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Overview of the lady beetle tribe Diomini (Coleoptera: Coccinellidae) and description of a new phytophagous, silk-spinning genus from Costa Rica that induces food bodies on leaves of *Piper* (Piperaceae)

NATALIA J. VANDENBERG[1,3] & PAUL E. HANSON[2]

[1]*c/o Department of Entomology, Smithsonian National Museum of Natural History, P.O. Box 37012, MRC-168, Washington, DC, USA. E-mail: VandenbergN@si.edu or Natalia.Vandenberg@ars.usda.gov*
[2]*Escuela de Biologia, Universidad de Costa Rica, San Pedro, San Jose, Costa Rica. E-mail: phanson91@gmail.com*
[3]*Corresponding author*

Abstract

A new genus of lady beetle, *Moiradiomus* **gen. nov.** (Coleoptera: Coccinellidae Latreille, 1807: Diomini Gordon, 1999), and four new species are described from Costa Rica, representing the first known occurrences of obligate phytophagous lady beetle species outside of the tribe Epilachnini Mulsant, 1846 (sens. Ślipiński 2007). The new species are described, illustrated and keyed, and their life histories discussed. Each species of *Moiradiomus* occurs on a separate species of *Piper* L., 1753 (Piperaceae Giseke, 1792), where the larva constructs a small silken tent between leaf veins and inside this shelter induces the production of food bodies, which are its exclusive source of food. Background information is provided on lady beetle trophic relations and other insect/*Piper* symbioses. The taxonomic history of *Diomus* Mulsant, 1850 and related species in the tribe Diomini is reviewed and existing errors in observation, interpretation, identification, and classification are corrected in order to provide a more meaningful context for understanding the new genus. The tribe Diomini is rediagnosed and recircumscribed to include *Diomus*, *Decadiomus* Chapin, 1933, *Heterodiomus* Brèthes, 1925, *Dichaina* Weise, 1923, *Andrzej* Ślipiński, 2007, and *Moiradiomus*. *Magnodiomus* Gordon, 1999 and *Erratodiomus* Gordon, 1999 are removed from Diomini and transferred to Hyperaspidini Costa, 1849, subtribe Selvadiina Gordon, 1985 stat. nov. *Mimoscymnus* Gordon, 1994 and *Planorbata* Gordon, 1994, originally described in Coccidulini Mulsant, 1846 are also transfered to Hyperaspidini and placed in Mimoscymnina subtribe nov. (type genus *Mimoscymnus*). The main morphological characters distinguishing Diomini and Hyperaspidini are described and illustrated. A key to genera of Diomini sensu novo is provided. The identification of the Australian *Diomus* species illustrated in Gordon's publication on North American lady beetles is corrected from *D. pumilio* Weise, 1885 to *D. tenebricosus* (Boheman, 1859), however specimens recently collected in California do not match these genitalic illustrations and are identified as true *D. pumilio*. The following species of *Diomus* are transferred to *Decadiomus* as new combinations: *D. balteatus* (LeConte, 1878), *D. floridanus* (Mulsant, 1850), *D. amabilis* (LeConte, 1852), *D. liebecki* (Horn, 1895), *D. myrmidon* (Mulsant, 1850), *D. humilis* (Gordon, 1976), *D. pseudotaedatus* (Gordon, 1976), *D. taedatus* (Fall, 1901), *D. bigemmeus* (Horn, 1895), and *D. austrinus* (Gordon, 1976). *Decadiomus seini* Segarra, 2014 is placed as a junior synonym of *D. austrinus*. The following new species of *Moiradiomus* are described: *M. clotho* **sp. nov.**, *M. lachesis* **sp. nov.**, *M. atopos* **sp. nov.**, *M. nanita* **sp. nov.**

Key words: ants, black pepper plants, ladybug, ladybird, *Diomus*, *Decadiomus*, *Heterodiomus*, *Dichaina*, *Andrzej*, *Magnodiomus*, *Erratodiomus*, Hyperaspidini, *Selvadius*, *Mimoscymnus*, *Planorbata*

Introduction

Four new species of the lady beetle family Coccinellidae Latreille, 1807 were discovered during field studies in Costa Rica. The beetles were reared from silken enclosures constructed by the larvae between leaf veins on the undersides of the leaves of pepper plants (Piperaceae Giseke, 1792: *Piper* L., 1753) and the beetles appear to correspond to the "tent beetles" documented by previous authors (Gastreich & Gentry 2004). In the present work, we discuss the interesting phytophagous habits of these lady beetles and the silk-spinning abilities of their larvae.

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This is the second example of an obligate phytophagous clade within the lady beetle family Coccinellidae. A brief overview of lady beetle food preferences are provided along with a summary of the known symbiotic relationships between *Piper* and various other insect species. The new species are described and placed in a new genus in the tribe Diomini Gordon, 1999. The morphology, anatomy, and classification of the Diomini are reviewed and a number of errors (in observation, interpretation, identification, and classification) are corrected in order to provide a more meaningful context for understanding the new genus. Keys to the genera of Diomini and species of the new genus are provided.

Material and methods

The following acronyms are used in the text to indicate specimen depositories and institutional affiliations:

USNM	United States National Entomological Collection, U.S. National Museum of Natural History, Washington, D.C., USA
MZUCR	Museo de Zoología, Universidad de Costa Rica, San Pedro, San José, Costa Rica

Dissections were performed with the aid of a stereomicroscope and standard dissection tools (forceps, scalpel, needle). Whole specimens were card or point mounted on insect pins after being removed from alcohol and soaked overnight in ethyl acetate to prevent the bodies from shriveling and the setae from matting upon drying. When a suitable series of specimens was available, one or more exemplars were disarticulated to allow individual structures (e.g. mouthparts, antennae, genitalia) to be slide mounted for closer examination. Structures were first soaked in a 10% solution of KOH to dissolve excess tissue and partially clear opaque areas. Temporary slide mounts were prepared in glycerin or KY Glycerin Lubricating Jelly. After examination, the structures were placed in a genitalia vial mounted on an insect pin for permanent storage. Additional genitalia dissections were prepared by removing the abdomen from specimens softened in water, then re-drying the main body and clearing the abdomen only. Digital illustrations were created in Adobe Photoshop CS2 based on reference digital photographs and camera lucida sketches made with a drawing tube attached to a Zeiss Discovery V8 stereo microscope or Zeiss compound microscope. Digital photographs were captured with a BK Imaging System using Infinity Optics (K2) and a Canon 40D Digital SLR camera (Visionary Digital). The Canon RAW files were processed in Photoshop Lightroom 1.2 (Adobe Systems Inc.) and exported as lossless TIF files (300 dpi, 8-bit). Digital photographs were taken at multiple focal planes and combined (montaged) with the software application Helicon Focus Pro (Helicon Soft Ltd.). Habitus illustrations representing particular specimens have been idealized, posed, and "repaired," with the elytra shown in a symmetrical and locked position even if the specimen had the elytra open, or was based in part on disarticulated structures. Morphological and anatomical terminology used in the descriptions follows Vandenberg (2002) or Ślipiński (2007) with cross-referencing when appropriate. Measurements were made using an ocular micrometer attached to a dissecting microscope for dissected structures, or a hand held micrometer for whole body measurements.

