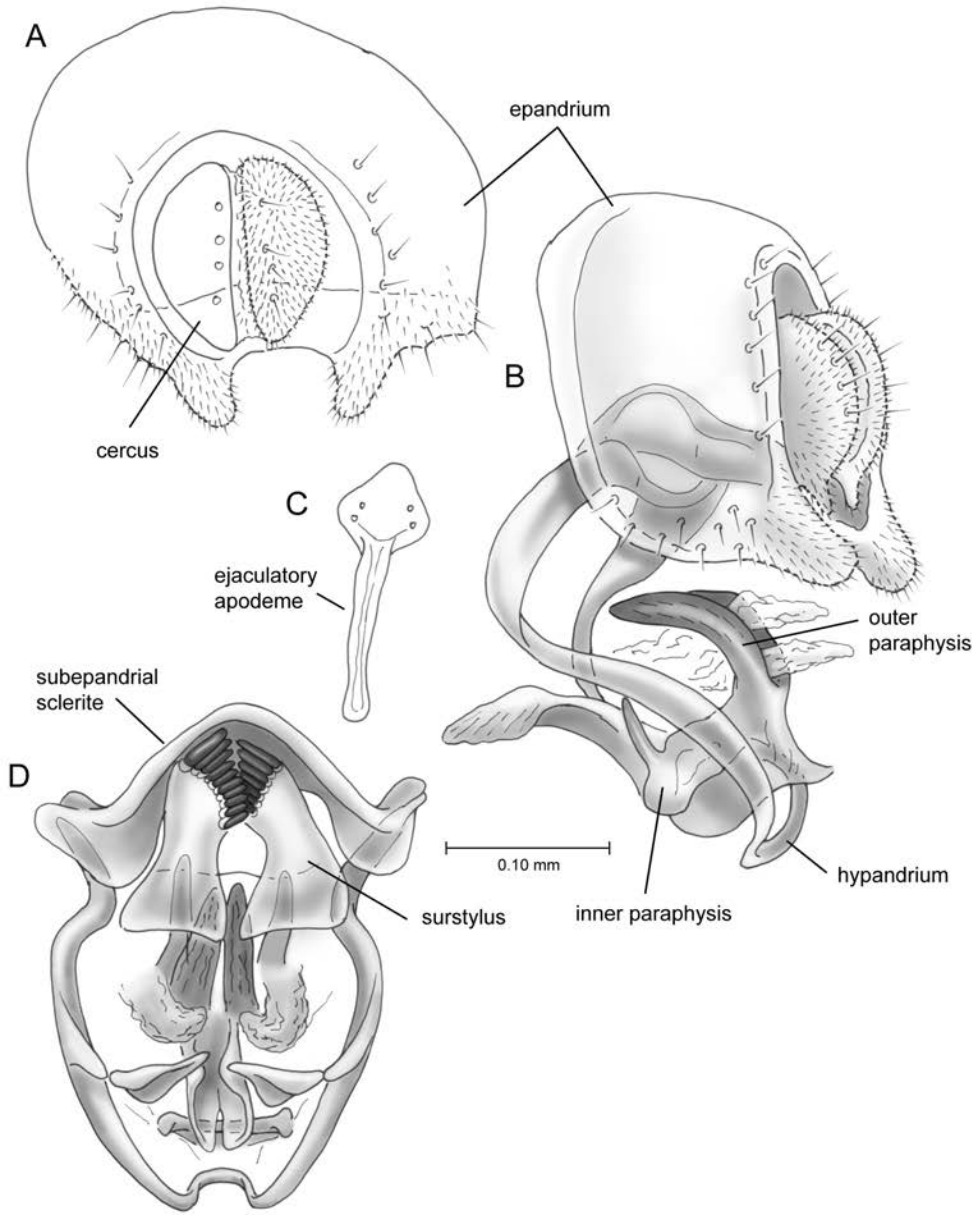


FIG. 67. Male terminalia, *A. rari pennis*. **A.** Epandrium and cerci. **B.** Lateral view. **C.** Ejaculatory apodeme. **D.** Ventral view. (Am 298, holotype).

Subepandrial sclerite large, nearly as long as the aedeagal apodeme; with thin, spindle-shaped central appendage. Outer paraphysis very complex: posterior portion a moderately long, laterally flattened lobe with a small preapical dorsal hook; base of lobe with patch 4–5 sensilla; lateral to lobe, a small appendage, facing posteriorly; anterior portion of outer paraphysis bifurcate, 2 long, darkly sclerotized rods, tapering to point, facing ventrally. Inner paraphysis narrow, simple, wedge shaped, immediately anterior to outer paraphyses. Aedeagal apodeme long, shieldlike, anterior 1/3 curved; distal end widely flared with a concave depression; 2 lobes near the base, large, as wide as distal lobes. Hypandrium simple; lateral arm with large gonopod, oriented dorsally. Ejaculatory apodeme 0.5× length of epandrium. Head and thorax measurements: ( $n = 5$ ; Am 13, 14, 17, 18, 20) FL/FW 0.63 (0.59–0.75), EL/EW 1.37 (1.30–1.48), EL/CW 6.12 (5.46–6.18), FML/FMW 0.38 (0.33–0.44), PR/RR 0.58 (0.46–0.77), ThL 1.63 (1.54–1.71 mm).

**TYPE MATERIAL:** **Holotype:** Data taken from Wheeler (1952): “♂, No. 2170.5, from Mill Canyon, Magdalena Mts., near Magdalena, New Mexico, taken by the writer in June, 1951,” [not examined]. Deposited in National Museum of Natural History, Washington D.C. (USNM). **Paratypes:** Localities and numbers of paratype specimens in AMNH differ slightly from Wheeler (1952) in some cases: “6, with same data as holotype” [Mill Canyon, Magdalena Mts., S. Magdalena, VI/26–VI/27/51, 2170.5, W.B. Heed/M.R. Wheeler, paratype], [34.008746, -107.201329], 2♂ and 2♀ (Am 14–16, 17\*, AMNH); “Cherry Creek Camp near Silver City (4)” [12 mi. N. Silver City, Aug 1950, M.R. Wheeler, paratype], [33.019248, -108.263582], [all specimens are *A. nebojsa* Máca, see Comments], 4♂ (specimen numbers under *A. nebojsa* Máca, AMNH); “Long Valley in Coconino National Forest (2)” [Arizona: Clover Springs, Coconino Nat'l. Forest, 50 mi. S. Flagstaff, VI/22–VI/23/51, W.B. Heed/M.R. Wheeler, paratype], [34.506258, -111.362842], 1♂ and 1♀ (Am 18\*, 19, AMNH); “Mogollon Road south of Flagstaff (4)” [Mogollon Rim

Road, Arizona, June 1951, M.R. Wheeler and W.B. Heed, 2169.8, paratype], [34.326000, -110.958445], 3♂ and 1♀ (Am 7.5\*, 12, 13\*, 20, AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the type series.

**DISTRIBUTION:** This species seems to be restricted to the Arizona Mountains Forest ecoregion in Arizona and New Mexico.

**COMMENTS:** The paratype series of *A. buccata* Wheeler at the AMNH contains another species. The four specimens from 12 mi. N. of Silver City are of *A. nebojsa* Máca. While the holotype specimen at the USNM has not been dissected for confirmation, its identity is assumed to be the same as the paratypes taken from the same series as the holotype.

### *Amiota didens*, sp. nov.

Figures 68E–F, 72C, 75, 95A

**DIAGNOSIS:** Small to medium-sized fly (ThL 0.99–1.44 mm), dark brown, legs yellow; frons dark with frontal half slightly silvery; arista with sparse, short plumosity; subepandrial sclerite appendage with broad, roughly cordate apex; outer paraphysis short, laterally flattened, with preapical dorsal hook, large proximal-dorsal spine near base that is twice the length of apical hook; inner paraphysis lost.

**DESCRIPTION:** Small to medium-sized fly (ThL 0.99–1.44 mm), dark brown, legs yellow. Frons slightly silvery, dark. Cheek whitish gray posteriorly. Palp yellow. Arista: Short, plumose; longest branches D2, D3; A.R. 0.35; 5 dorsal branches (apical 2 very short), 2–3 very short ventral branches; none pointed mediad/laterad; arista trunk with medium-length microtrichia, bare on apical third. Epandrium with middorsal margin evanescent, grading into surrounding membrane below. Cercus small, crescentic, margins distinct, flattened in lateral view. Surstylus roughly square, the middle region with scattered setulae; 9–10 prensisetae, apices blunt, closely spaced, comblike. Subepandrial sclerite with short subepandrial

appendage that is drop-shaped in full ventral view; pair of microtrichose, membranous lobes flanking subepandrial appendage, apparently attached to genital complex. Outer paraphysis symmetrical, short, heavily sclerotized, laterally flattened, with preapical dorsal hook; several sensilla in small cluster on lateral side; large proximal-dorsal spine, twice the length of apical hook. Inner paraphysis lost. Aedeagal apodeme bent at 45° angle. Hypandrium faint, incomplete or very faintly sclerotized in middle; with large, bulging gonopod in middle of posterior margin. Ejaculatory apodeme 0.6× length of epandrium. Head and thorax measurements: (n = 3; Am 444, 1418, 1429) FL/FW 0.63 (0.60–0.64), EL/EW 3.11 (1.26–6.62), EL/CW 14.42 (13–17), FML/FMW 0.28 (0.25–0.30), PR/RR 0.56 (0.50–0.62), ThL 1.18 (0.99–1.44 mm).

TYPE MATERIAL: **Holotype:** male: MEXICO, Morelos: #7, 14 mi. N. Cuernavaca, [19.188745, -99.228691], 7300', 29 July 1963, leg. George W. Byers, Am 444, [glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH).

OTHER MATERIAL EXAMINED: **Mexico: Sinaloa:** Portrerillos, 15 mi. W El Palmito, 5000', 1964-07-08, leg. J.F. McAlpine, 1♂ (Am 1429\*, CNC); 1964-07-011, leg. J.F. McAlpine, biting man, 1♂ (Am 1418\*, CNC).

ETYMOLOGY: Formed from *di*, Greek for "two," and *dens*, Latin for "tooth or prong," in reference to the lateral view of the outer paraphysis of the male genitalia.

DISTRIBUTION: *Amiota didens* is known only from the states of Morelos and Sinaloa in Mexico.

COMMENTS: This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

*Amiota floridiensis*, sp. nov.

Figures 69A–B, 72E, 76, 95B

DIAGNOSIS: Small fly (ThL 1.11 mm), frons narrow, dull; arista with medium branches dorsally and ventrally; genitalia very distinctive:

outer paraphysis with hornlike spine projecting dorsally; inner paraphysis armlike, projecting dorsolaterally, broadened at distal end into 5 pointed spines, the middle spine longer than the other 4; aedeagal apodeme faint and lightly sclerotized, long and rectangular, length almost 2.5× width, distal end narrower than midsection.

DESCRIPTION: Small fly (ThL 1.11 mm), thorax jet black [faded to rusty ochre in the holotype], legs light yellow. Frons slightly pollinose, dark brown, narrow. Cheek white. Palp yellow. Katepisternum lighter than rest of pleuron. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branch D2; A.R. 0.42; 5 long dorsal, 3 long ventral branches, none pointed mediad/laterad; arista trunk with short microtrichia, bare on apical half. Male genitalia: Epandrium wide ventrally, with 8–13 crowded long setae, 5–6 setae forming a single row leading to the apex, dorsal bridge of epandrium barely present. Cercus distinct from surrounding membrane. Surstylus with 9 prenisetae, apices blunt, all of roughly equal size; triangular lobe, pointed, arising on lateralmost area of surstylus, extending over prenisetae, with ca. 9 long setulae. Subepandrial sclerite forming a small scoop, extending ventrally just below epandrium, but not appendicular. Outer paraphysis laterally flattened, with heavily sclerotized hornlike spine arising at base, proximal tooth at midpoint; distal portion of outer paraphysis forming rounded lobe with ca. 7 sensilla. Inner paraphysis armlike, darkly sclerotized, sinuous in anterior view, dorsolaterally projecting, distally flattening to 5 pointed spines, the middle one longest. Aedeagal apodeme very distinctive: slender, lightly sclerotized, length 2.5× width, slightly bent in lateral view (not strongly arched); distal portion small, almost rectangular, narrower than midsection, not widely flared and without concave depression. Hypandrium simple, a squared U-shape, thickness consistent; lateral arms not thickened. Ejaculatory apodeme not studied. Head and thorax measurements: (n = 1, Am 174) FL/FW 0.86, EL/EW 1.52, EL/CW 15.25, FML/FMW 0.35, PR/RR 0.54, ThL 1.11 mm.

**TYPE MATERIAL: Holotype:** male: FLORIDA: Lake Hall 5 mi. N. Tallahassee, [30.521947, -84.258074], VI/12-V/14/50, T.C. Hsu and Stephens, 2007.16, Am 174, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** In reference to Florida (United States), the state of the type locality.

**DISTRIBUTION:** This species is only known from the panhandle of Florida.

**COMMENTS:** Wheeler (1952) referred to this undescribed species as “*Amiota* species C” but refrained from describing it.

*Amiota humeralis* Loew, 1862

Figures 69C–D, 71, 72D, 77, 95C

*Amiota humeralis* Loew, 1862a: 229 (original description); Malloch and McAtee, 1924: 29 (key and description is male of *A. hsui*); Wheeler, 1952: 168 (key to Nearctic species, discussion); Wheeler, 1949: 260 (discussion); Wheeler, 1957: 110 (discussion); Wheeler, 1965: 761 (Nearctic catalog); Brake and Bächli, 2008: 252 (world catalog).

*Stegana humeralis* (Loew): Sturtevant, 1921: 57 (comb. nov. by Sturtevant).

*Phortica humeralis* (Loew): Malloch, 1921: 312 (comb. nov. by Malloch).

*Amiota setigera* Malloch, 1924: 51 (original description; type locality: USA, Illinois, Savoy; Deposited in Illinois Natural History Survey, Champaign, Illinois, INHS); Wheeler, 1952: 169 (key to Nearctic species); Wheeler, 1957: 110 (discussion); Wheeler, 1965: 761 (Nearctic catalog); Máca, 2003: 265 (redescription and male genitalia figured); Brake and Bächli, 2008: 255 (world catalog); syn. nov.

**DIAGNOSIS:** Very distinctive, small to medium-sized fly (ThL 1.20–1.29 mm); frons in

male narrow, reflective, and silvery (frons in female slightly wider and not as shiny, glossier); hind femur of male with ca. 3–5 long upright setae (females without long dorsoventral setae on femur); inner paraphyses unique, flanking inner lateral margins of the hypandrium, each side with ca. 8–10 thick, heavily sclerotized, feather-shaped lobes.

**DESCRIPTION:** Small to medium-sized fly (ThL 1.20–1.29 mm), dark brown to black, somewhat pollinose, legs yellow. Frons narrow (FL/FW 0.96–1.25), brilliant silvery from direct anterior view; ocellar triangle black, slightly pollinose. Cheek small, milk white. Palp yellow. Katepisternum lighter in color than rest of pleuron. Hind femur with 3–5 upright setae, more than 2× longer than diameter of femur. Arista: Very long, plumose; longest branch D3; A.R. 0.46; 5 dorsal, 2 ventral branches, none pointed mediad/laterad; arista trunk with medium microtrichia, bare on apical half. Male genitalia: Epandrium not separated dorsally, lower 2/3 with long setae. Cercus long, grading into surrounding membrane and almost continuous with epandrium. Surstylus longer than broad; 7 prensisetae, apices blunt, prensisetae becoming smaller from middle laterally and medially; prominent lateral thumblike lobe extending out and at angle to prensisetae (slightly hooked), creating gap; covered in setulae. Subepandrial sclerite simple, shield shaped, extending dorsally over surstyli, lacking subepandrial appendage. Outer paraphysis large and elaborate, ventral portion laterally flattened, with ca. 13 sensilla, distal portion with an apical claw, bridge arising proximal to apical claw joining to dorsal portion of outer paraphysis; dorsal portion consisting of 2 thickened, heavily sclerotized projections, the apices finely serrated and jagged, the distal end of dorsal portion consisting of a keellike extension with a deep cleft. Inner paraphysis elaborate: flanking inside margin of lateral arms of hypandrium, each half with 8–10 darkly sclerotized, feather-shaped appendages branching from the paraphysis stem. Aedeagal apodeme typical, slightly longer than wide, “distal plate” of aedeagal

apodeme flared, distal margin slightly concave. Hypandrium simple; incomplete at apex, diameter of consistent thickness, lateral arms not thickened. Ejaculatory apodeme of moderate size, length  $\sim 0.4 \times$  the depth of epandrium. Head and thorax measurements: ( $n = 5$ ; Am 183, 324, 465, 656, 737) FL/FW 1.09 (0.96–1.25), EL/EW 1.24 (1.01–1.38), EL/CW 21.58 (17.25–25), FML/FMW 0.42 (0.31–0.53), PR/RR 0.62 (0.45–0.80), ThL 1.24 (1.20–1.29 mm).

**TYPE MATERIAL:** **Holotype:** female: USA: District of Columbia: Loew Coll., “humeralis m.,” “Type 13406,” [barcode] MCZ-ENT00013406, [leg. C.R. Osten-Sacken], [not examined, only photomicrographs reviewed]. Deposited in the Harvard Museum of Comparative Zoology, Cambridge (MCZC).