Taxon sampling: Nearly 6,000 USNM specimens from around the World were examined in order to verify morphological and anatomical character states of the genera of Diomini (sens. nov.). The USNM holdings are especially rich in North, Central, South American, and West Indian specimens, with limited material from Africa, Australia, Egypt, Europe, and Asia. All Diomini genera are represented therein except for the two monotypic Australian genera, *Andrzej* Ślipiński, 2007 and *Dichaina* Weise, 1923, which fortunately are well documented photographically in Ślipiński (2007). Exemplars of USNM material belonging to *Bulaea* Mulsant, 1850 (Coccinellini Latreille, 1807, sens. Escalona *et al.* 2017) and the following genera of Hyperaspidini Costa, 1849 (sens. nov.) were also examined: *Hyperaspis* Redtenbacher, 1844; *Tenuisvalvae Duverger, 1989; Hyperaspidius* Crotch, 1873; *Blaisdelliana* Gordon, 1970; *Thalassa* Mulsant, 1850; *Helesius*, Casey, 1899; *Diazonema* Weise, 1926; *Brachiacantha,* Dejean 1837; *Dilatitibialis Duverger*, 2001; *Tiphysa Mulsant*, 1850; *Serratitibia Gordon & Canepari*, 2013; *Cleothera Mulsant*, 1850; *Cyrea* Gordon & Canepari, 2013; *Mimoscymnus* Gordon, 1994; *Planorbata Gordon*, 1994; *Selvadius Casey, 1899*; *Erratodiomus* Gordon, 1999; *Magnodiomus Gordon, 1999*.

Background information

Coccinellidae trophic relations. In most species of lady beetles (Coccinellidae) both larvae and adults are predatory, and the family has an illustrious history of use in biological control (Obrycki & Kring 1998). However, it is now generally recognized that most of these so-called predators feed facultatively on honeydew, pollen, nectar and fungi, and many species regularly ingest small amounts of plant tissue even in the presence of abundant prey (Hodek & Honek 1996; Moser *et al*. 2008; Giorgi *et al*. 2009).

Modern molecular studies have proven an invaluable method for reconstructing the evolution of lady beetle feeding preferences (Giorgi *et al*. 2009; Magro *et al*. 2010; Seago *et al*. 2011; Escalona *et al*. 2017). These studies corroborate the monophyly of a single obligate phytophagous clade within Coccinellidae, corresponding to the tribe Epilachnini Mulsant, 1846 (sens. Ślipiński, 2007) (=subfamily Epilachninae sens. Sasaji, 1968). The complete transition to plant feeding in an otherwise predaceous family has been accompanied by elaborate modifications to the mandibular dentition of both larval and adult stages. Outside of the epilachnines, the genus *Bulaea*, placed by various authors in the tribe Bulaeini Savoiskaya, 1969, Tytthaspidini Savoiskaya, 1969, or a more broadly defined Coccinellini Latreille, 1807 (Escalona *et al.* 2017), is sometimes categorized as phytophagous (Kovář 1996; Hodek & Honek 1996; Iqbal *et al*. 2017). However, although the latter genus contains known plant pests, the species are predominantly pollinivorous, and some have been reported to consume aphids under laboratory conditions (Giorgi *et al*. 2009) or even in the field (Ali *et al*. 2014). In contrast to the epilachnine mandible (Fig. 21), that of *Bulaea* (Fig. 22) closely resembles the mandible of many entomophagous species (Fig. 24) except for the addition of numerous minute blunt teeth on the incisor edge. A similar dentition to that of *Bulaea* can be found in the related genus *Tytthaspis* Crotch, 1874, which has a mycophagous (mildew-feeding) or microphagous habit, while a second mycophagous lineage including *Psyllobora* Chevrolat in Dejean, 1837 and allies (traditionally segregated in a separate tribe Psylloborini Casey, 1899, or Halyziini Mulsant, 1846) have the additional serrations restricted to the ventral tooth of the bifid apex.

In the present work, we document the occurrence of a new phytophagous genus and four new species in the tribe Diomini. Until now, all species in this tribe were known to be predators, especially of mealybugs (Pseudococcidae Heymons, 1915), but also of other Coccoidea Handlirsch, 1903 (Coccidae Stephens, 1829; Diaspididae, Maskell, 1878; Monophlebidae Signoret, 1875; and Ortheziidae Green, 1896), aphids (Aphididae Latreille, 1802), whiteflies (Aleyrodidae Westwood, 1840) and even ant brood (Formicidae Latreille, 1809) (Gordon 1999; Segarra-Carmona & Otero 2014; Vantaux *et al*. 2010). The larvae of the four new species are restricted to certain species of *Piper* (Piperaceae) where they construct silken tents between leaf veins (Figs. 40–42) and within these shelters induce the production of food bodies. This behavior has been mentioned previously (Gastreich & Gentry 2004), but the coccinellid was not identified.

***Piper* food bodies and their insect associates.** Food bodies, also known as pearl bodies or pearl glands, are plant cells or tissues that provide a nutritional reward to arthropods that potentially protect the plant, for example ants, although non-beneficial arthropods can also utilize them (Paiva *et al*. 2009). Food bodies therefore have a function similar to that of extrafloral nectaries, but they have been less well studied. In a survey of 243 species of dicotyledonous plants in Panama, 44 (18%) had food bodies (Schupp & Feener 1991). Most, if not all, species of *Piper* (Piperaceae) are thought to produce food bodies, which are scattered across the undersides of leaves and on floral spikes (Tepe *et al*. 2007b). *Piper* food bodies are liquid-filled, translucent spheres that vary in size from 0.1 to 0.9 mm (Rickson & Risch 1984; Gastreich & Gentry 2004), and contain mostly lipids (41–48% dry mass) and proteins (17–24% dry mass) (Fischer *et al*. 2002).

The genus *Piper* (which includes the culinary spice, black pepper) is one of the most species-rich genera of flowering plants, comprising approximately 2,000 species worldwide, with the greatest diversity in the American tropics, followed by southern Asia (Quijano-Abril *et al.* 2006; Jaramillo *et al.* 2008). These shrubs, vines, and herbaceous plants often dominate the understory of tropical forests (Gentry 1990). Five Central American species of *Piper* are myrmecophytes, having a mutualistic relationship with *Pheidole bicornis* Forel, 1899 (Formicidae). The queen ant colonizes a young *Piper*, where she and her brood occupy the hollow petioles (sheathing leaf bases tightly folded into a tube; Tepe *et al.* 2007b). As the colony grows the workers gradually extend the nest site by excavating into the stem (Risch *et al.* 1977), which contains a specialized pith (Tepe *et al.* 2007a). The ants induce the production of food bodies on the inner surface of the hollow petiole and if *P. bicornis* are excluded from the *Piper* petiole, food body production is reduced to very small numbers (Risch & Rickson 1981). Other ant species are rarely encountered in the petiole chamber, but when present, they do not induce food body production

(Letourneau 1991). *Pheidole bicornis* has never been found anywhere else except on these five species of *Piper*; the ant obtains a nest site and a food source, while the plant benefits through reduced herbivory and fungal infection (Risch 1982; Letourneau 1983, 1998).

Two groups of beetles are also capable of inducing the production of food bodies on *Piper*, but they are not known to have a mutualistic relationship with the plant. Larvae of one or more undescribed species of Cleridae Latreille, 1802 (referred to in the literature under the manuscript name *Tarsobaenus letourneauae* Barr, nom. nud., or as a species of *Phyllobaenus* Dejean, 1837) are sometimes found inside the petiole cavities of myrmecophytic *Piper*. They are capable of killing adult *Pheidole bicornis* (though they do not consume them) and feeding on the ant larvae, but food bodies appear to be the primary component of their diet (Letourneau 1990, 1991). In addition to this clerid beetle, two unidentified coccinellid larvae have been reported inducing food body production on non-myrmecophytic *Piper*, one inside the hollow petioles of *P. marginatum* Jacquin, 1788 in Panama (Dyer *et al.* 1999) and the other inside tents on the undersides of leaves of *P. urostachyum* Hemsley, 1882 in Costa Rica (Gastreich & Gentry 2004). The latter authors noted that food body size and density were much higher under the tents than on the leaf surface. These coccinellids probably belong to the new genus described below, but specimens were not available for examination. The mechanism by which ants, clerids and coccinellids stimulate the proliferation of food bodies on *Piper* is not known.

Historical Review of *Diomus* and allies. *Diomus* Mulsant, 1850 is a cosmopolitan genus of small to minute pubescent lady beetles whose greatest diversity lies in the tropical and subtropical regions of the world. *Diomus* is one of the most speciose genera in the family Coccinellidae (Pang & Ślipiński 2009) and the number of described species has increased dramatically in the last couple of decades (Gordon 1999; Chazeau 1987, 1993; Pang & Ślipiński 2009, 2010; González & Honour 2011). Unfortunately, the small size of specimens, together with their dense pilosity, tends to obscure cuticular features especially in greasy or matted specimens, and the taxon has suffered, perhaps more than most, from misinterpreted or misreported character states (Tables 1, 2).

Diomus was first proposed as a subgenus of *Scymnus* Kugellan, 1794, originally distinguished by the form of the abdominal postcoxal line curving posterolaterally and merging with the posterior margin of the first ventrite. Weise (1895) elevated *Diomus* to full generic status, but a number of cataloguers and revisers continued to treat it as a subgenus of *Scymnus* (Casey 1899; Leng *et al.* 1920; Korschefsky 1931; Mader 1955; Wingo 1952; Chapin 1974) and still others (Iablokoff-Khnzorian 1976; Fürsch 1987) placed it as a subgenus of *Nephus* Mulsant, 1846.

Brèthes (1925) described seven new species of *Diomus* from Chile and Brazil, and also proposed a new genus *Heterodiomus* Brèthes for two new species, one from Brazil and one from Uruguay. Surprisingly, although his choice of the new generic name suggests a close relationship to *Diomus*, Brèthes did not compare or contrast the character states of these two genera in his publication.

Chapin (1933) separated the species *Diomus bahamicus* Casey, 1899 and four newly described species from the Caribbean Islands with a reduced number of antennomeres (10 instead of 11) in a new genus *Decadiomus* Chapin, 1933. He also stated that *Diomus* possesses 4 tarsomeres (=cryptotetramerous or pseudotrimerous) and *Decadiomus* only 3 (=trimerous) (Table 1), and provided comparative illustrations of slide mounted material to support his assertion.

Gordon recognized sixteen valid species of North American *Diomus* as part of a larger work treating the tribe Scymnini of the United States and Canada (Gordon 1976). His generic discussion did not make any reference or comparison to the allied genus *Decadiomus* which, at the time, had not been recorded from the latter two countries. Gordon's diagnosis of *Diomus* (10 antennomeres, 3 tarsomeres) corresponds with Chapin's characterization of *Decadiomus* rather than *Diomus*. Gordon informally divided the North American species of *Diomus* into the *floridanus* group, the *xanthaspis* group, and one transitional group, the *bigemmeus* group based on characteristics of the male and female genitalia. Later, in a treatment of the entire North American family Coccinellidae (Gordon 1985), he added one introduced species from Australia, which he identified as *Diomus pumilio* Weise, 1885.

Pang and Gordon (1986) examined the slide-mounted material upon which Chapin had diagnosed the genera *Diomus* and *Decadiomus* and found that Chapin had incorrectly assessed the number of tarsomeres in his exemplars of *Diomus thoracicus* (F., 1801) (=*Coccinella thoracica* F., type species of *Diomus*). They stated that the exemplars of both genera have trimerous tarsi, but concluded that it would be important to examine the actual type material of *C. thoracicus* and review *Diomus* material from around the world. They retained a broad definition of *Diomus* in their redescription, allowing for multiple states for both the antennomeres (10 or 11) and tarsomeres (3 or 4).

Gordon and Hilburn (1990) revised the Coccinellidae of Bermuda, recognizing a single species each of *Diomus* and *Decadiomus*. They attempted to differentiate the two genera based on the number of antennomeres and tarsomeres (Table 1) but, in reality, their broad circumscription of *Diomus* did not provide any definitive characters to exclude members of *Decadiomus* (Table 1).

Gordon (1999) completed an ambitious project revising *Diomus* and allies of South America in which he treated 268 species names, and included 234 newly described species. He proposed a new tribe Diomini (Scymninae Mulsant, 1846) for *Diomus* and included five genera: *Diomus*, *Heterodiomus* and *Decadiomus*, which he diagnosed with trimerous tarsi (type material examined) and a shared configuration of the abdominal postcoxal line; and two newly described genera, *Magnodiomus* Gordon, 1999 and *Erratodiomus* Gordon, 1999, which differ from the other Diomini in possessing cryptotetramerous tarsi, an abdominal postcoxal line that does not reach the hind margin of the ventrite, and an unusually long and convoluted cornu of the spermathecal capsule in the female genitalia. Vandenberg (2002) stated that the newly circumscribed Diomini is polyphyletic with respect to another tribe, Selvadiini, proposed by Gordon in his revision of North American Coccinellidae (1985). She also confirmed Gordon's rediagnoses of *Diomus* and *Decadiomus* with respect to the tarsal and antennal characters, but agreed with Pang and Gordon (1986) that the generic placement of some North American *Diomus* species treated in Gordon (1976, 1985) would need to be reassessed. At this point Gordon had already recurated the North American Diomini housed at the USNM, and reassigned members of the *floridanus* and *bigemmeus* groups to *Decadiomus*. Unaware of these reassignments, other workers (Peck & Thomas 1998; Peck 2016) continued to list those species in *Diomus*.