**OTHER MATERIAL EXAMINED:** **USA: Alabama:** Clay Co., Talladega Nat. For., 33.443496, -85.839339, 2018-08-15, leg. L.E. Jones, swept around head, 1 ♀ (Am 923, AMNH); Lawrence Co., Bankhead Nat. For., 434.308325, -87.395084, 2018-08-15, leg. L.E. Jones, swept around head, 1 ♀ (Am 913, AMNH); Wilson Dam F.Q., 1942-07-12, leg. J.N. Belkin, 2 ♀ (Am 670, 671, LACM). **Arkansas:** Johnson Co., Ozark Nat. For., 35.673036, -93.453114, 2018-08-09, leg. L.E. Jones and J.L. Hughes, swept around head, 2 ♀ (Am 825, 826, AMNH); 2018-08-09, leg. J.L. Hughes and L.E. Jones, swept around head, 1 ♀ (Am 839, AMNH); Logan Co., Magazine Mt., 2750 ft., 1992-07-06, leg. D. Grimaldi, 1 ♂ and 7 ♀ (Am 318, 324\*, 327, 330, 344, 359, 360, 363, AMNH); Garland Co., Ouachita Nat. For., 34.540121, -93.352490, 2018-08-09, leg. J.L. Hughes and L.E. Jones, 1 ♂ (Am 736\*, AMNH). **Georgia:** Towns-White Cos., Unicoi Pk., 1954-10-02, leg. H.R. Dodge, 3 ♀ (Am 411, 413, 414, WSU). **Illinois:** Hardin Co., Shawnee Nat. For., 37.594631, -88.382478, 2018-08-08, leg. L.E. Jones and J.L. Hughes, swept around head, 4 ♂ and 27 ♀ (Am 647\*, 737\*, 738\*, 739\*, 755–759, 761–765, 767, 768, 770–774, 776, 778, 779, 781–783, 785, 786, 788, 790, AMNH); 2018-08-08, leg. J.L. Hughes and L.E. Jones, swept around head, 1 ♂ and 15 ♀ (Am 734\*, 791, 796–798, 1151–1156, 1158–1162, AMNH); Mason Co., Sand Ridge State Park, 1976-06-12, leg. M.E. Irwin, 1 ♂ (Am 1601\*, INHS); Savoy, 1916-05-23, [leg. J.R. Malloch], on sap, INHS Insect Collection 238.815, [Holotype of *Amiota setigera* Malloch], 1 ♂ (no number, INHS); St. Clair Co., Stemler Cave

Woods Nat. Pres., 38.464886, -90.155530, 2019-05-24, leg. L.E. Jones, swept around head, 1 ♀ (Am 996, AMNH); Union Co., Trail of Tears State Forest, 37.499757, -89.340117, 2018-08-08, leg. L.E. Jones and J.L. Hughes, swept around head, 1 ♂ and 3 ♀ (Am 807, 808, 811, 813, AMNH); 2018-08-08, leg. J.L. Hughes and L.E. Jones, swept around head, 1 ♀ (Am 820, AMNH); White Heath, 1920-08-12, [leg. J.R. Malloch], [paratype of *Amiota setigera* Malloch], 1 ♀ (Am 1612, INHS); White Heath, 1920-08-12, leg. J.R. Malloch, INHS Insect Collection 238.814, [Allotype of *Amiota setigera* Malloch], 1 ♀ (no number, INHS). **Indiana:** Harrison Co., O'Bannon Woods St. Pk., 38.194962, -86.267880, 2018-08-14, leg. L.E. Jones, swept around head, 3 ♂ and 2 ♀ (Am 655\*, 656\*, 888, 889, 894, AMNH); Perry Co., Hoosier Nat. For., 38.195597, -86.613230, 2018-08-14, leg. L.E. Jones, swept around head, 1 ♀ (Am 865, AMNH). **Kansas:** Leavenworth, 1935-06-17, leg. L.S. Henderson, 1 ♀ (Am 450, SEMC). **Mississippi:** 8 mi. S. Columbus, 1941-09, leg. G.B. Mainland and R.P. Wagner, 1 ♀ (Am 70, AMNH); Yalobusha Co., George P. Cossar St. Pk., 34.131206, -89.887945, 2018-08-12, leg. J.L. Hughes and L.E. Jones, swept around head, 1 ♀ (Am 855, AMNH). **Missouri:** Carter Co., Ridge Road at Road C, 4.5 mi SW of Van Buren, 1967-08-04, leg. H.B. Leech, 3 ♀ (Am 382–384, CAS); Franklin Co., Meramac Caverns, 1966-07-06, leg. P.H. Arnaud Jr., 1 ♀ (Am 385, CAS); Lithium, 1955-06-29, leg. M.R. Wheeler, 1 ♂ and 7 ♀ (Am 44, 47–51, 67, 188, AMNH); Taney Co., Drury Conservation Area, ex. Buttonbush Pond., 36 34 2.28 N, 93 4 33.60 W, 280 m, 2019-06-06, leg. B.J. Sinclair, CNC 1450129, 1 ♂ (Am 1296, CNC). **Ohio:** Lawrence Co., Wayne State Forest, Vesuvius Recreation Area, 1989-07-13, leg. S.A. Marshall, 1 ♀ (Am 747, DEBU); Vinton, 1900-06-05 through 1900-06-12, [collector unknown], 2 ♂ and 1 ♀ (Am 464, 465, 467, SEMC). **Tennessee:** Rutledge, 1954-07, leg. M.R. Wheeler, 1 ♂ (Am 183\*, AMNH). **Texas:** Austin, 1958-10, leg. L. Throckmorton, 1 ♀ (Am 109, AMNH).

**DISTRIBUTION:** *Amiota humeralis* inhabits an area comprised of the Ozark Mountains, lower Midwest, portions of the southern Appalachia Mountains, the upper American South, and extends into the Great Plains; a unique distribution. The holotype of *A. humeralis* was collected in the District of Columbia, suggesting a greater historical range for this species in the east.

COMMENTS: The name *A. humeralis* Loew has been misapplied in the literature to many small, dark species of the genus. Wheeler (1952) erroneously cited *A. humeralis* as the type species of *Amiota* Loew, which was later amended (Wheeler, 1957); the type species is *A. leucostoma* Loew, as designated by Coquillett (1910). The holotype of *A. humeralis* designated by Loew in the MCZC is a female (fig. 71). Examination of photographs of the holotype revealed a frons on the female that is reflective and golden pruinose. This reflective frons is also found in the male of *A. setigera* Malloch (type at INHS), although much more brilliant and silvery. Detailed distribution maps of both sexes with shimmering frons overlap and are nearly identical. This morphological and distributional is compelling evidence that the male of *A. setigera* Malloch is the male of *A. humeralis* Loew, and that taxonomic conclusion is adopted here. Wheeler (1957) alluded to this possibility as well. Females of *A. humeralis* are commonly collected, and in some cases, can outnumber the males caught at a given locality by up to 8:1 (L.E.J., personal obs.), so it is no surprise that a female of this species would have been among the first collected and described in the genus. *Amiota humeralis* exhibits a number of external characters that make its identification easy without the dissection of genitalia including the narrow, silvery frons, as well as the long setae on the hind femora. This species exhibits the characteristic behavior of attraction to the eyes and face common to many *Amiota*.

***Amiota imperator*, sp. nov.**

Figures 69E–F, 72F, 78, 96A

DIAGNOSIS: Large fly (ThL 1.60–1.73 mm), honey to light brown, legs white, middle tibia with comb of ~20 upright setae; arista with medium to long plumosity; epandrium squat, broader than deep, dorsally complete, cercus pendulous; subepandrial sclerite with pair of slender, spinelike appendages that project for-

ward; aedeagal apodeme long and slender, length almost 2× width of base; inner paraphysis with distal, globose lobe densely covered in membranous scales.

DESCRIPTION: Large fly (ThL 1.60–1.73 mm), color always light, varying from golden honey to light brown (darkening in older museum specimens), abdomen darker, legs brilliant milky white (sometimes yellowing in older material), setation on body jet black. Cheek milky white posteriorly. Palp yellow. Katepisternum darker than rest of pleuron. Middle tibia with comb composed of ~20 setae, length of longest setae approximately equal to width of tibia, central setae slightly longer than those flanking the ends of the comb. Tergites 1 and 2 lightly colored. Arista: Medium, plumose; longest branches D3–D4; A.R. 0.36; 6 dorsal, 2–3 ventral branches; D5 pointed laterad; arista trunk with very long microtrichia that shorten apicad. Male genitalia: Epandrium squat, width ~0.7× height; dorsally complete, not medially split; ventral lobe rounded, with ~15 medium-length setae, ~8–9 setae clustering near apex of epandrium, long setae absent from medial area of epandrium. Cercus grading into surrounding membrane, not recessed into epandrium, pendulous (ventral margin overhanging surstyli). Surstylus with 7 prenisetae, apices blunt, becoming smaller dorsally, spinelike seta arising below the most medial preniseta; entire surstylus distally setulose. Subepandrial sclerite moderately sclerotized, shield-like; with pair of long, slender, spinelike processes arising from anterior portion, pointing backward. Outer paraphyses (?) apparently fused distally into a small membranous lobe that is bifid and with a deep notch, lateral surfaces each with pair of sensilla. Inner paraphysis a heavily sclerotized digitiform lobe, the apex with a globose membrane densely covered in minute lanceolate scales. Aedeagal apodeme distinct, slender, length more than 2× width of base; tapering past middle point, “distal plate” expanding, almost circular, not wider than base; single flange forming a central column. Hypandrium simple, incomplete in middle; lateral arms slightly thick-

ened with membranous, ventrally pointed gonopod. Median membranous structure between paraphyses (?aedeagus), with central swale and covered with setulalike projections. Ejaculatory apodeme small and stout, sclerotized, length  $\sim 0.4 \times$  depth of epandrium. Head and thorax measurements: (n = 5; Am 291, 507, 562, 642, 703) FL/FW 0.66 (0.61–0.74), EL/EW 1.37 (1.20–1.50), EL/CW 14.68 (12–18), FML/FMW 0.38 (0.37–0.41), PR/RR 0.54 (0.46–0.61), ThL 1.66 (1.60–1.73 mm).

**TYPE MATERIAL:** **Holotype:** male: USA: MI: Marquette Co., Huron Mtns., Huron Mtn. Club property vicinity, 46.874950, -87.891717, Leg. T. Werner, 6–12.vii.2018, Am 680, [specimen glued to paper point, dissected]. Deposited in the American Museum of Natural History (AMNH). **Paratypes:** USA: MI: Marquette Co., Huron Mtns., Huron Mtn. Club property vicinity, 46.874950, -87.891717, Leg. T. Werner, 6–12.vii.2018, 5 ♂ (Am 703\*, 1072, 1584–1586\*, AMNH).

**OTHER MATERIAL EXAMINED:** **Canada:** **Ontario:** Algonquin Provincial Park, Swan Lake Station, Scott Lake Survey, 1993-06-19 through 1993-06-31, leg. Larson/Marshall/Barr, pan A3, hemlock, clubmoss, 1 ♂ (Am 530, DEBU); Algonquin Provincial Park, W.R.S. A (B3), 1994-07-01, leg. R. Bonduriansky, 1 ♂ (Am 610\*, DEBU); Hald.-Norfolk Reg., Turkey Point Provincial Park, site 1, 2011-05-31 through 2011-06-15, leg. Brunke and Paiero, forest malaise pans, debu01153255, 1 ♂ (Am 613, DEBU); Northumberland Co., Peter's Woods Provincial Nature Preserve, front woods, 2011-07-12 through 2011-07-26, leg. Brunke and Paiero, forest malaise pans, debu01153255, 1 ♂ (Am 614, DEBU); Peterboro Co., Keene, Mill St. Trail, 2001-07-14, leg. W.J. Crins, 1 ♂ (Am 562\*, DEBU); Rattlesnake Pt. Conservation Area, 43 28 N, 79 55 W, 2010-06-19, leg. B.J. Sinclair, forest, 1 ♂ (Am 1268, CNC); Smith's Bay, Nr. Picton, 1970-01-07, leg. J.F. McAlpine, 2 ♂ (Am 1187, 1193, CNC). **Nova Scotia:** Cape Breton Islands N.P., Lone Shieling, Over small stream in maple forest, 1983-07-01, leg. J.R. Vockeroth, PG732859, 1 ♂ (Am 1397\*, CNC). **Quebec:** Gatin-eau Park, Lac Phillippe, 2014-07-05, leg. O. Lonsdale, 1 ♂ (Am 1305, CNC); Hull, 1958-06-30, leg. W.W. Moss, 1 ♂ (Am 1381, CNC); Mont Tremblant,

3000', 1959-07-15, leg. B.V. Peterson, 1 ♂ (Am 1380, CNC); PN de la Jacques-Cartier, Le Confluence Tr., 47 11 30 N, 71 22 43 W, 2019-07-15, leg. B.J. Sinclair, CNC1700874, 1 ♂ (Am 1223, CNC); Old Chelsea, Summit King Mtn., 1965-06-20, leg. D.M. Wood, 1 ♂ (Am 1534, CNC). **USA: Alabama:** Haleyville, 1953-07-06, leg. M.R. Wheeler, [illegible description], 1 ♂ (Am 296\*, AMNH). **Arkansas:** Newton Co., Buffalo Na. River, Lost Valley, Clark Creek, 335m, 36 0 36 N, 93 22 28 W, 2019-06-04, leg. B.J. Sinclair, CNC 1556621, 1 ♂ (Am 1303, CNC). **Connecticut:** River-ton, 1980-07-01, leg. S.A. Marshall, debu01081399 [Am 602], 2 ♂ (Am 558\*, 602, DEBU). **Georgia:** Indian Spring State Park, Indian Spgs., 1950-06-21 through 1950-06-22, leg. T.C. Hsu and Stephens, "=*Steyskal leucostoma* 3," 2015.9, 1 ♂ (Am 291\*, AMNH). **Indiana:** Wayne Co., Richmond, 1962-08-26, leg. T.R. Marsh, 1 ♂ (Am 1593\*, INHS). **Maine:** Guerette, [no date, likely 07-1948], [collector unknown, likely T.C. Hsu and M.R. Wheeler], [genitalia on slide, no pinned specimen] 1 ♂ (AMNH). **New Hampshire:** Franconia, [no date], leg. A.T. Slosson, Ac. 26226, 1 ♂ (Am 127\*, AMNH). **New York:** Bronx Co., New York Bot. Garden, 40.864029, -73.875571, 2018-08-02, leg. L.E. Jones and L. Li, swept around head, 1 ♂ (Am 642\*, AMNH); Monroe Co., Rochester, Highland Pk., 43.132600, -77.602784, 2018-07-26, J. Jaenike, 1 ♂ (Am 722\*, AMNH); N. Evans, 1912-07-04, leg. M.C. van Duzee, 1 ♂ (Am 388\*, CAS); Trumansburg, 1983-07-19, D. Grimaldi, 2 ♂ (Am 125\*, 126\*, AMNH). **North Carolina:** Graham Co., Robbinsville, 1976-06-09, leg. G.E. Bohart, 3 ♂ (Am 505–507\*, EMUS); Highlands, 1902-08-15, [collector unknown], 1 ♂ (Am 292, AMNH); Highlands, Skittle Creek, 1957-07-19, leg. W.R. Richards, 1 ♂ (Am 1384, CNC); Rich Mt., 2000', 1957-07-31, leg. W.R. Richards, 1 ♂ (Am 1382, CNC). **Ohio:** Portage Co., West Branch State Park, 1988-07-17, leg. B.A. Foote, 2 ♂ (Am 315\*, 316, AMNH).

**ETYMOLOGY:** From *imperator*, Latin meaning "emperor, commander-in-chief, ruler," in reference to the size of this new species, among the largest in Eastern North America, and its distinctiveness.

**DISTRIBUTION:** *Amiota imperator* is found throughout Eastern North America. Of note, this striking, new species was collected in the Thaines Family Forest of the New York Botanical Garden, located in the Bronx, New York City.

COMMENTS: Pinned specimens of this species can look remarkably similar to species of the *rufescens* species group in size and color. *Amiota imperator* can be separated from these species by the comb on the midtibia of the males. This species is uncommon in most localities, usually collected as one individual rather than a series. Three specimens (DEBU) were caught via malaise and pan traps. *Amiota imperator* is likely the species referred to as “*Amiota* species B” by Wheeler (1952), although none of the specimens collected in Maine have been seen except for the genitalia of a male on a slide (no pinned material) in the collections of the AMNH. This species exhibits the characteristic behavior of attraction to eyes and face common to many *Amiota*.

***Amiota laevifurca*, sp. nov.**

Figures 70A–B, 72G, 79, 96B

DIAGNOSIS: Large fly (ThL 1.59 mm), dark blackish brown; frons dark, dull, wide; arista with 4 long dorsal and 2 ventral branches; femora and tibiae light brown; outer paraphyses asymmetrical, left one with hornlike spine on dorsal margin, both with short, sclerotized, preapical lobe; inner paraphysis roughly L-shaped, left side with a bifurcated end; subepandrial appendage well developed, apex roughly heart shaped in posterior view; aedeagal apodeme rectangular; epandrium with wide dorsomedial gap; ejaculatory apodeme large, length equal to height of epandrium.

DESCRIPTION: Large fly (ThL 1.59 mm), dark brown, uniformly so, including entire pleura (except for white postpronotal and subalar spots). Femora and tibiae light brown, tarsi yellow. Frons dull blackish brown. Facial marking large, depth 0.5× width. Cheek whitish gray posteriorly. Palp brown. Haltere bright yellow. Tergite 1 lightly colored. Arista: Long, plumose; longest branch D1; A.R. 0.37; 4 dorsal, 2–3 shorter ventral branches; no branches pointed

mediad/laterad; arista trunk with long microtrichia to apex. Male genitalia: Epandrium mid-dorsally separated by wide membranous gap. Cercus large, long oval; margins discrete from surrounding membrane; cercus occupying virtually all of space surrounded by epandrium. Surstylus with 10 prensisetae, apices blunt, lateral thumblike lobe present; ventral margin, area above prensisetae, and lobe covered with scattered setulae. Subepandrial sclerite wide, shieldlike; subepandrial appendage well developed, projecting ventrally from epandrium, apical portion roughly heart shaped in full posterior view. Outer paraphysis possibly small, simple lobe at base of outer paraphyses (best seen in posterior view). Inner paraphysis roughly L-shaped; distal end of left side bifurcated, with a long, upper spinelike lobe, lower lobe having a small dorsal tooth; proximal end of right inner paraphysis has small fork, distal end like left paraphysis except without large, dorsal spinelike lobe. Aedeagal apodeme long, rectangular, length 2× width; hardly expanded on distal end, depression very shallow; lateral and anterior margins very slightly concave. Hypandrium apex posterodorsally curved around outer paraphysis; lateral arms and gonopod very wide, almost triangular in lateral. Ejaculatory apodeme large, slightly longer than epandrium. Head and thorax measurements: (n = 1; Am 1416) FL/FW 0.68, EL/EW 1.38, EL/CW 11.43, FML/FMW 0.39, PR/RR 0.33, ThL 1.59 mm.