Ślipiński (2007) published a book documenting the diversity and biology of the Australian Coccinellidae with keys, descriptions and numerous SEMs and color photographs. He placed *Amidellus* Weise, 1923 as a junior synonym of *Diomus* and added two additional Australian genera, *Dichaina* Weise, 1923, and a new genus *Andrzej* Ślipiński, 2007, to Diomini. He also remarked that both *Erratodiomus* and *Heterodiomus* "probably do not belong [in Diomini]," but did not elaborate. Further along in the same paper, he partially contradicted this earlier statement by admitting that his own diagnosis of *Diomus* would include *Heterodiomus*. Although Ślipiński provided much more complete generic and tribal diagnoses than many previous authors, the character states reported showed some inconsistencies between hierarchical levels, involving such characters as the number of antennomeres in the club, presence or absence of an ocular canthus, and the presence or absence of a stylus and "infundibulum" in the female genitalia (Table 2).

Pang and Ślipiński (2009, 2010) completed two parts of a four part series aimed at treating the entire Australian *Diomus* fauna, estimated at around 140 species. The authors indicated that an important goal of these works is to establish the identity of previously described species, a number of which are represented by single female specimens with abraded vestiture (Pang & Ślipiński 2010). They continued to follow the tribal concept of Diomini presented by Gordon (1999) (comprising *Diomus*, *Heterodiomus*, *Decadiomus*, *Magnodiomus*, and *Erratodiomus*) with the addition of the two monotypic Australian genera (*Dichaina*, and *Andrzej*) added by Ślipiński (2007), but cast doubt on the validity of *Heterodiomus* and *Decadiomus* as distinct from *Diomus*. They indicated that the diagnoses of these two genera depend on character states which have not been assessed in the majority of the world diomine fauna. In particular, they noted that some Australian *Diomus* species that normally have 11 antennomeres have occasional individuals with only 10 antennomeres.

Many shorter works have contributed to the elucidation of the world's Diomini fauna. A new species of *Heterodiomus* was described from Chile by Gordon and González (2003). González and Honour (2011) described 10 new *Diomus* from South America and reviewed progress on the descriptions of new species from the Palearctic region, India, China, and New Guinea (Chazeau 1993; Poorani 2002; Eizaguirre 1998; Pang *et al.* 2004). González (2015, 2016) contributed 12 more *Diomus* species from South America. A recent paper by Segarra-Carmona and Otero (2014) added four new species of *Decadiomus* from Puerto Rico and commented on the diagnosis of the genus in relation to *Diomus*, stating that number of antennomeres is a stable character at least in the Puerto Rican diomine fauna that was studied.

Molecular analyses have provided some insight into the higher relations of *Diomus* to other coccinellid taxa. A molecular analysis by Giorgi et. al (2009) groups Diomini, Hyperaspidini, Brachiacanthini Mulsant, 1850, Aspidimerini Weise, 1900, and Platynaspidini Mulsant, 1846 together in a single clade, and an analysis by Magro *et al.* (2011) shows strong support of a sister-group relationship between *Diomus* (Diomini) and *Hyperaspis* (Hyperaspidini). A study of the superfamily Cucujoidea Latreille, 1802 (Robertson *et al.* 2015) also places *Diomus* in a clade with members of Hyperaspidini and Platynaspidini, but a study by Seago *et al.* (2011) failed to recover these associations and places *Diomus* instead with *Amida* Lewis, 1896 and *Ortalia* Mulsant, 1850 (Ortaliini Mulsant, 1850).

TABLE 1. Conflicting reports on the number of antennomeres and tarsomeres in adults of two Diomini genera: *Diomus* and *Decadiomus*.

	Diomus		*Decadiomus*	
	Antennomeres	Tarsomeres	Antennomeres	Tarsomeres
Chapin 1933:95	11	4	10	3
Gordon 1976:319	10	3		
Gordon 1978:231		3		4
Gordon 1985:316	10	3		
Pang and Gordon 1986:192	10 or 11	3 or 4	10	3
Gordon & Hilburn 1990:277	10 or 11	3 or 4	10	3
Gordon & Hilburn 1990:279	11	3 or 4	10	3
Yu 1996:277	10 or 11	3		
Gordon 1999:4	11	3	10	3
Vandenberg 2002:379	11	3	10	3
Ślipiński 2007:87,89	11	3		
Hong and Ślipiński 2009:643	10 or 11			

TABLE 2. Morphological and anatomical character states of Australian Diomini adults as reported in Ślipiński (2007).

Diomini	coxites with styli absent	interfacetal setae absent	ocular canthus lacking	antennal club with 3 antennomeres	infundibulum present
Diomus	coxites with styli absent	interfacetal setae absent or indistinct	ocular canthus extending slightly into eye	antennal club with 3 antennomeres	infundibulum present
Dichaina	coxites with styli present	interfacetal setae absent or indistinct	ocular canthus extending slightly into eye	antennal club with 4 antennomeres	infundibulum absent
Andrzej	not known	interfacetal setae absent or indistinct	ocular canthus extending slightly into eye	antennal club with 1 antennomere	not known

Systematics

Tribe Diomini Gordon, 1999
(Figs. 1a–d)

Diomini Gordon 1999:3. Type genus: *Diomus* Mulsant, 1850

Included taxa (new circumscription, excluding *Magnodiomus* and *Erratodiomus* which we transfer to Hyperaspidini; see "*Remarks*," below): *Diomus*, *Decadiomus*, *Heterodiomus*, *Dichaina*, *Andrzej*, and the new genus described herein

Diagnosis. Size minute to small (1.1–3.5 mm), pubescent; antenna (Figs. 1a,b) composed of 10 or 11 antennomeres; pedicel bead like, articulated with and slightly narrower than scape, antennomere 3 elongate, 1.5–3× as long as antennomere 4; distal 3, 4, or 5 antennomeres forming slightly flattened asymmetrical compact club with oblique to truncate apex bearing concentration of short sensory setae (=sensilla). Mentum (Fig. 1a) subtrapezoidal, tapered posteriorly, typically with anterior margin concave or bicuspidate. Terminal maxillary palpomere in repose free, not partially inserted beneath mentum, more or less expanded distally with sensory surface directed anteriorly or anteromedially. Tarsi trimerous (Fig. 1c). Tibial spurs lacking. Abdomen with 6 visible ventrites; ventrite 1 and 2 partially fused medially. Abdominal postcoxal line (Fig. 1d) curving posterolaterally, merging with posterior margin of ventrite. Male genitalia with basal lobe (=penis guide sens. Ślipiński) distinctly asymmetrical to roughly symmetrical at least in outline; penis capsule with outer arm distinct to obsolete (Figs. 9–12). Female genitalia with spermathecal capsule well developed, except vestigial or absent in some Australian species; capsule with simple angular or C-shaped form, vermiform throughout or with swollen basal chamber; cornu of moderate length, not convoluted; ramus and nodulus sessile to weakly projecting; ramus with or without short beak-like projection (apodeme) overhanging attachment of accessory gland. Coxites teardrop or rhombus-shaped, with widely arcuate posterior margin.

Members of Diomini are most easily confused with other small pubescent lady beetles. The shape of the abdominal postcoxal line and wide posterior margin of the coxites will distinguish diomines from both *Scymnus* and *Nephus* (including its subgenera sens. Gordon 1985 which are now often accorded full generic status). In *Scymnus* and *Nephus* the postcoxal line does not reach the hind margin of the ventrite and the outer end is often recurved toward the base of the ventrite; the coxites are narrow and distally tapered rather than broad. Among New World species, the basal lobe of Diomini is distinctly asymmetrical, while that of *Scymnus* is bilaterally symmetrical. Furthermore, *Scymnus* can be distinguished from Diomini by the possession of cryptotetramerous tarsi, and *Nephus* is distinct in having the basal two antennomeres fused or tightly joined (non-articulated).

Pubescent members of the newly recircumscribed tribe Hyperaspidini (see "Remarks," below) differ from Diomini in possessing an antenna with a fusiform club (Figs. 2a,b) bearing a proliferation of setae in a membranous area on the inner (medially facing) surface of the terminal antennomere and smaller membranous area on the inner distal margin of the penultimate antennomere (antennae directed anteriorly); terminal maxillary palpomere in repose (Fig. 2a, left side of image) with inner edge contiguous with or partially inserted beneath anterolateral lobe of large cordate mentum, with oblique sensory surface facing dorsally and pressed against ventral surface of head, and tarsi cryptotetramerous (Fig. 2c). Also in Hyperaspidini the abdominal postcoxal line (Fig. 2d) does not reach the posterior margin of the ventrite and/or the outer end is recurved and directed toward or attains the anterior margin of the ventrite (see corresponding character states for Diomini (Fig. 1) listed in the paragraph above this one). Members of the subtribe Selvadiina (Hyperaspidini) can further be distinguished from Diomini based on the extremely elongate and convoluted cornu of the female spermathecal capsule (Figs. 3–4).

Remarks. Ślipiński (2007) diagnoses the Diomini as lacking interfacetal setae, an ocular canthus, and stylus of the coxites (=female genital plates or hemisternites) (Table 2). Our own random sampling of Diomini exemplars in the USNM suggests that these structures are normally present, but at times difficult to see or lost through abrasion. Published digital images of Australian species also document the presence of these structures, at least in some species (e.g. Ślipiński 2007:figs. 298 & 309; Pang & Ślipiński 2010:25d, showing coxites bearing styli; Pang & Ślipiński 2009:fig. 17b, showing frontal view of specimen with eyes bearing canthi and interfacetal setae). Other character states involving the number of antennomeres in the club and the presence or absence of an infundibulum in the female genitalia are difficult to assess because no consistent method for delineating the club has been presented, and the term "infundibulum" has not been well defined nor treated consistently by various authors. When Ślipiński (2007) indicated that certain genera "probably do not belong in Diomini" we assume from his later remarks that he intended to name the two taxa related to *Selvadius*—*Erratodiomus* and *Magnodiomus*—but instead mentioned *Erratodiomus* and *Heterodiomus*.

Gordon (1985) originally misinterpreted the unusual convoluted cornu of the spermathecal capsule in *Selvadius* (Fig. 3) as a continuation of the spermduct, and assumed that the spermatheca was lacking. He correctly interpreted the homologous structures in *Magnodiomus* and *Erratodiomus* (Fig. 4) (Gordon 1999) but failed to consider their placement in Selvadiini, possibly due to his original misinterpretation. Gordon placed his new tribe Selvadiini in the subfamily Scymninae, but discussed similarities between *Selvadius* and certain hyperaspidines, even referring to them as Hyperaspidinae in his tribal diagnosis. Vandenberg (2002) indicated that Selvadiini would be better placed in the Hyperaspidinae along with Hyperaspidini and Brachiacanthini. These similarities had been previously noted by Whitehead (1967) who suggested that *Selvadius* may bear a closer affiliation to *Hyperaspidius* than to *Scymnus*.

In addition, Vandenberg and Perez-Gelabert (2007) noted that two South American genera, *Mimoscymnus* and *Planorbata*, originally placed in Coccidulini (Coccidulinae) (Gordon 1994), also belong in Hyperaspidinae. Ślipiński (2007) concurred about the improper placement of *Planorbata* but referred to it as "a 'Scymninae' genus," possibly using the latter subfamily in the broad sense of Sasaji, which would have included *Hyperaspis* and allied genera. Seago *et al.* (2011) reduced Hyperaspidinae to tribal level and placed Brachiacanthini as a synonym of Hyperaspidini. This action was followed by Gordon *et al.* (2014), although inconsistently within that paper, and mentioned but not employed in a subsequent work in that series (Canepari *et al.* 2016). We follow Seago *et al.* (2011) and various other modern authors in treating the Hyperaspidini at tribal level, but recognize four distinct subtribes: Hyperaspidina, Brachiacanthina, Selvadiina stat. nov. (for *Selvadius*, *Magnodiomu*s and *Erratodiomus*) and Mimoscymnina subtribe nov. (for *Mimoscymnus* and *Planorbata*; type genus=*Mimoscymnus*), as distinct lineages each defined by one or more autapomorphies of the male and female genitalia. The placement of the Selvadiina in Hyperaspidini is supported by the molecular phylogenies of Seago *et al.* (2011) and Robertson *et al.* (2015) who show *Selvadius* as clustering more closely with *Brachiacantha* and *Hyperaspis* than with *Diomus.* The placement of Mimoscymnina in Hyperaspidini is provisional, and based only on external morphological characters (Fig. 2) as there has not yet been a molecular study involving either *Mimoscymnus* or *Planorbata*. Members of Mimoscymnina can be readily distinguished from other members of Hyperaspidini by the elongate triangulate coxites of the female genitalia, and the male genitalia with the trabes much longer than the basal lobe and basal piece combined.

Key to World genera of Diomini sens. nov.

(excluding *Erratodiomus* and *Magnodiomus* (Hyperaspidini) (Figs. 1–2))

1\. Antenna with 10 antennomeres 2

1’. Antenna with 11 antennomeres 4

2\. Species restricted to the New World 3

2’. Species occurring outside the New World . . . . *Diomus* Mulsant, *in part*

3\. Female genitalia (Fig. 5) with sperm duct generally long, convoluted; spermatheca vermiform throughout, lacking bulbous basal chamber. Male genitalia (Fig. 7) with main tube of penis completing half to three-quarters turn or more within basal ½, somewhat spiraliform; penis bearing long or short apical flagellum; penis capsule (Figs. 7, 11–12) with long slender inner arm that may be strongly procurved (Fig. 12); outer arm truncated or obliterated (Fig. 11), leaving large oval orifice to mark its place; some species with fragment of outer arm present but not enclosing ejaculatory duct (Fig. 12). Predators on Sternorrhyncha (Pseudococcidae, Coccidae, Diaspididae, Monophlebidae, Ortheziidae). Larvae free-living . . . . *Decadiomus* Chapin

3’. Female genitalia (Fig. 6) with sperm duct of moderate length, may be weakly sinuous; spermatheca with bulbous basal chamber. Male genitalia (Figs. 8, 29–32) with main tube of penis completing half turn within basal ½, forming fishhook shape; penis lacking apical flagellum; inner and outer arms of penis capsule (Fig. 10) equally well developed, broadly consolidated into fan-like shape with sinuous distal margin; ejaculatory duct enters penis capsule through small opening in outer angle of capsule. Parasites of *Piper* plants that feed on food bodies. Larvae develop in silken tents constructed between leaf veins (Figs. 40–42) . . . . *Moiradiomus* **gen. nov.**