TYPE MATERIAL: **Holotype:** male: Portrerillos, Sin. [Sinaloa], 15 mi. W. El Palmito, MEX., [23.578657, -106.216630], 5000', “8.VII.”1964, J.F. McAlpine, Am 1416, [specimen glued to pin, dissected]. Deposited in the Canadian National Collection (CNC).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: From Latin *laevus* for “left” and *furca* for “fork,” in reference to the forked inner paraphysis on the left side of the asymmetric male genitalia. Used as a feminine noun in apposition.

**DISTRIBUTION:** *Amiota laevifurca* is currently only known from the state of Sinaloa in Mexico.

**COMMENTS:** This species is superficially similar to *Amiota barretti* (Johnson), another species from Mexico, but *A. barretti* is externally separable by being black with metallic bluish highlights (vs. dark brown), the femora and tibiae are nearly black (vs. light brown), *A. barretti* has a wider cheek (vs. narrow); and, perhaps most distinctive of all, *A. barretti* has short branches on the arista, *A. laevifurca* has long branches (i.e., AR 0.17 vs 0.37, respectively).

*Amiota sinaloensis*, sp. nov.

Figures 70C–D, 72H–I, 80, 96C

**DIAGNOSIS:** Small to medium-sized fly (ThL 1.02–1.18 mm); dark brown, including entire pleura; frons dark, dull, wide; legs yellow; cheek deep, light brown; postpronotal lobe marking faint, subalar spot very faint or absent; arista with few, very short branches; cerci flattened, positioned low, ventral margins in line with ventral level of epandrium; surstylus apically narrow, with ca. 5 prensisetae; subepandrial appendage well developed; outer paraphyses asymmetrical, relatively short, forming L-shaped structure in lateral view, ventrally with 2 basal ostia; inner paraphysis lost.

**DESCRIPTION:** Small to medium-sized fly (ThL 1.02–1.18 mm), body dark brown, uniformly so, even entire pleura including katapisternum; legs yellow. Frons dark, blackish-brown dorsally, light brown ventrally at lateral corners; relatively narrow (FML/FMW 0.20–0.28). Cheek deep (EL/CW 7.57–7.62), very light brown. Palp yellow. Postpronotal lobe marking faint, subalar spot extremely faint to absent. Arista: Short, plumose; longest branch D2; A.R. 0.28; 2 dorsal branches at base, 2 ventral branches preapically; branch D3 pointed mediad; arista trunk with short to medium-length microtrichia to apex. Male genitalia: Epandrium dorsally complete, margin discrete

from membrane below; row of long ventral setae in lateral view. Cercus wedge shaped, flattened, dorsally narrow, ventrally expanded with flat margin, extending slightly beyond epandrium in lateral view; very large membranous area dorsally. Surstylus with broad base, apical half a narrow lobe; row of setulae on medial and lateral margins; 5 short prensisetae, apices blunt. Subepandrial appendage present, U-shaped, each distal end connected to membranous sheath bearing microtrichia; roughly heart shaped. Outer paraphyses asymmetrical; short, stout, heavily sclerotized; bases broad, narrowed apically; right paraphysis with bifid spine projected posteriorly, plus 2 smaller, simple ventral spines; left one with 3 short spines; 1 long preapical trichoid sensilla on each, plus several smaller ones, ventrally with 2 small ostia near base. Inner paraphysis lost. Aedeagal apodeme flared with a concave depression; basal end with deep V-shaped notch, heavily sclerotized “flange” arising at the base and connecting to the midpoint; bent nearly 90° in lateral. Hypandrium thin at apex, forming distinct, wrinkled wings adjacent to paraphyses. Ejaculatory apodeme large, equal to depth of epandrium; heavily sclerotized. Head and thorax measurements: (n = 3; Am 433, 1415, 1419) FL/FW 0.69 (0.62–0.73), EL/EW 1.25 (1.23–1.27), EL/CW 7.58 (7.57–7.62), FML/FMW 0.24 (0.20–0.28), PR/RR 0.41 (0.40–0.44), ThL 1.10 (1.02–1.18 mm).

**TYPE MATERIAL:** **Holotype:** male: Portrerillos, Sin. [Sinaloa], 15 mi. W. El Palmito, MEX., [23.578657, -106.216630], 11.VII.1964, J.F. McAlpine, 5000', Am 1419, [glued directly to pin, dissected]. Deposited in the Canadian National Collection (CNC). **Paratype:** Portrerillos, Sin. [Sinaloa], 15 mi. W. El Palmito, MEX., 8.VII.1964, J.F. McAlpine, 5000', 1 ♂ (Am 1415\*, CNC).

**OTHER MATERIAL EXAMINED:** **Mexico: Chiapas:** Finca Prusia (33km S. Jaltenango), 1000m, 1985-05-10 through 1985-05-12, leg. A. Freidberg, 1 ♂ (Am 433\*, AMNH); 9 mi SW Teopisca Hwy 24, 1969-05-23, leg. B.V. Peterson, 1 ♂ (Am 1503\*, CNC).

**ETYMOLOGY:** Derived from Sinaloa State in Mexico, location of the type series.

**DISTRIBUTION:** *Amiota sinaloensis* is currently known from Sinaloa and Chiapas states in Mexico.

**COMMENTS:** It is unknown whether this species is attracted to the eyes and face as in other *Amiota*.

## DISCUSSION

Most surprising is how a genus that interacts with humans, many on a daily basis, and literally eye to eye, has been ignored for so long, especially in one of the best biotically inventoried regions of the world. *Amiota* is common throughout certain parts of the United States and can form swarms in some areas. As random as taxonomic efforts can be, interaction with humans is often a good predictor to a taxon receiving attention. Culicidae (mosquitoes) and other families of biting species, for example, are among the most-studied flies (Harrington et al., 2001), especially since they are vectors for many deadly diseases, parasites, and infections. *Amiota* is not known to harbor any deadly diseases, but given its placement in Drosophilidae, with so many models in basic science, one would assume that it would have attracted more study before now.

And ripe they are for study: this study identified 36 new Nearctic species. This is probably the largest number of new species for any genus of Drosophilidae left to be discovered in North America. The new species were evenly split between eastern and western North America at nine each, with one shared between east and west. Mexico also has a large share of new species at 19 (of these, two shared with the United States).

Since the description of the genus by Loew with American species, 15 names have been associated with the American fauna. Twelve of these species were encountered during this study, either collected or consulted from existing museum collections. One species from Canada, *A. subtusradiata* Duda, has not been fully addressed yet, as

only the type specimen of its synonym *quadrata* (deposited in Tokyo) is currently known. We hope to see material for a future supplement. Two previous names can now be excluded, *Amiota steganoptera* Malloch and *Amiota setigera* Malloch. *Amiota steganoptera*, which was originally described from Costa Rica (Malloch, 1926), was presumed by Wheeler (1965) to be in the southern United States, but dissections of Central American species are quite different from the species in the southern United States, so it can likely be excluded from the Nearctic (see Comments under *A. raripennis*). Only one species is synonymized in this work, *A. setigera*, which is now understood to be the male of *A. humeralis* Loew (see COMMENTS under *A. humeralis*).

Within North America, *Amiota* diversity appears constrained by elevation and vegetation type. These areas occur in the interior of the continent, e.g., southwestern United States, Appalachia, Ozarks, Ontario, interior highlands of Mexico, with the diversity and number of individuals dropping closer to the coasts and along the Atlantic and Gulf Coastal Plains, especially in the American South. Other areas with little to no diversity, or few individuals collected, include the Rocky Mountains, the Great Plains, the Great Basin, and the far west, like California. These coastal and interior regions are usually low in elevation or dominated by coniferous forests (Olsen et al., 2001). *Amiota* seems to be exclusively associated with broadleaf trees (Krivoshchina, 2008; Máca, 1980; Malloch, 1924), with no known associations with conifers. Less clear is why elevation would be involved, although it could be due to precipitation or microclimate.

The habits of male *Amiota* allow convenient sampling of species. As a result, there is excellent geographic spread of sampling and data on species distributions, though not without lacunae. In the following biogeographic summary, official names of North American ecoregions are given in capital letters, some of them from the North American Atlas of Ecological Regions (CEC, 1997; fig. 97).

**AREAS OF DIVERSITY:** Greatest species diversity occurs in the temperate forests of

eastern North America (19 species), the montane forests of southwestern North America (9 species), and the temperate Sierran forests of Mexico (19 species). Details on these distributions are given below.

**GREAT PLAINS AND DESERT SCARCITY:** *Amiota* is very scarce in the North American Great Plains in the center of the continent, and absent from the hot, dry, lowland desert regions of Nevada, Arizona, New Mexico, Utah, California, and Mexico. The few records of *Amiota* from the Great Plains are of *A. minor* (Malloch) (one record in Nebraska, another in southernmost Manitoba) and of *A. hsui* Máca (one in Oklahoma). It is possible that sparse Plains populations subsist in wooded areas of cottonwoods (*Populus* spp.) along riverine habitats.

**PACIFIC COASTAL SCARCITY:** Another area of (surprising) scarcity involves Marine West Coast forests of British Columbia, Washington, Oregon, and northern California. Despite the rainfall and moisture in these coastal areas, and an abundance and substantial diversity of oaks (*Quercus* spp.) in at least California, the only predominant species in this area is *Amiota occidentalis*. The only species known just from this area is *A. mcalpinei* (one record from southernmost British Columbia).

**ROCKY MOUNTAIN SCARCITY:** There are surprisingly few species or records from Rocky Mountain forests, and no records at all from Colorado and Wyoming. *Amiota occidentalis* is the only species found thus far in this area. This scarcity is likely due to the coniferous trees that dominate the environments such as the Colorado Rockies forests (CEC, 1997) and other northward-stretching regions, where few or no *Amiota* have been collected. Aspens, however, are also abundant in this region, and presumably these trees are suitable as breeding sites.

**SOUTHEASTERN SCARCITY:** The only species from the subtropical Coastal Plains of the southeast (Georgia, Florida) is *A. floridiensis*, sp. nov. (and possibly *A. raripennis*), known as a single record from the panhandle of Florida. Curiously, *Amiota* do not seem diverse in this relatively low subtropical area. This phenomenon is consistent

with lower diversity in the Caribbean and other lower elevation tropical areas (L.E.J. and D.A.G., personal obs.). This region is characterized by the southeastern conifer forests, which is a mix of broadleaf and pine trees (Ware et al., 1993).

**TRANSCONTINENTAL SPECIES:** There are two species whose distributions extend to both coasts of North America: *Amiota hsui* Máca (from New York state and North Carolina to California, but oddly not in northern areas of the west); and *A. minor* (Malloch), from the entire eastern North America, where it is very abundant, to Arizona and Washington state, where it is scarce. *Amiota minor* is the most abundant and widespread species in the Nearctic Region. The Great Plains and desert regions of southwestern North America clearly are a major barrier to most species of *Amiota*.

**WIDESPREAD EASTERN SPECIES:** Species of the Eastern Temperate Forests are much more widespread than those in other regions of the United States and Canada. This is expected, given that there are moderate differences in temperature, rainfall, and plant diversity between lowland and montane forests in this region. Some of the eastern species are rare, i.e., *Amiota fulvitibia*, *A. raripennis*, and *A. tessae*; in addition, *A. nanonigrescens* is known only from a single record in southern Ontario. Additional sampling is necessary to confirm whether these species truly have narrow distributions. *Amiota humeralis* Loew appears to be concentrated in the Mississippi and Ohio River basins. The westernmost extension of four species is in the Ozark Mountains of Arkansas: *A. communis* Chen and Steyskal, *A. imperator*, *A. mariae* Máca, and *A. steyskali* Máca.

**SOUTHEASTERN EXTENSIONS:** Some northeastern species have their southernmost extensions into the southern Appalachians of Virginia, the Carolinas, and Tennessee. These include *Amiota communis* Chen and Steyskal, *A. fulvitibia*, *A. lineiventris* Máca, and *A. zalis-koi*. Two species extend to the southern Appalachians as well as to the Ozark Mountains of Missouri and Arkansas (*A. imperator* and *A.*

*mariae* Máca). Southern extensions into montane areas are expected based on the cooler climate. An unusual exception to this pattern is *Amiota raripennis*, which occurs in the Virginia Appalachians as well as the Gulf Coastal Plain of southern Mississippi and Alabama (and likely Florida).

**TEMPERATE SIERRA DIVERSITY:** The *Amiota* species of Temperate Sierra forests of Arizona, New Mexico, and northern Mexico, and the Semi-Arid Highlands of southwest Arizona are surprisingly diverse for an area of comparatively small size. We attribute this to the geographic and ecological isolation of montane forests ("sky islands") in these areas, separated by large areas of dry, lowland desert uninhabitable to *Amiota*. Together these mountains form a sky-island effect (Warshall, 1995), with the genus absent from the dry, arid lowlands.

Five species restricted to these two areas are *Amiota antitortum*, *A. buccata* Wheeler, *A. cruciatum*, *A. nebojsa* Máca, and *A. tormentum*. Two additional species are known only from the highlands of western Texas: *A. texas* and *A. wheeleri*. Two other species occur in the area but extend well into Mexico (*A. amputata* and *A. incurva*).

**HIGH DIVERSITY IN SIERRA MADRE:** Despite the limited geographic sampling, preliminary indications are that there is very high *Amiota* diversity in the forests of the western Sierra Madre of Mexico. This is based on the sampling by McAlpine and other Canadian dipterists in the 1960s in a few areas in Durango and Sinaloa. The interior of Mexico is dominated by Sierra Madre Occidental pine-oak regions (Gonzalez-Elizondo et al., 2013). Conifers dominate the highest elevations of mountainous areas, with combinations of aspen, cottonwood, and oak dominating middle elevations. In these areas of Mexico, oaks in particular are very diverse, nearly 165 species (Nixon, 2006), where *Amiota* can be caught in great numbers.

Nineteen species are now known from northern to central Mexico (we included records of southern, tropical portions of Mexico in this

study only for those species that occur farther north). Seven of these species are widespread, extending in the north from southern Arizona and New Mexico to Chiapas: *Amiota amputata*, *A. barretti* (Johnson), *A. biacuminis*, *A. incurva*, *A. latilabrum*, *A. onyx*, and *A. sinaloensis*. Species with a distribution that appears more limited, to Durango and areas surrounding Mexico City, include *A. didens*, *A. forceps*, *A. subnebojsa*, and *A. uniacuminis*. Eight species have a single record, from either Durango, Sinaloa, or Michoacan: *A. avipes*, *A. cervites*, *A. durangoensis*, *A. elsaltoensis*, *A. laevifurca*, *A. multiplex*, *A. oviaptor*, and *A. pseudominor*, indicative of great diversity in this area.

**UNUSUAL DISJUNCTIONS:** Two species show dramatic disjunctions between eastern and southwestern North America: *Amiota nigrescens* Wheeler (southern Ontario and Québec; and Arizona and New Mexico) and *A. hyalou*. (southern Illinois and Ontario; and New Mexico, Arizona, and southern California). We could not find morphological differences between flies from the disjunct areas for either of these species, but it would be useful to sequence some specimens for confirmation.

**HISTORICAL BIOGEOGRAPHY:** As to which biogeographic realm was on the receiving end of some of these similar species is untested and unknown (in biogeography there is a common assumption of the Palaearctic giving rise to Nearctic forms, and perhaps this comes from the historical paths of humans). Speculation by some authors has posited southwestern China as a possible place of origin for the genus (Chen et al., 2005; Zhang and Chen, 2006). This is based on the extraordinary diversity of the genus in the Hengduan Mountains, where more than 50 species occur, more than the known number of species in the Nearctic. This assumption hasn't been tested phylogenetically and is only based on the large number of species there. One of the more basal lineages in the morphology-based phylogenies of Chen and Toda (2001), the *rufescens* species group, has three representatives in the Nearctic (two new to science), which suggests this matter is not settled.

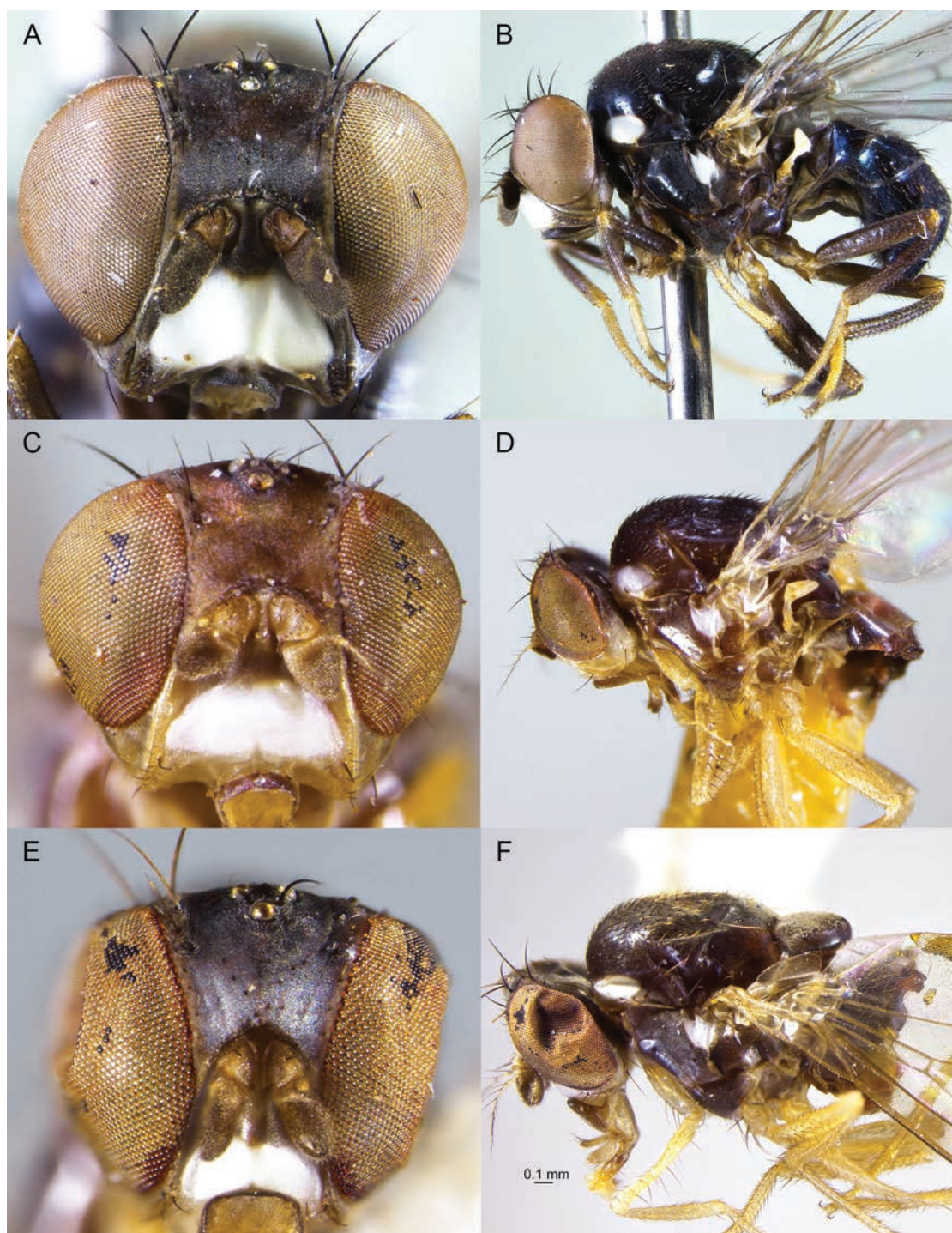


FIG. 68. Heads and lateral views, ungrouped species. A–B. *A. barretti* (Johnson) (Am 1490). C–D. *A. buccata* Wheeler (Am 14, paratype). E–F. *A. didens*, sp. nov. (Am 444, holotype, lateral image flipped).