4\. Length of terminal antennomere approximately equal to twice width, longer than basal 3 antennomeres combined . . . . *Andrzej* Ślipiński

4.’ Length of terminal antennomere (Figs. 1a,b) less than twice width (except in *Diomus sedani*), much shorter than basal 3 antennomeres combined 5

5\. Pronotum with sharp submarginal carinae separating the anterolateral pronotal angles from the disc. Australia . . . . *Dichaina* Weise

5.’ Pronotum without submarginal carinae 6

6\. Prosternum T-shaped, long anterior to coxal cavities (subequal to length of cavity), with short carinae not extending to apex. Female genitalia with bulbous base to spermatheca, with distally tapered sclerotized sheath in basal half of sperm duct (similar to *Moiradiomus*; Fig. 6). Restricted to the New World . . . . *Heterodiomus* Brèthes

6.’ Without the above combination of characters. Distributed world wide . . . . *Diomus* Mulsant

Diomus Mulsant, 1850

Scymnus (*Diomus*) Mulsant 1850: 951. Type species: *Coccinella thoracica* Fabricius, 1801, by subsequent designation of Korschefsky 1931.

Diomus: Weise 1895:144.

Nephus (Diomus): Iablokoff-Khnzorian 1976:377.

Amidellus Weise 1923: 141. Type species: *Scymnus ementitor* Blackburn, 1895 by original designation. Synonymised by Ślipiński 2007: 87.

(see Gordon 1976, and Pang & Gordon 1986 for a more complete bibliography)

Diagnosis. In the New World fauna, *Diomus* species can be distinguished from other Diomini by the combination of: antenna composed of 11 antennomeres (Figs. 1a,b), prosternum shaped like a short stemmed Y, short anterior to coxal cavities (about ½ diameter of cavity), intercoxal process with carinae extending to anterior margin or nearly so.

Remarks. This is a large and diverse genus with no known autapomorphies to define it relative to the other Diomini genera. It constitutes more than 90% of the documented Diomini from the New World, nearly 97% of those currently described from Australia, and 100% of the Diomini recorded from the rest of the World. It is almost certainly polyphyletic. Presumably as the fauna becomes better known the lineages within this large group will become better defined, perhaps with the aid of molecular studies. Gordon (1985) informally recognizes eight different groups within the South American members of the genus, each defined exclusively by characteristics of the male genitalia; however, he speculates that only about half of these represent monophyletic groupings. Much of the Australian *Diomus* fauna elucidated by Pang and Ślipiński (2009, 2010) through detailed descriptions and imagery cannot be assigned to any one of these groups. It is interesting to note that the type species of *Diomus*, *Coccinella thoracica* F., is actually an atypical member of the genus with highly derived larvae that inhabit ant nests, chemically mimic them, and feed on their brood (Vantaux *et al.* 2010).

The identification of the Australian *Diomus* species whose genitalia are illustrated in Gordon (1985) is corrected from *D. pumilio* to *D. tenebricosus* (Boheman, 1859); however, we have no evidence that *D. tenebricosus* was ever established in North America. Gordon (1985) documents multiple releases of *Diomus pumilio*, and Australian "*Diomus* sp." in North America between 1959–1974. It is possible that some of these releases contained *D. tenebricosus* or other exotic *Diomus* species. Pang and Ślipiński (2009) indicate that *D. pumilio* and *D. tenebricosus* can only be reliably separated by examining the male genitalia. We were not able to find North American specimens of *D. tenebricosus* in the USNM that might have formed the basis of the drawings in Gordon (1985). There is a series collected in El Cerrito, CA and identified as *D. pumilio* by Ken Hagen (University of California, Berkeley; deceased) as part of a biological control release-and-recapture program; they do not have the same genitalia as those illustrated in Gordon's work, but agree instead with the digital images for *D. pumilio* in Pang and Ślipiński (2009). Recent field collected material submitted for identification by A. Goldmann from several California localities has also proven to be *D. pumilio*.

Heterodiomus Brèthes, 1925

Heterodiomus Brèthes 1925:155. Type species: *Heterodiomus darwini* Brèthes, 1925, by subsequent designation of Korschefsky 1931.

Diagnosis. This genus was described but not diagnosed by Brèthes (1925). The species currently included (Gordon 1999; Gordon & González 2003) are distinguished from other members of the New World Diomini by the combination of: antennae composed of 11 antennomeres, prosternum shaped like a short stemmed T, long anterior to coxal cavities (subequal to length of cavity), intercoxal process with carinae short, not extending to anterior margin, and suture between abdominal ventrites 1 and 2 partially obliterated. Members of *Heterodiomus* are strongly united by the shape of the female genitalia which have a bulbous base to the spermatheca and distally tapered sclerotized sheath in the basal half of the sperm duct (= "thorn-like infundibulum" sens. Gordon 1999). Although this combination of genital characteristics does not occur in the other Diomini illustrated in Gordon (1999), the corresponding structures in most species have not yet been evaluated, and a very similar configuration (Fig. 6) is found in the new genus described herein.

Decadiomus Chapin, 1933

Decadiomus Chapin 1933:96. Type species: *Diomus bahamicus* Casey, 1899, by original designation.

Diagnosis. In the New World fauna, *Decadiomus* species can be distinguished from most previously known Diomini by the combination of: antenna composed of 10 antennomeres, prosternum shaped like a short stemmed Y, short anterior to coxal cavities (about ½ diameter of cavity), intercoxal process with carinae extending to anterior margin or nearly so.

Decadiomus differs from the new genus described in the present paper (which also has only 10 antennomeres) by having free living, predatory larvae, and also by characteristics of the male genitalia: penis with apical flagellum (Fig. 7), and outer arm of capsule truncated or strongly reduced and not enclosing the ejaculatory duct prior to its entry into the main penis tube (Figs. 11–12).

Genital characteristics of *Decadiomus* males and females are included in the generic key, below, and also discussed by Gordon (1976) (as *Diomus*, *floridanus* group and *bigemmeus* group), and by Segarra-Carmona and Otero (2014). These characteristics may serve to differentiate *Decadiomus* species from the occasional occurrence of Diomini with 10 antennomeres from areas outside of the New World (e.g. in some individuals of *Diomus flavolaterus* (Lea) from Australia).

Remarks. The following species previously classified in *Diomus* are hereby transferred and represent new combinations within *Decadiomus: D. balteatus* (LeConte, 1878), *D. floridanus* (Mulsant, 1850), *D. amabilis* (LeConte, 1852), *D. liebecki* (Horn, 1895), *D. myrmidon* (Mulsant, 1850), *D. humilis* (Gordon, 1976), *D. pseudotaedatus* (Gordon, 1976), *D. taedatus* (Fall, 1901), *D. bigemmeus* (Horn, 1895), and *D. austrinus* (Gordon, 1976). *Decadiomus seini* Segarra, 2014 is placed as a junior synonym of *D. austrinus* based on the original type descriptions and illustrations, and a comparison between specimens from Puerto Rico and the type material of *D. austrinus.*

Dichaina Weise, 1923

Dichaina Weise 1923:145. Type species: *Dichaina inornata* Weise, 1923, by monotypy.

Diagnosis. This monotypic genus is very similar to *Diomus*, but can be easily distinguished by the sharp submarginal carinae separating the anterolateral pronotal angles from the disc.

Andrzej Ślipiński, 2007

Andrzej Ślipiński 2007:92. Type species: *Andrzej antennatus* Ślipiński, 2007, by original designation.

Diagnosis. This monotypic genus is based on a single male specimen that has 11 antennomeres and the terminal antennomere extremely large and elongate (length more than 2× width).

Remarks. In a more recent work by Pang and Ślipiński (2009), another species, *Diomus sedani* (Blackburn,1889), is diagnosed with similar proportions to the terminal antennomere, although less enlarged overall than that of *A. antennatus*. Unfortunately, the latter species is known from females only, so characteristics of the male genitalia diagnosed for *Andrzej* cannot be compared with it. Ślipiński (2007) indicates that the antennal club of *A. antennatus* consists of a single antennomere; however, we observed that the antennomeres gradually increase in width beginning with antennomere 9, and therefore consider that the last 3 antennomeres together constitute the club.

Moiradiomus gen. nov.

(Figs. 6, 8, 10, 13–20, 23, 25–42)

Type species: *Moiradiomus clotho* sp. nov.

Diagnosis. Distinguished from other members of the tribe Diomini by the combination of morphological, anatomical, and behavioral traits: antenna consistently comprised of 10 antennomeres, distal antennomere not greatly enlarged or elongated relative to penultimate, pronotal anterolateral angles lacking submarginal carinae (Figs. 13–20), prosternum (Figs. 25–28) shaped like a short stemmed Y, short anterior to coxal cavities, about ½ diameter of cavity, with carinae of intercoxal process extending to anterior margin, male genitalia (Figs. 29–32) with basal lobe (=penis guide) asymmetrical (Figs. 29b, 30b, 31b, 32b), penis (=siphonal) capsule (Fig. 10) well developed, with inner and outer arms broadly joined into single wedge-shaped structure with sinuous distal margin, capsule enclosing ejaculatory duct prior to its entry into the main penis tube, penis apex lacking flagellum (Figs. 8, 29c, 30c, 31c, 32c), larva silk spinning, adult and larva phytophagous, parasitic on plants in the genus *Piper*, inducing and feeding on *Piper* food bodies.

The reduced number of antennomeres (10 as opposed to 11) will distinguished the new genus from all other Diomini except *Decadiomus* and a few species or individuals presently classified in *Diomus*. From these latter two genera, *Moiradiomus* can be distinguished by the highly consistent configuration of the penis of the male genitalia (as described above), and by the unusual life history and trophic relations shared by its members. Thus far the known *Moiradiomus* species all have a similar elytral color pattern (Figs. 13–20) consisting of a medium to dark brown background with apex suffusely lightened or bearing a distinct band of pale yellow. The elytral color patterns in *Decadiomus* are more variable, with either a dark or light background and often with contrasting maculae. The tarsal claw is sexually dimorphic in the known species *Moiradiomus*, but this characteristic occurs in some *Diomus* and *Decadiomus* as well.

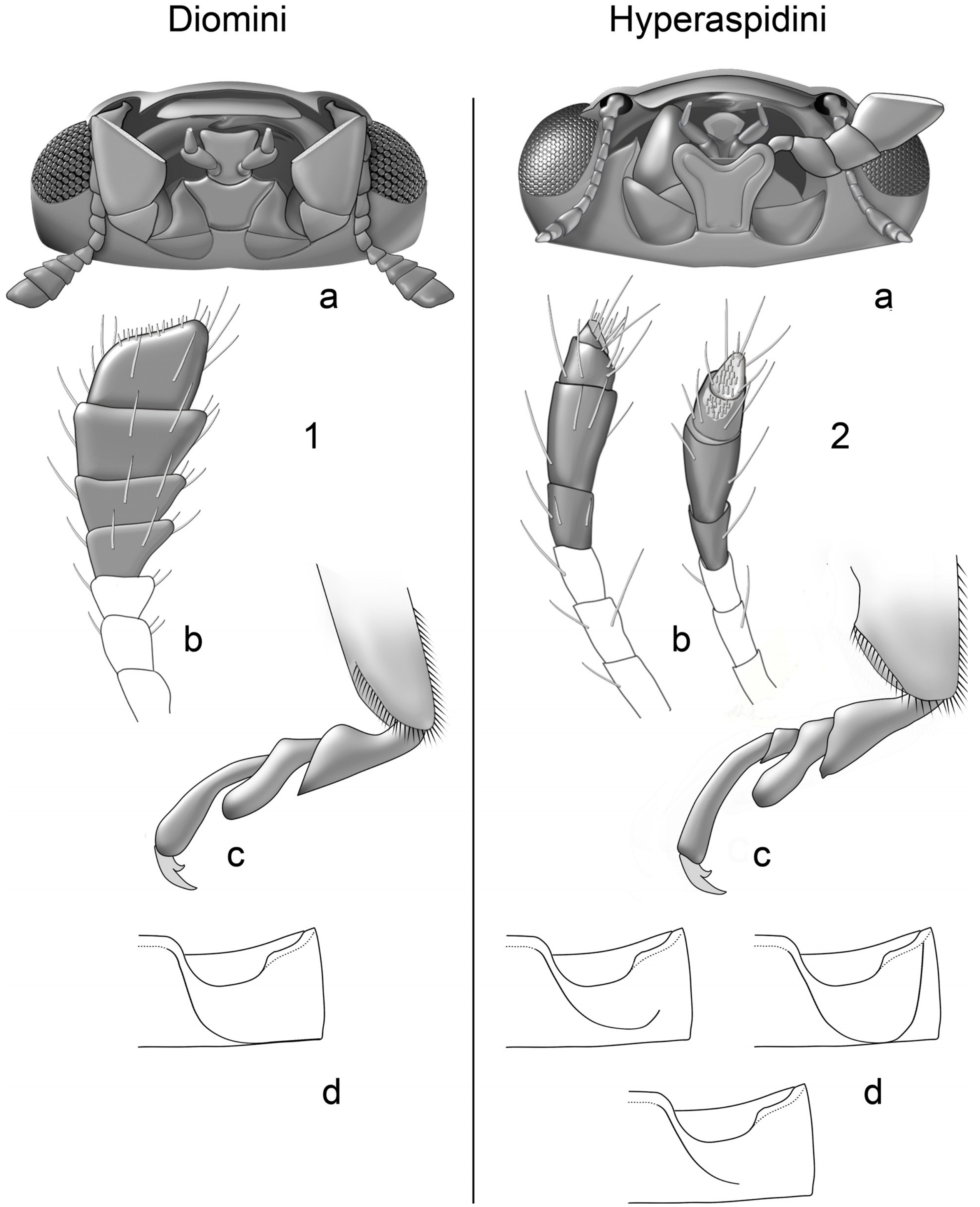
Description. Form (Figs. 13–20) broadly oval to elongate, length 1.1–2.0 mm, weakly to moderately convex, pubescent. Color pattern simple, unsaturated; predominantly brown with yellow; female pronotum generally darker than in male. Head transverse; eyes finely facetted, well separated dorsally, bearing interfacetal setae, with interocular distance greater than eye width in frontal view, weakly emarginated near antennal insertions by small rounded eye canthus; antenna short, approximately ½ head width, clavate, composed of 10 antennomeres with last 4 or 5 forming irregular club; scape normal; pedicel bead like, slightly narrower than scape; antennomere 3 elongate, longer than 4, with distal antennomere subequal to or only slightly longer than penultimate. Mandible (Fig. 23) with bifid apex, with about 40 minute blunt teeth on incisor blade; molar part with curved tooth near top (=basal tooth sens. Ślipiński 2007). Maxillary palp with 4 palpomeres; terminal palpomere moderately to strongly expanded distally. Labial palp with 3 palpomeres.