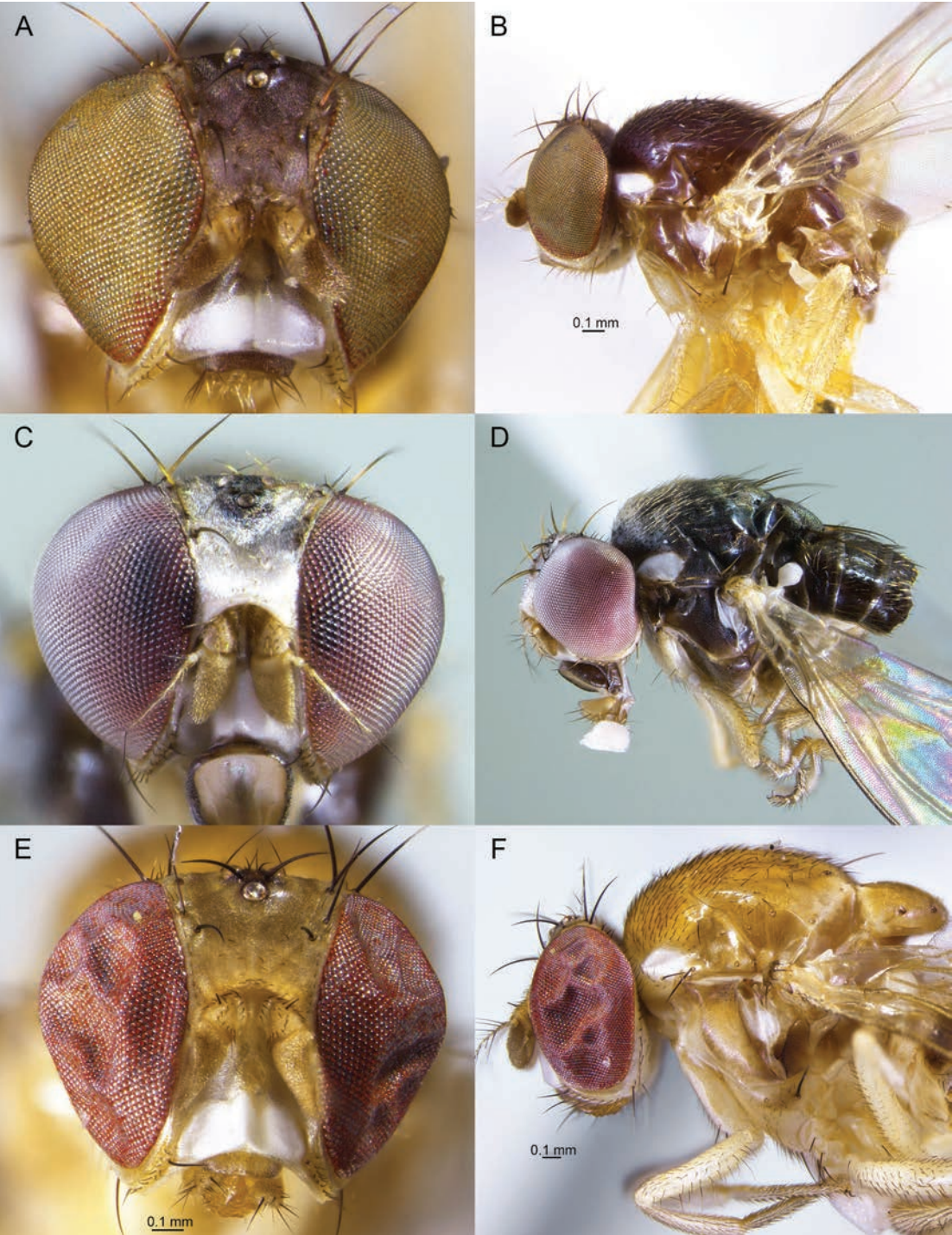


FIG. 69. Heads and lateral views, ungrouped species. A–B. *A. floridiensis*, sp. nov. (Am 174, holotype, lateral image flipped). C–D. *A. humeralis* Loew (Am 739). E–F. *A. imperator*, sp. nov. (Am 562, lateral image flipped).

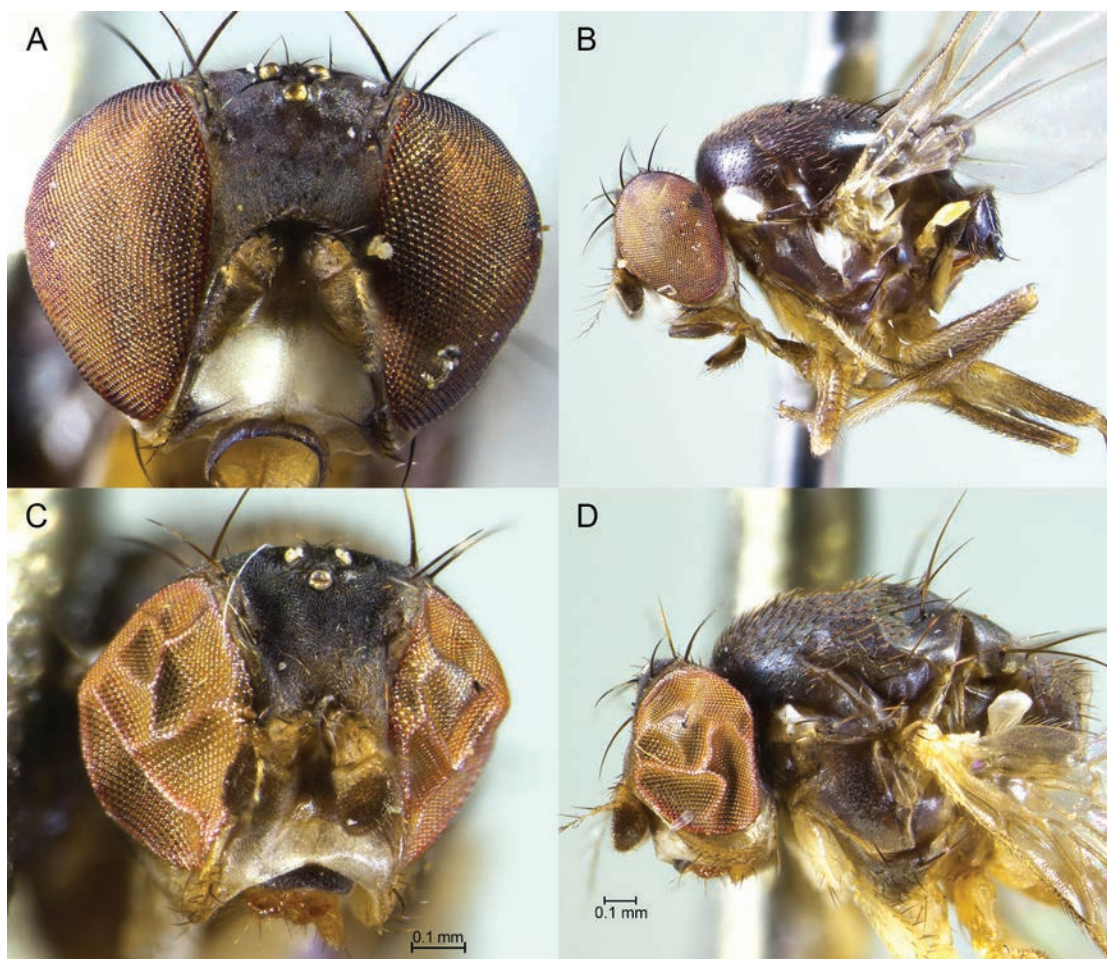


FIG. 70. Heads and lateral views, ungrouped species. A–B. *A. laevifurca*, sp. nov. (Am 1416, holotype). C–D. *A. sinaloensis*, sp. nov. (Am 1419, holotype).

Among the few patterns of Nearctic *Amiota* based on species relationships perhaps the most interesting is a contrast between the northern (U.S. and Canada) and southern (Mexico) areas. The United States and Canada share some species groups with Europe and Asia; these include the *alboguttata* group, *nagatai* group, and *rufescens* group. Moreover, the morphological cladogram (fig. 3) shows additional European and Asian species scattered among other, unplaced North America species. The only U.S./Canada lineage that is endemic to a region is the *nigrescens* group, which is largely in the northeastern United States.

*Amiota* species of the Southwest and Mexico, in contrast, have several groups endemic to that region: *cervites* species group (three species), *avipes* species group (six species), and *nebojsa* species group (five species). Thus, there has been probably more diversification within Mexico than in any other region of the Nearctic. This is probably due to several factors, including a large area of sky-island isolation as well as a great abundance and diversity of temperate tree taxa in montane regions, especially oaks (Fagaceae) (Nixon, 2006).

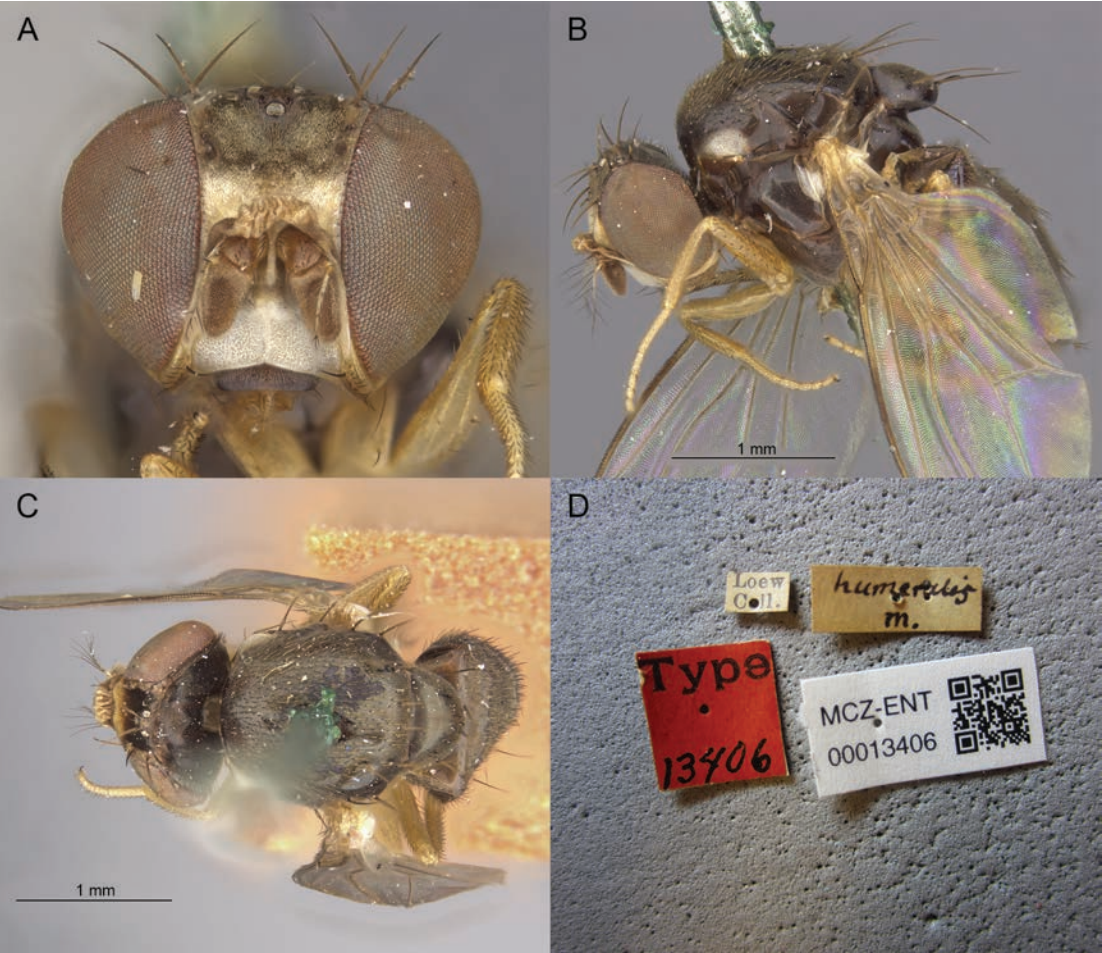


FIG. 71. Holotype of *A. humeralis* Loew (MCZC), Museum of Comparative Zoology, Harvard University. Photographs by Charles Farnum. A. Head. B. Lateral view. C. Dorsal view. D. Specimen labels and barcode.

CONCLUSIONS

Future prospects for research in this genus are rich, beginning with additional fieldwork and species exploration. Many regions in the western United States have not been systematically collected for *Amiota*, and more species are likely to be found in the mountains of Arizona and New Mexico. The potential of the Mexican highlands, where many new species occur, is completely open, and neotropical species are essentially unstudied. Western areas of Canada also need better surveying, with the possibility

that species—or new species closely related to them—are shared with the eastern Palaearctic. Even in the northeastern U.S. and southeastern Canada there are several very rare species, indicating that further sampling will produce important distributional records and perhaps several more species. GIS studies could help determine the relative roles of climate, vegetation, and altitude in *Amiota* distributions. Phylogenetic construction using sequence data can clarify many relationships, not just within *Amiota*, but among Steganinae genera broadly (O’Grady and DeSalle, 2018). Previous cladistic studies within

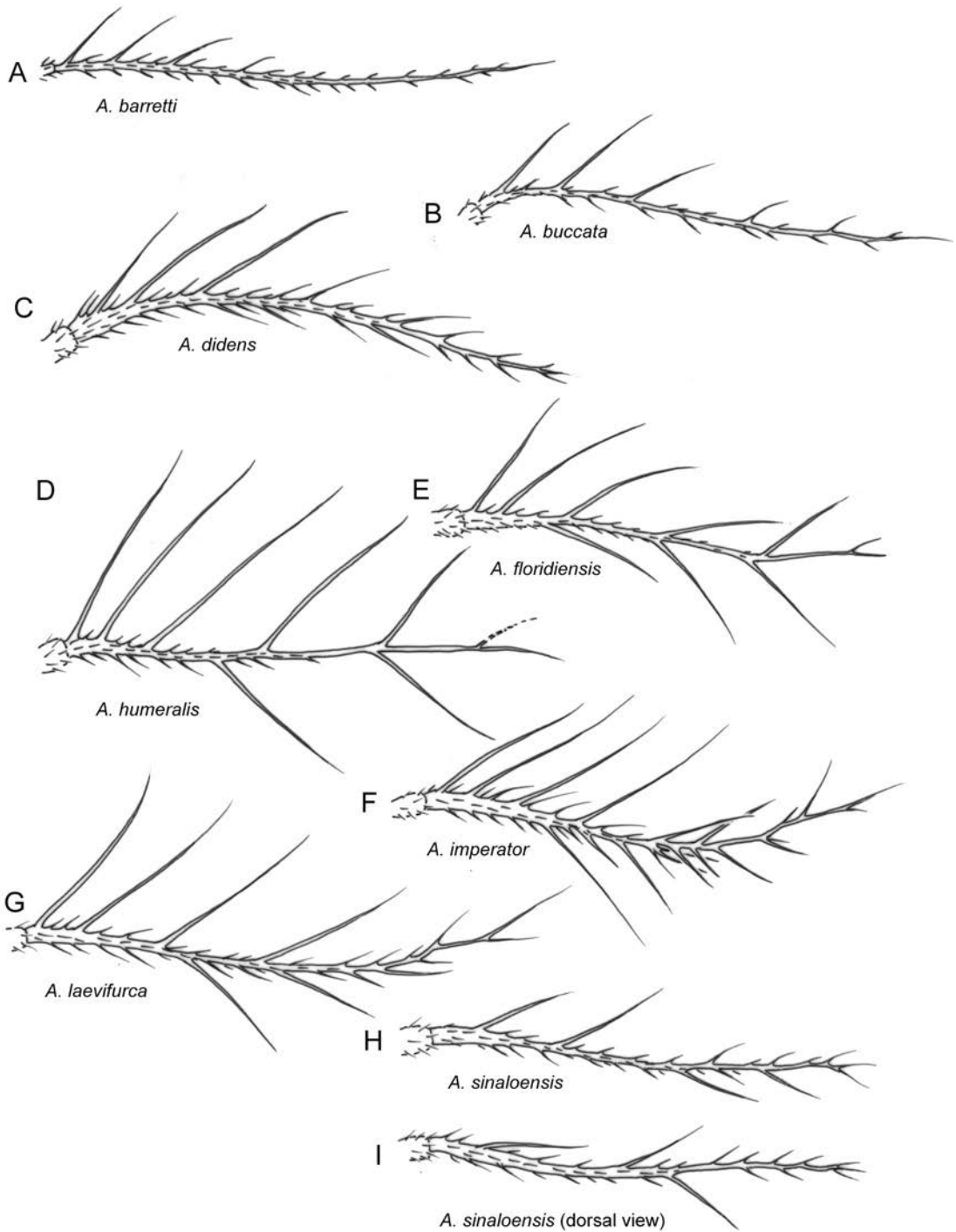


FIG. 72. Aristae, ungrouped species. A. *A. barretti* (Johnson). B. *A. buccata* Wheeler. C. *A. didens*. D. *A. humeralis* Loew. E. *A. floridiensis*. F. *A. imperator*. G. *A. laevifurca*. H–I. *A. sinaloensis*. Not to the same scale.

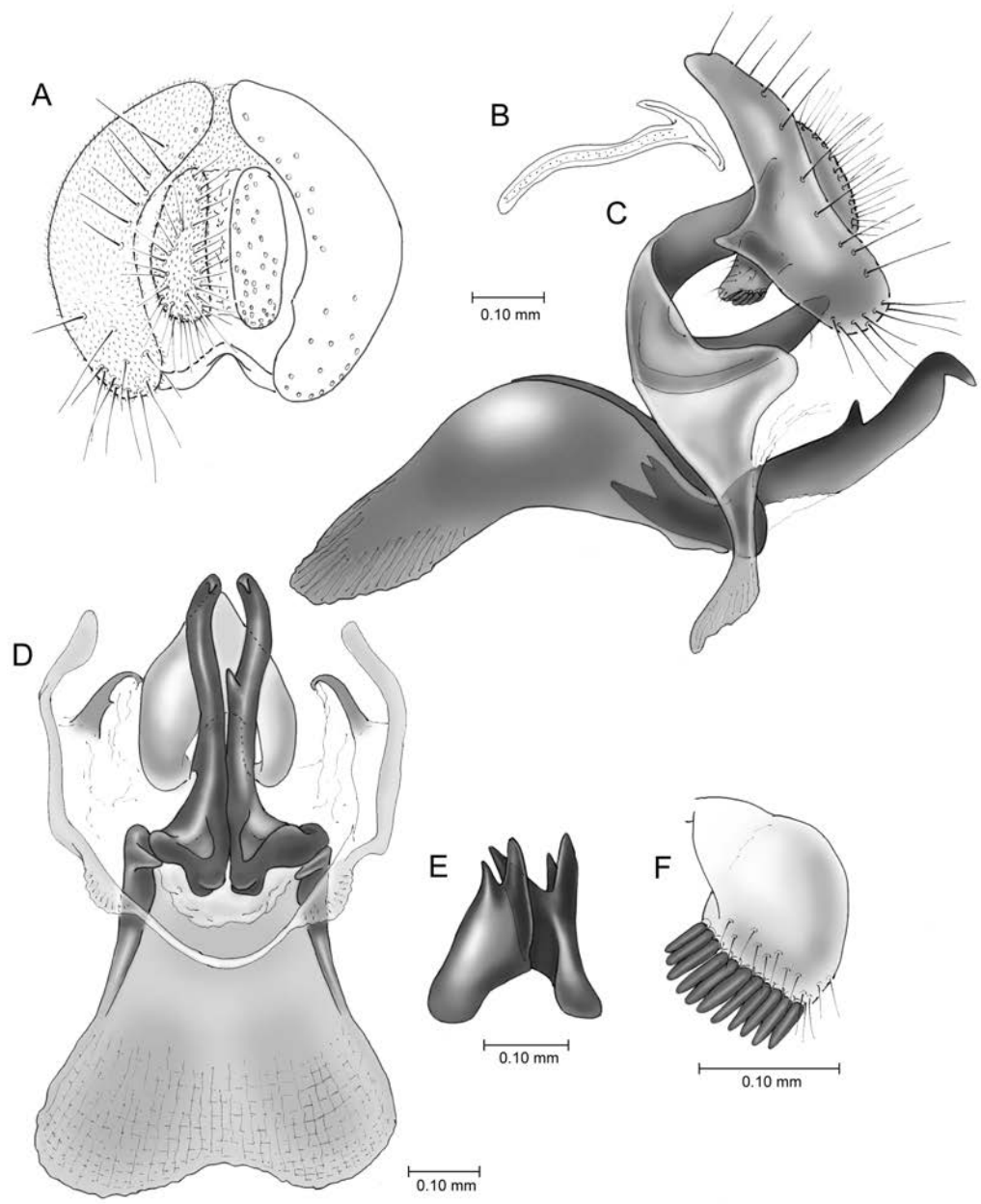


FIG. 73. Male terminalia, *A. barretti* (Johnson). **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Ventral view. **E.** Inner paraphyses. **F.** Surstylus. (Am 1423).

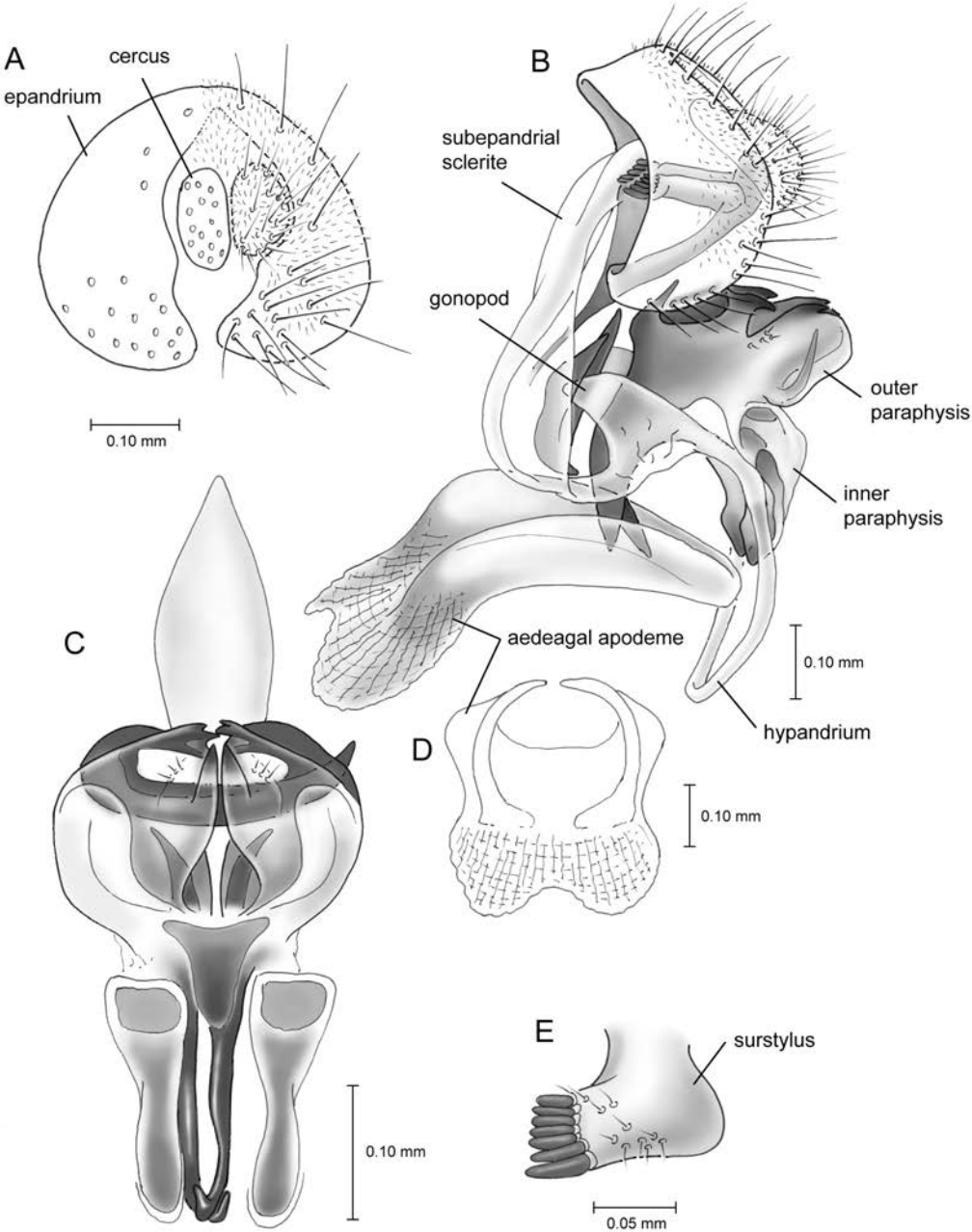


FIG. 74. Male terminalia, *A. buccata* Wheeler. A. Epandrium and cerci. B. Lateral view. C. Ventral view. D. Aedeagal apodeme. E. Surstylus. (Am 14, paratype).

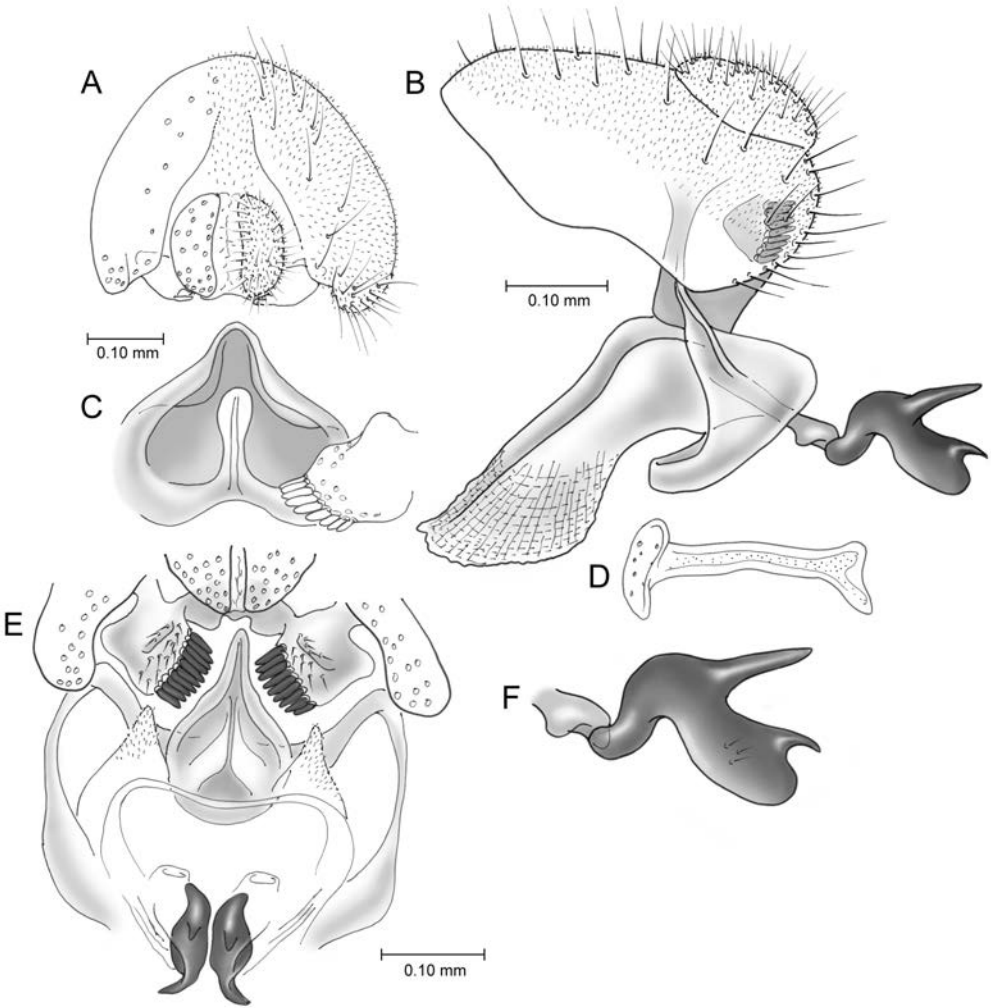


FIG. 75. Male terminalia, *A. didens*. **A**. Epandrium and cerci. **B**. Lateral view. **C**. Subepandrial sclerite and surstylus, ventral view. **D**. Ejaculatory apodeme. **E**. Posterior view. **F**. Outer paraphysis, lateral view. (Am 444, holotype).

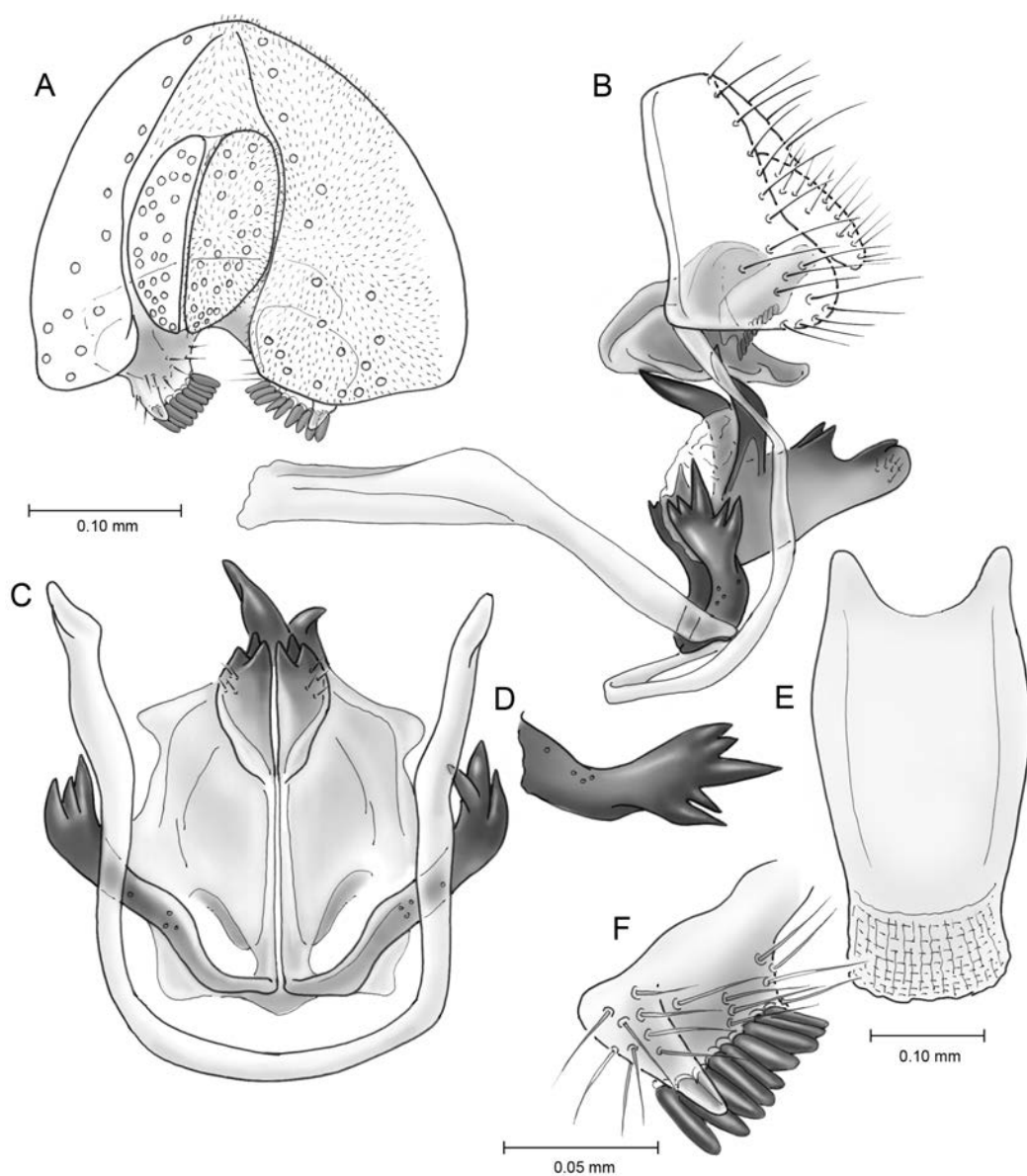


FIG. 76. Male terminalia, *A. floridiensis*. A. Epandrium and cerci. B. Lateral view. C. Ventral view of hypandrium, paraphyses, and subepandrial sclerite. D. Inner paraphysis. E. Aedeagal apodeme. F. Surstylus. (Am 174, holotype).

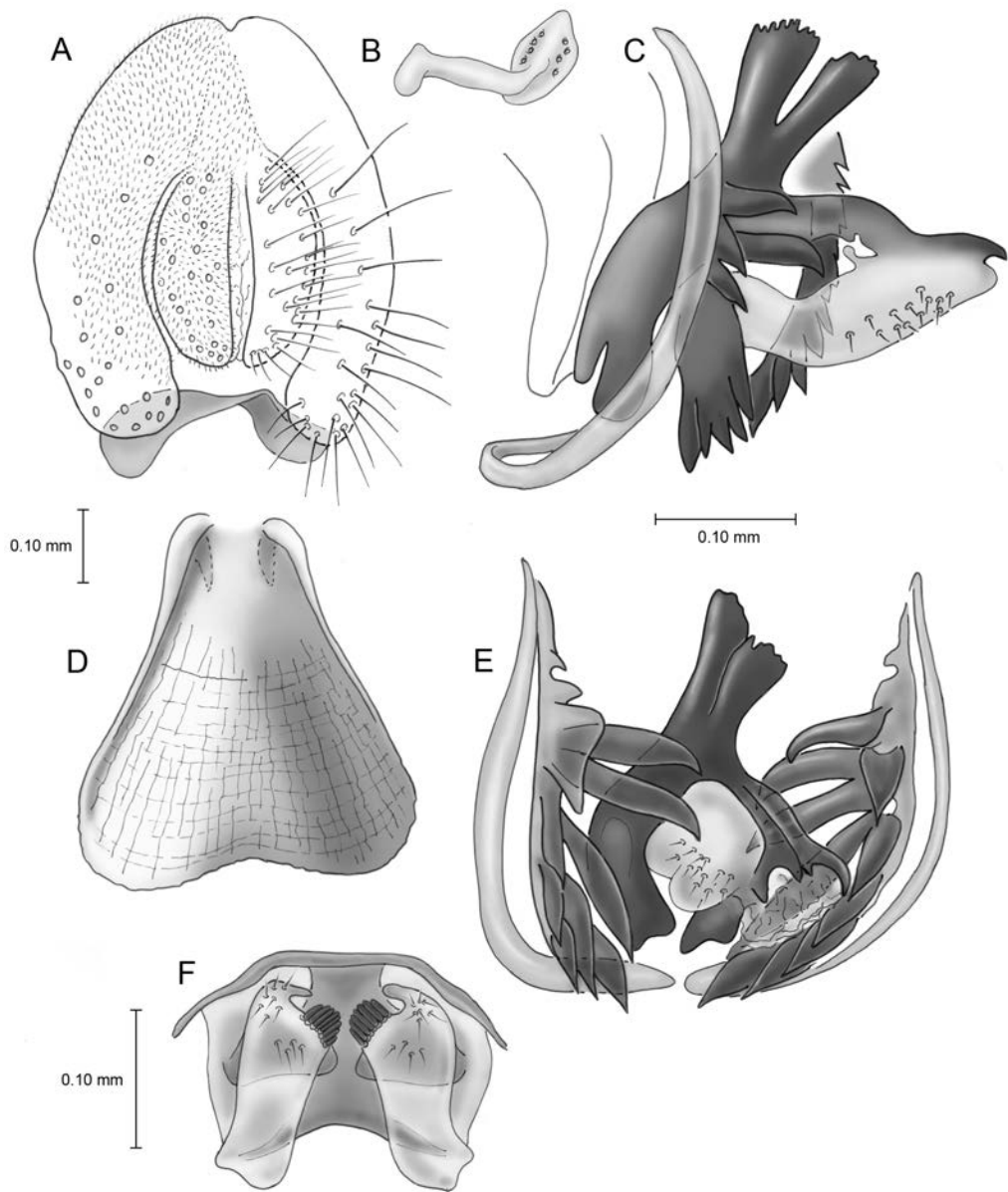


FIG. 77. Male terminalia, *A. humeralis* Loew. **A.** Epandrium and cerci. Subepandrial sclerite shaded. **B.** Ejaculatory apodeme. **C.** Lateral view of hypandrium and paraphyses. **D.** Aedeagal apodeme. **E.** Posterior view of hypandrium and paraphyses. **F.** Surstyli and subepandrial sclerite, inner view. (Am 324).

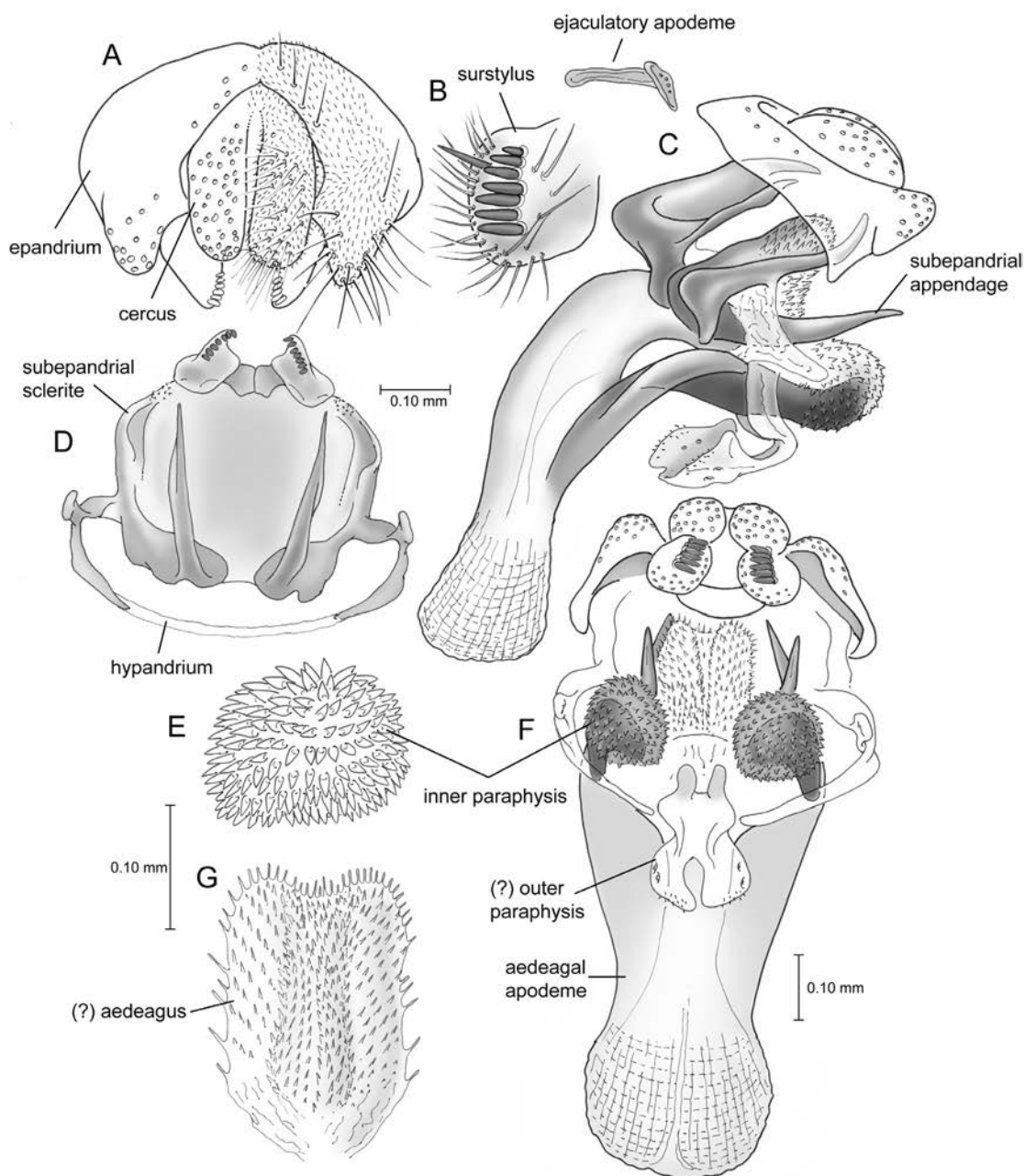


FIG. 78. Male terminalia, *A. imperator*. **A.** Epandrium and cerci. **B.** Surstylus. **C.** Lateral view, with ejaculatory apodeme. **D.** Surstyli, subepandrial sclerite, hypandrium, ventral view. **E.** Inner paraphysis and detail. **F.** Ventral view. **G.** (?) Aedeagus. (Am 315).

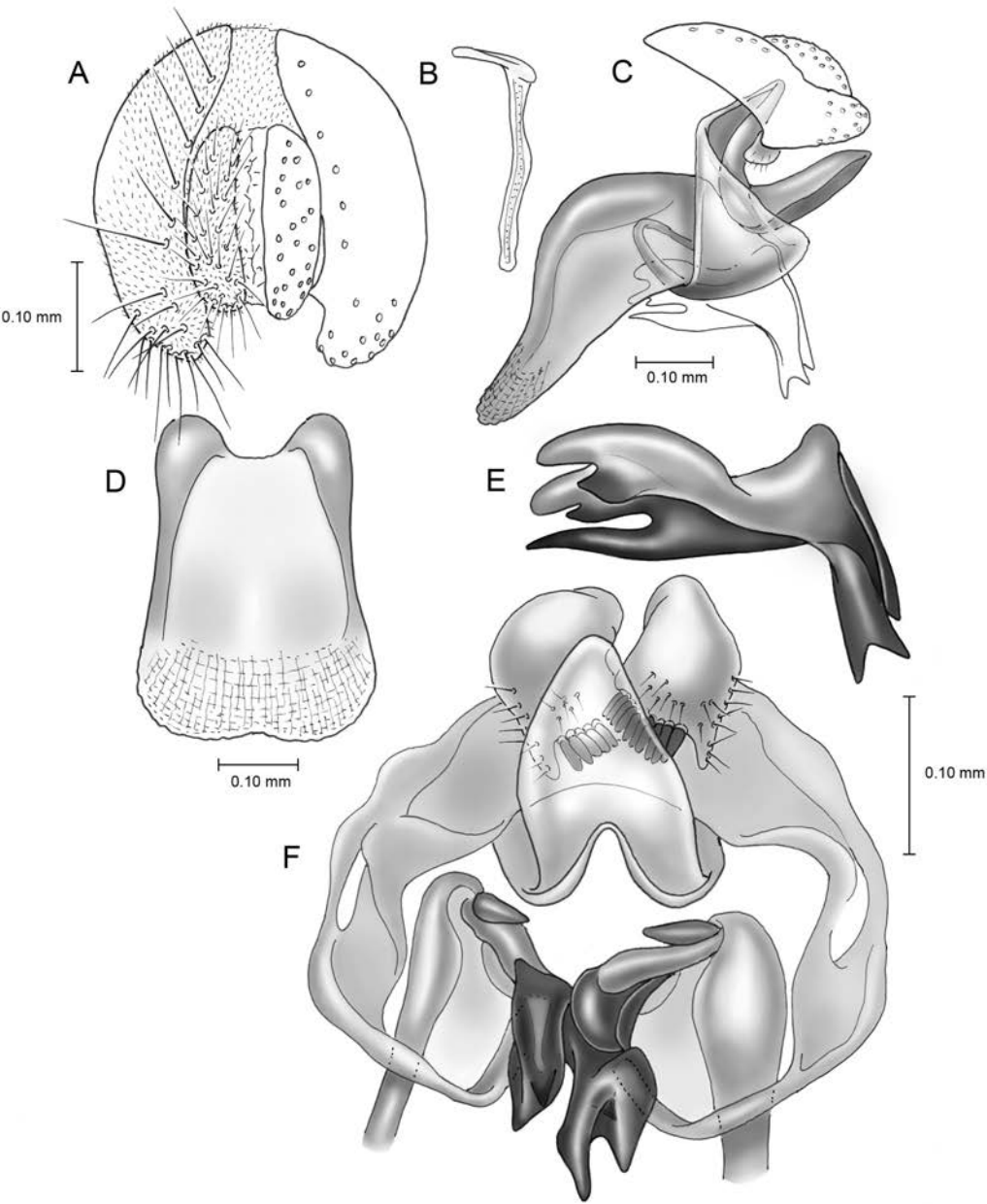


FIG. 79. Male terminalia, *A. laevifurca*. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Aedeagal apodeme. **E.** Paraphyses, lateral view. **F.** Ventral view. (Am 1416, holotype).

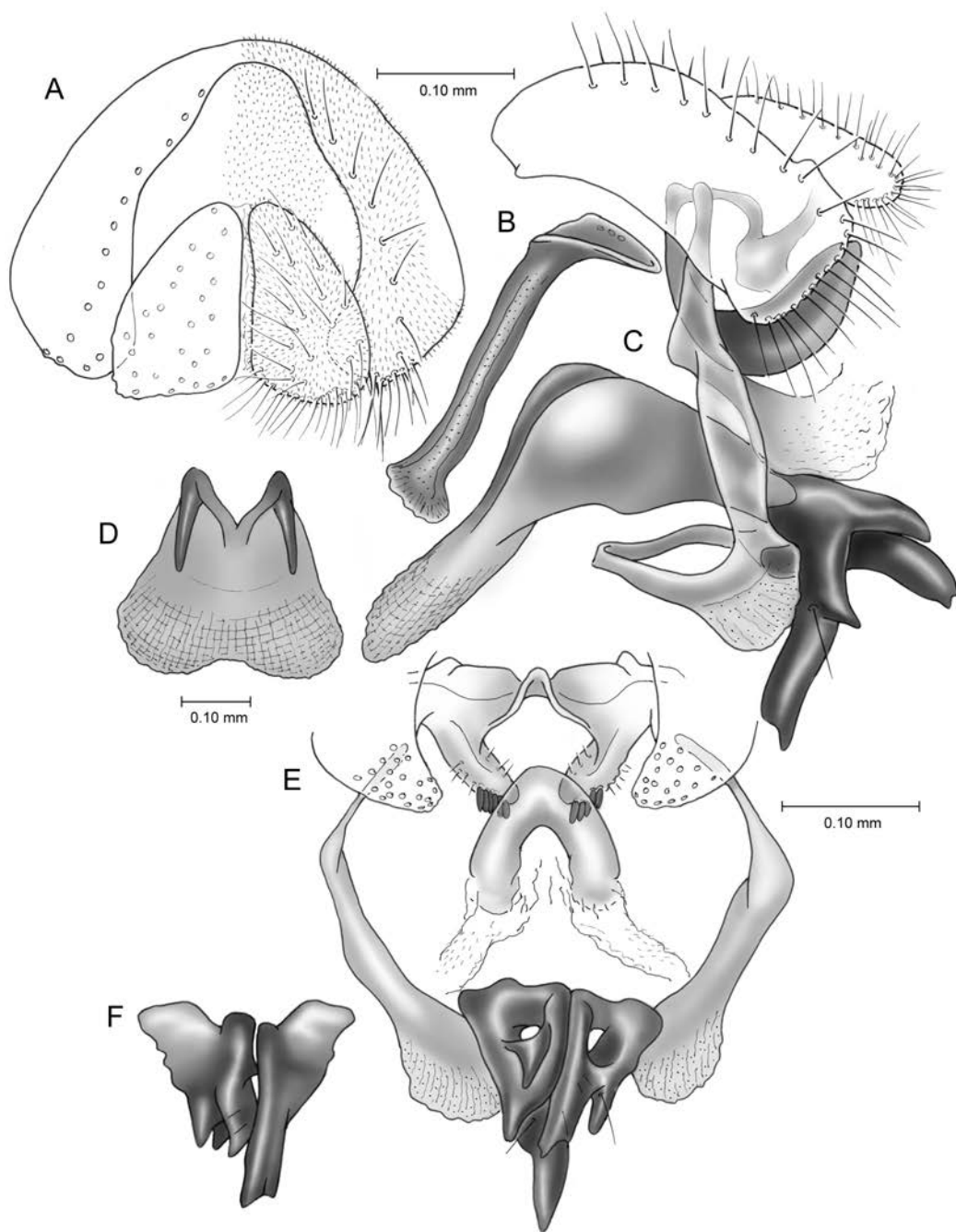


FIG. 80. Male terminalia, *A. sinaloensis*. **A.** Epandrium and cerci. **B.** Ejaculatory apodeme. **C.** Lateral view. **D.** Aedeagal apodeme. **E.** Ventral view, sursty, apex of subepandrial appendage, hypandrium, and paraphyses. **F.** Outer paraphyses, dorsal view. (Am 1419, holotype).

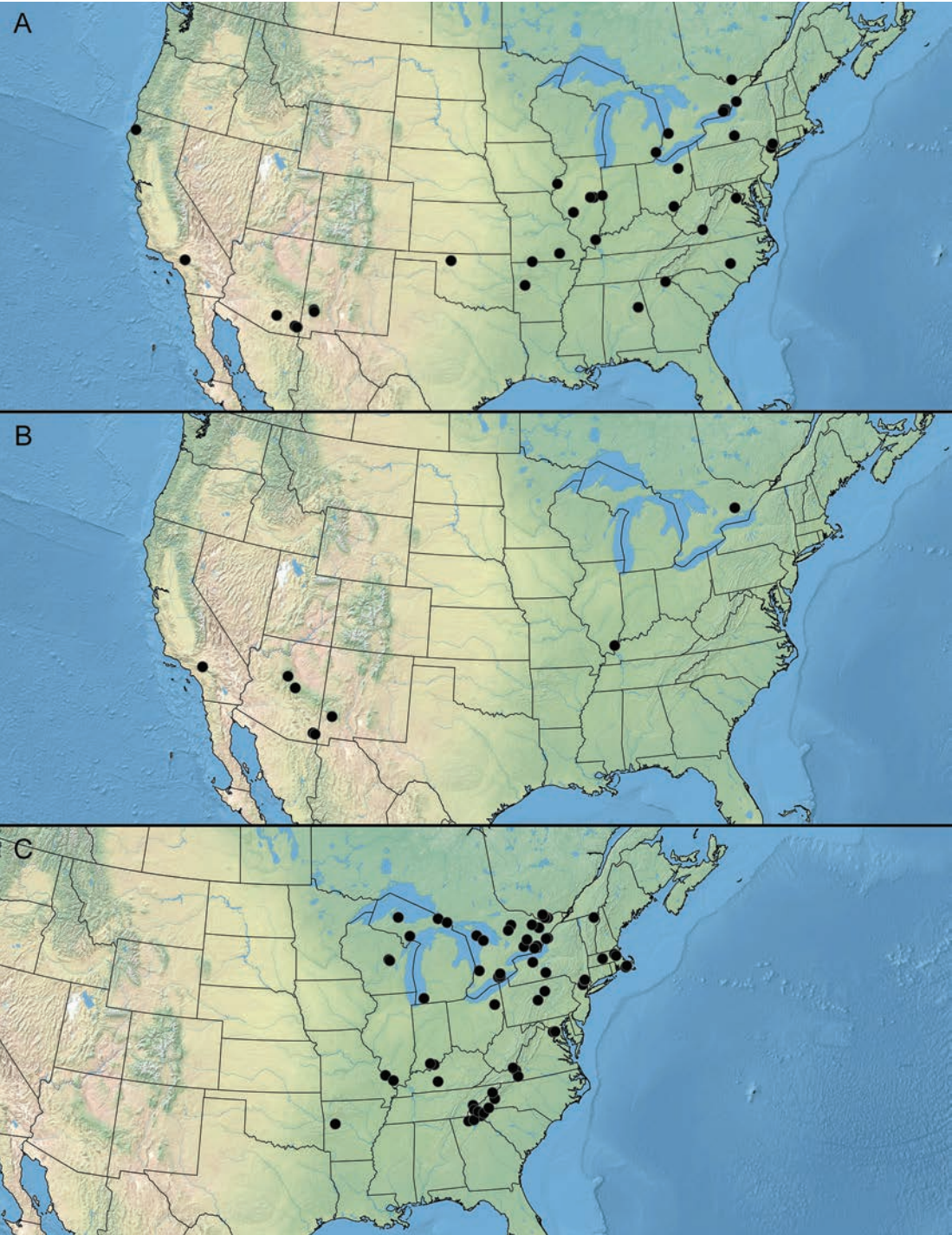


FIG. 81. Distribution maps, *A. hsui* species group. **A.** *A. hsui* Máca. **B.** *A. hyalou*. *A. alboguttata* species group. **C.** *A. communis* Chen and Steyskal.



FIG. 82. Distribution maps, *A. alboguttata* species group. A. *A. durangoensis*. B. *A. lineiventris* Máca. C. *A. steyskali* Máca.



FIG. 83. Distribution maps, *A. mariae* species group. A. *A. antitortum*. B. *A. brayi*. C. *A. cruciatum*.



FIG. 84. Distribution maps, *A. mariae* species group. A. *A. incurva*. B. *A. mariae* Máca. C. *A. texas*.

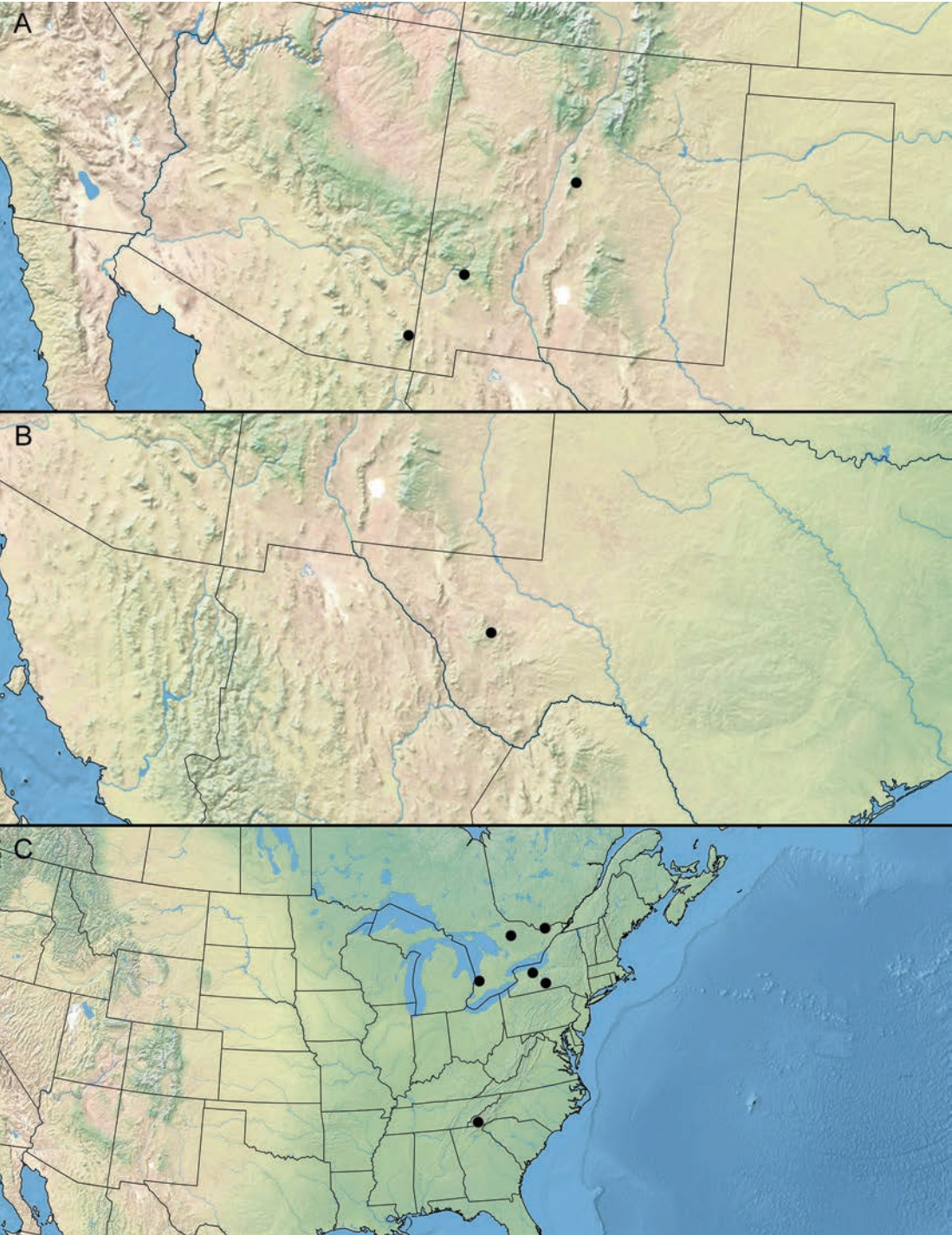


FIG. 85. Distribution maps, *A. mariae* species group. **A.** *A. tormentum*. **B.** *A. wheeleri*. **C.** *A. zaliskoi*.

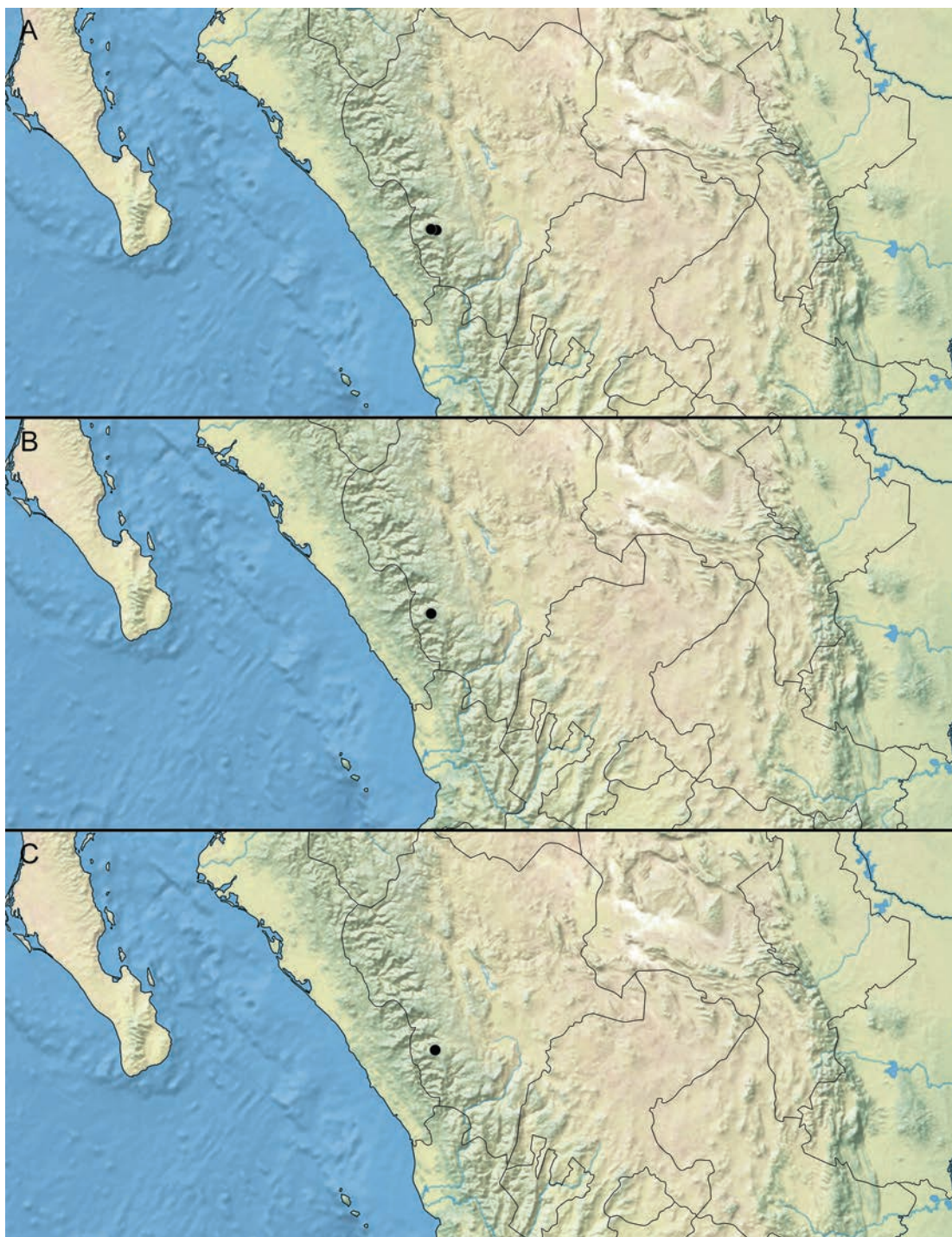


FIG. 86. Distribution maps, *A. cervites* species group. **A.** *A. cervites*. **B.** *A. elsaltoensis*. **C.** *A. multiplex*.

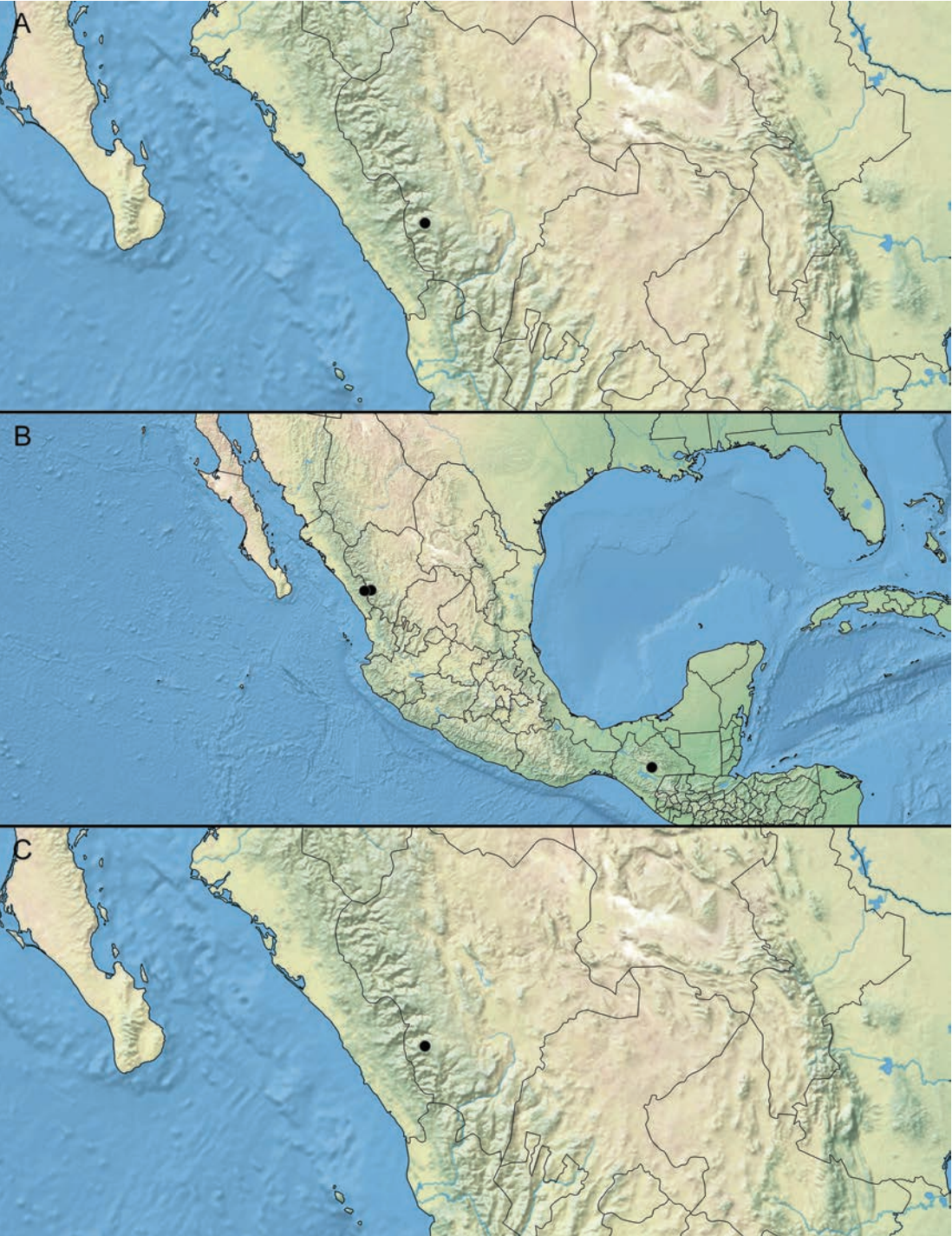


FIG. 87. Distribution maps, *A. avipes* species group. A. *A. avipes*. B. *A. biacuminis*. C. *A. forceps*.



FIG. 88. Distribution maps, *A. avipes* species group. A. *A. minor* (Malloch). B. *A. onyx*. C. *A. pseudominor*.



FIG. 89. Distribution maps, *A. avipes* species group. **A.** *A. uniacuminis*. *A. rufescens* species group. **B.** *A. leucostoma* Loew. **C.** *A. mcalpinei*.

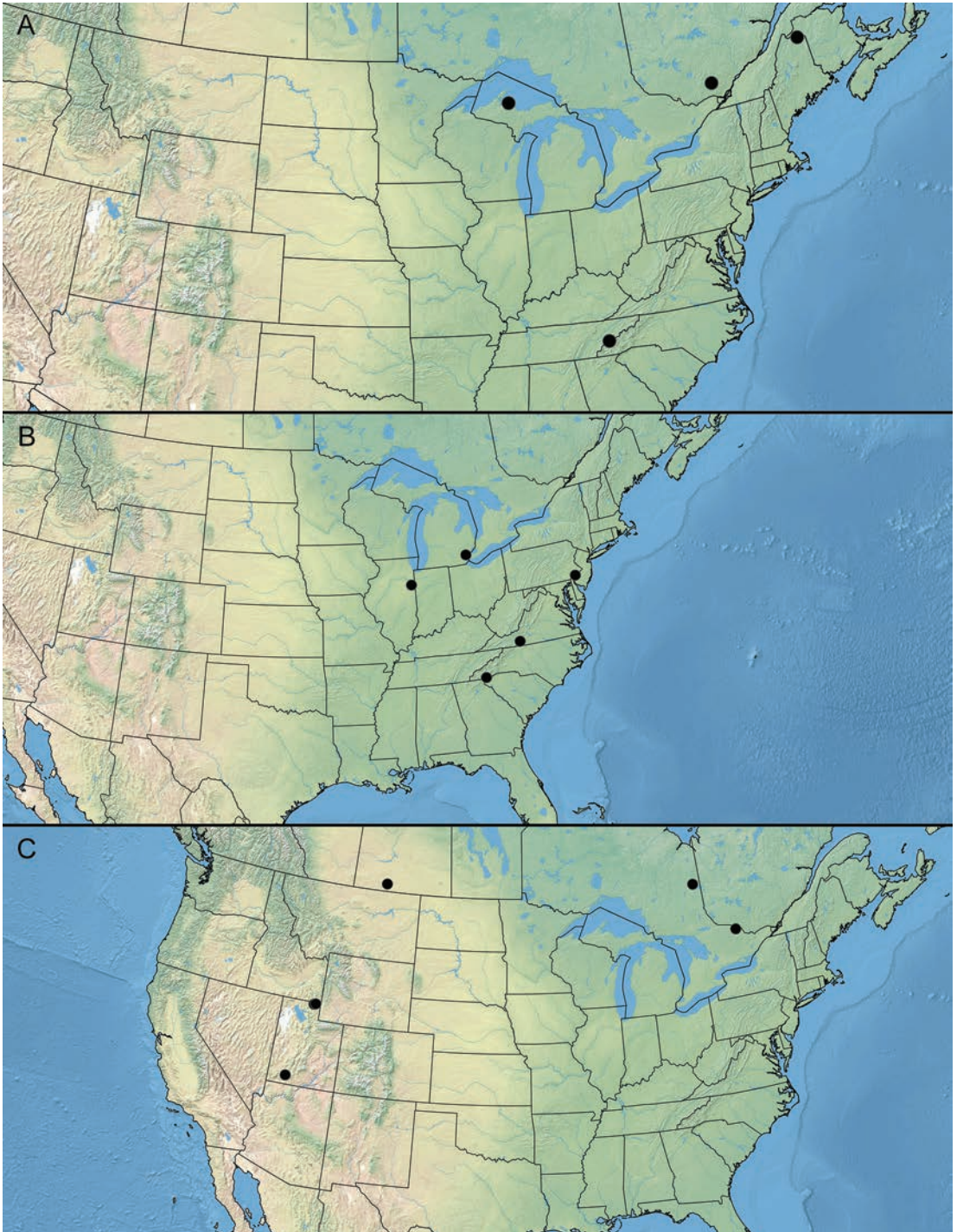


FIG. 90. Distribution maps, *A. rufescens* species group. A. *A. tessae*. *A. subtusradiata* species group. B. *A. byersi*. C. *A. tibialis*.

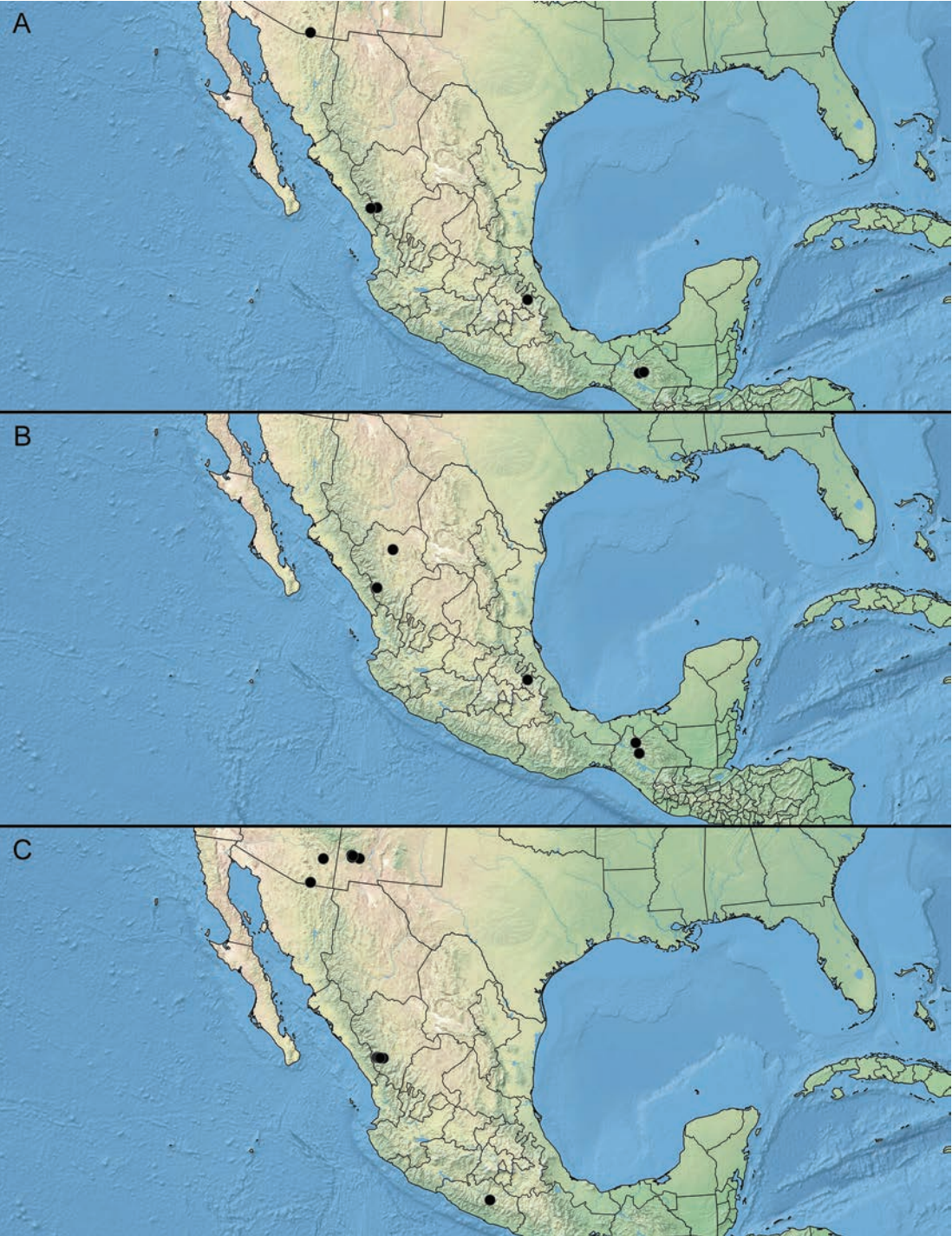


FIG. 91. Distribution maps, *A. nebojsa* species group. A. *A. amputata*. B. *A. latilabrum*. C. *A. nebojsa* Máca.



FIG. 92. Distribution maps, *A. nebojsa* species group. **A.** *A. occidentalis*. **B.** *A. oviraptor*. **C.** *A. subnebojsa*.



FIG. 93. Distribution maps, *A. nigrescens* species group. A. *A. fulvitibia*. B. *A. nanonigrescens*. C. *A. nigrescens* Wheeler.

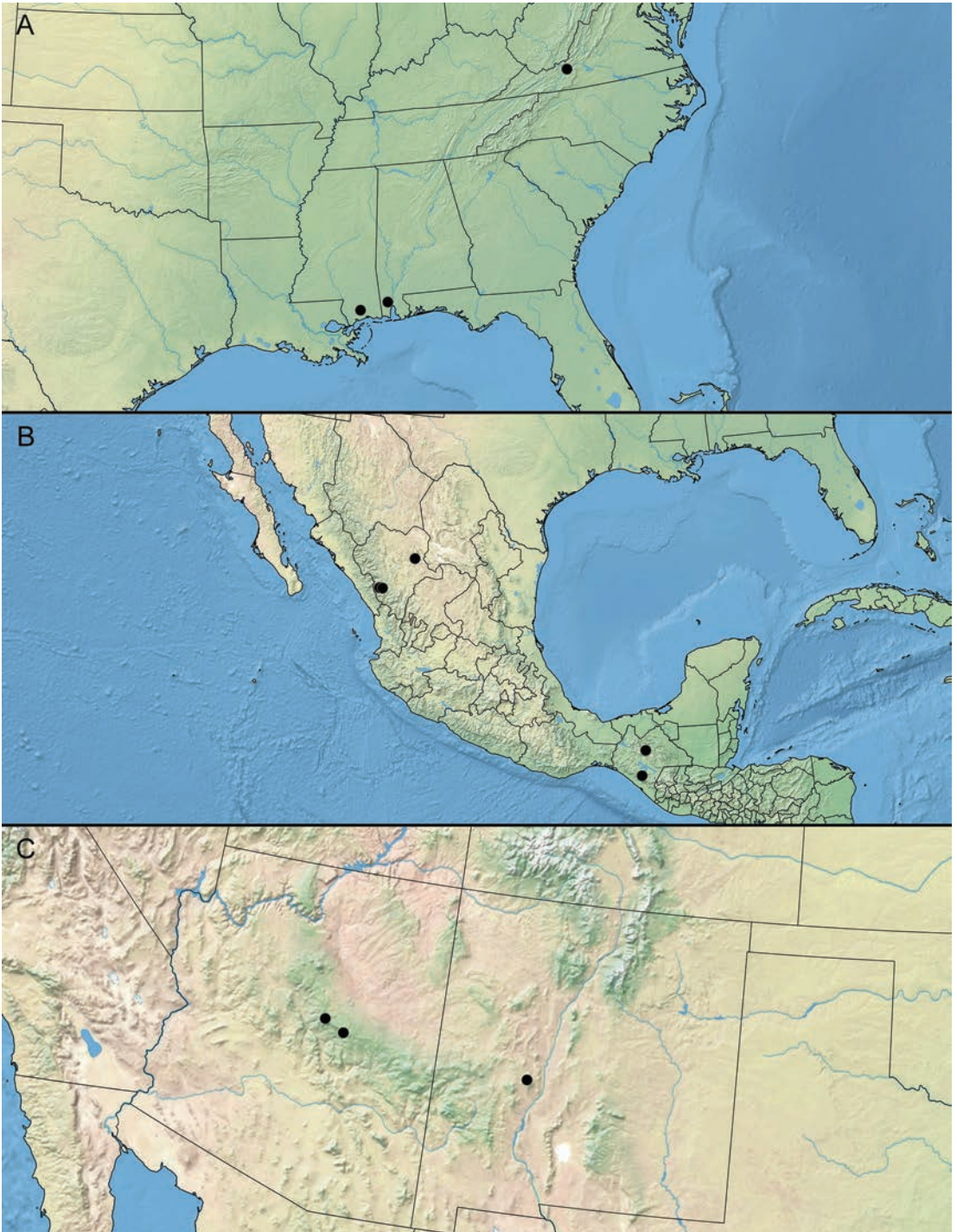


FIG. 94. Distribution maps, *A. nagatai* species group. **A.** *A. raripennis*. Ungrouped species. **B.** *A. barretti* (Johnson). **C.** *A. buccata* Wheeler.



FIG. 95. Distribution maps, Ungrouped species. A. *A. didens*. B. *A. floridensis*. C. *A. humeralis* Loew.

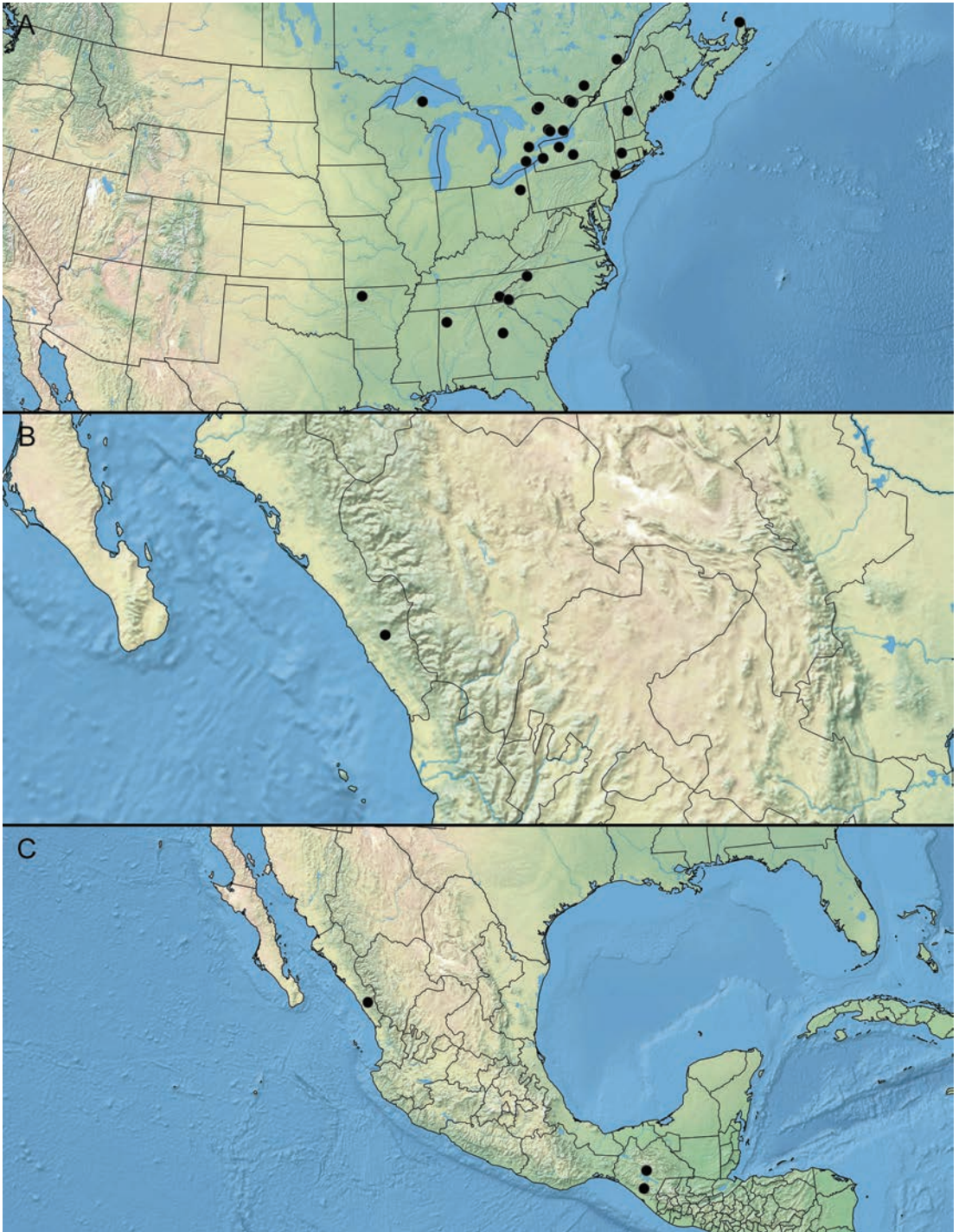


FIG. 96. Distribution maps, Ungrouped species. A. *A. imperator*. B. *A. laevifurca*. C. *A. sinaloensis*.

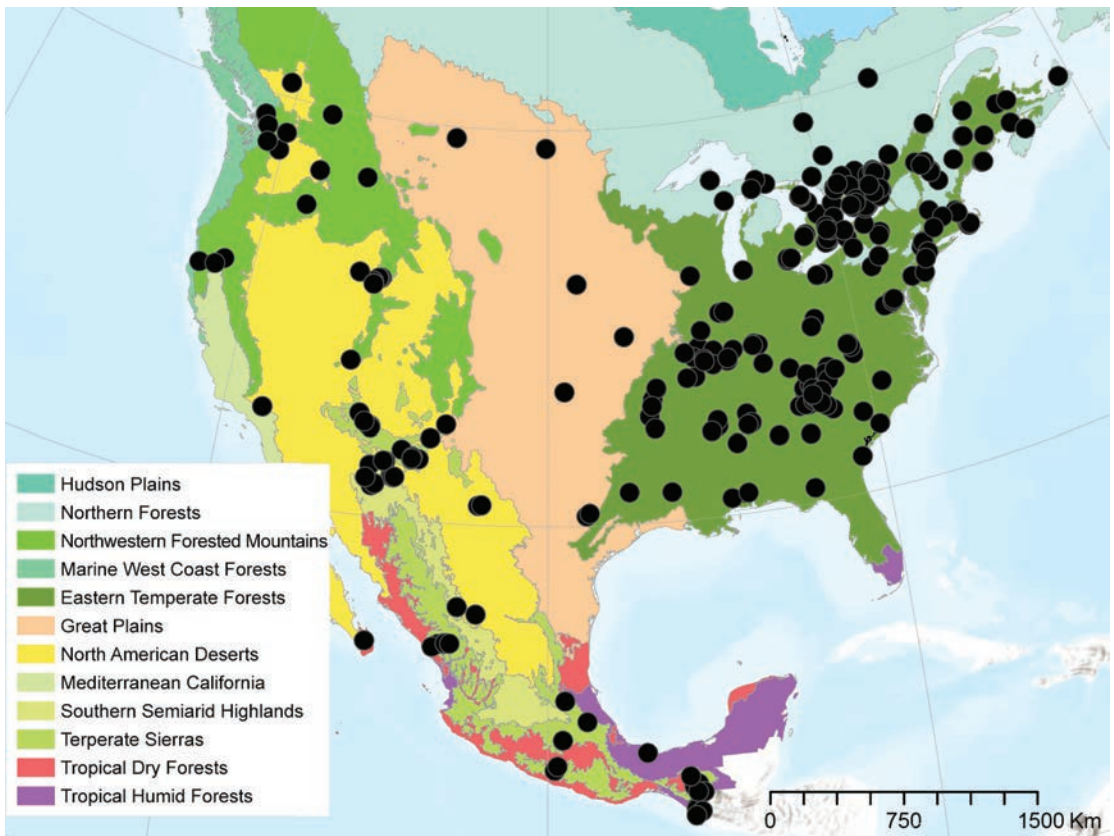


FIG. 97. Ecoregions map of North America. Based on the map of the Commission for Environmental Cooperation (CEC, 1997). Points represent specimens of *Amiota* used in this study

the genus have been almost exclusively carried out on Chinese species with morphology (Chen and Toda, 2001) or only one to two gene regions (He et al., 2009; Otranto et al., 2008; Shao et al., 2014; Wang et al., 2020; Zhao et al., 2013). Molecular phylogenetics will help to interpret patterns of species distribution and endemism.

Biology, particularly reproduction, remains perhaps the most intriguing aspect of *Amiota*; addressing this topic would probably require some methods of captive breeding of the flies. For example: Are the white spots used for general signaling? If so, then why aren't they species specific in size and location on the body? Is there much courtship? How do *Amiota* transfer sperm without an obvious aedeagus or do the elaborate paraphyses function somehow in

compensation? In species where a subepandrial appendage is highly developed the paraphyses are less elaborate—does this correlate with their respective functions? What is the purpose of the saclike sternite 6 in male *Amiota*? The musculature of male genitalia will probably be an important first step in addressing those questions. Also, if males are seeking sodium from eye secretions and perspiration, why not the females? Are males transferring the sodium to females during copulation? (Does the sternite 6 sac function in this regard?). Lastly, how are chiral variants in paraphyses explained? This is an extremely unusual phenomenon, which some COI data (Gong et al., 2018; Toda et al., 2020) and all the morphological evidence indicate is intraspecific variation. What is the devel-

opmental basis for this? Why is it confined to the *mariae* species group?

Basic taxonomic work usually always precedes all other studies that eventually come along, and it is hoped more and exciting opportunities will arise in the research on this fascinating genus of fruit flies.

#### ACKNOWLEDGMENTS

Both authors have numerous people to thank for their critical assistance with this project. At the AMNH: Steve Davis helped organize and plan laboratory work. A large part of this study would not have gone as smoothly without him. His friendship is appreciated, as well as the untold number of annoying questions, favors, and conversations (scientific and not) asked of him by L.E.J. Other AMNH colleagues include Courtney Richenbacher and Suzanne Rab Green, who fielded too many requests and questions to remember. Mary Knight offered nomenclatural assistance on all things Latin and Greek. Charlotte Holden, illustrator extraordinaire, rendered the shading for the genitalic plates from D.A.G.'s pencil sketches and line drawings. Lee Herman offered advice to L.E.J. on the nitty gritty of nomenclature and procedural taxonomy.

Lance's brother, Jessten Hughes, accompanied him on two large collecting trips. In total, 15 states were visited with him in this study from California to Mississippi. Over approximately 7000 miles of driving, Jesse managed to collect nearly five species, one new to science. Christian Liriano accompanied a trip in upstate New York. KeyLyn Song accompanied several trips around Florida. Lin Li accompanied many trips around the New York Botanical Garden. Kitty Sopow accompanied trips in southern Illinois.

Ryan Mannion generously laid out, labeled, and sized all the figures in this study. In addition, he accompanied Lance on a trip to Maine and New Hampshire. He also looked over parts of the manuscript. His kind attitude for the

intense nature over the past five years of this project is appreciated.

Amy Berkov (City College of New York-CUNY) is thanked for her help over the last five years. Amy served on the master's committee of the first author when this study was a thesis topic. Her patience, guidance, and encouragement pushed this study along in many ways. She imparted a love of urban and suburban biodiversity to a student who originally thought natural areas were the only places worthy of study. Amy's insight was prescient: insect taxonomy projects always end up becoming larger than one anticipates.

Staff at the AMNH Southwest Research Station (Michele Lanan), Black Rock Forest Consortium (William Schuster), and the New York Botanical Garden (Jessica Arcate-Schuler) are thanked for assistance and permissions for L.E.J. to conduct fieldwork. The American Museum of Natural History is greatly appreciated for their financial assistance of fieldwork through generous funding by a Theodore Roosevelt Memorial Fund Grant to L.E.J. The Williston Diptera Fund at the Smithsonian Museum of Natural History provided funds for L.E.J. to attend Fly School in California in 2017, where more collections of *Amiota* were made.

Countless collectors and their specimens form the foundation for this study, among them Marshall R. Wheeler, William B. Heed, Stephen Marshall, James F. McAlpine, and Donald M. Wood. Marshall R. Wheeler deserves special appreciation. His collections throughout the United States formed a significant proportion of all museum collections consulted for this study. Combined with his papers, his contributions to this study are huge—and would have been woefully incomplete without them. When the late George Steyskal learned of D.A.G.'s study on drosophilids, beginning 40 years ago, he offered up all his notes and drawings. Thomas Werner and John Jaenike graciously donated valuable series of specimens for study. The Museum of Comparative Zoology at Harvard (MCZC) provided photographs of Loew's type specimens and permitted their use in this text.

Numerous individuals contributed over the past five years through conversation and advice to L.E.J., among them: Kate Armstrong, Amy Berkov, Brian Brown, Steve Davis, Andrew Henderson, Lee Herman, John Jaenike, Sarah Kornbluth, Lin Li, Ronniel Pedales, Jeff Skevington, Neil Snow, Dennis Stevenson, Barbara Thiers, Thomas Werner, and Doug Yanega.

Thanks go to the many staff at institutions who loaned material: California Academy of Sciences (the late Paul Arnaud), Canadian National Collection (Bradley Sinclair), Illinois Natural History Survey (Tommy McElrath), L.A. County Museum of Natural History (the late Charlie Hogue), University of Guelph (Steve Marshall), University of Kansas (the late George Byers), Utah State University (Wil Hanson), Washington State University (Bill Turner).

For D.A.G., this was a work decades in waiting.

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