Pronotum transverse, evenly convex, base with raised border; pronotal anterolateral angle lacking submarginal carina. Elytron with raised lateral ridge; epipleuron narrow, oblique, not excavated to receive femoral apices, not reaching elytral apex. Prosternum (Figs. 25–28) shaped like short stemmed Y, short anterior to coxal cavities, about ½ diameter of cavity, with carinae of intercoxal process extending to anterior margin or nearly so. Mesoventrite with raised anterior border, with anterior face excavated to receive apex of prosternal intercoxal process. Tibial spurs lacking; tarsal claw sexually dimorphic in species thus far known, with short triangular tooth in female, longer scythe-like tooth in male. Abdomen with 6 ventrites in both sexes; abdominal postcoxal line curving posterolaterally, merging with posterior margin of ventrite. Male genitalia (Figs. 29–32) with outer margin of paramere densely setiferous; setae long, slender, flexible; basal lobe (=penis guide) asymmetrical, penis capsule (Fig. 10) well developed, with inner and outer arms broadly joined into single wedge-shaped structure with sinuous distal margin, capsule enclosing ejaculatory duct prior to its entry into main penis tube; penis apex lacking flagellum. Female genitalia (Fig. 6) with spermathecal capsule fully developed, bent in basal 1/2 with bulbous base; sperm duct moderately long with sclerotized distally tapered sheath enclosing basal 1/2.

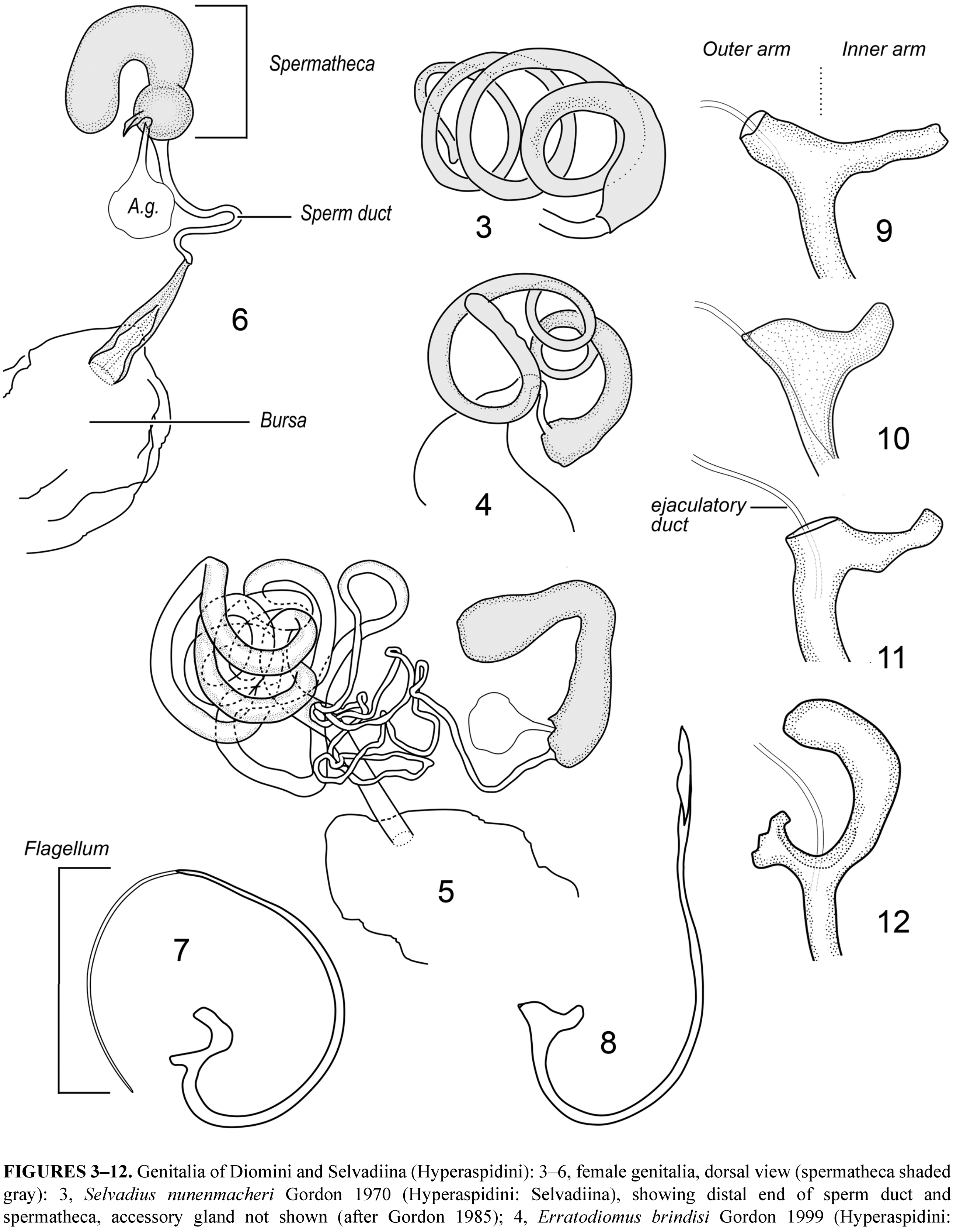
Larva, final (4th) instar (Figs. 33–39, based on *M. lachesis*). Body off white, pruinose, soft-bodied, subovate, weakly convex dorsally, setiferous. Setae (Fig. 37) minutely barbed, of variable form, some flattened, scale-like, falcate, spatulate, clavate or frayed. Head tapered anteriorly, bearing three stemmata on each side behind antenna; frontal arms of epicranial suture indistinct; epicranial stem absent; mandible (Fig. 36) falciform, with unidentate apex, shallow incisor groove, triangular plate-like angulation near middle of incisor edge, with simple rectangular molar region.

Antenna (Fig. 35) 3-segmented, short; scape annular; pedicle narrower, nearly as long as wide, bearing conical sensorium, pair of preapical setae present; flagellum with long apical seta. Mala small, apically rounded. Maxilla (Fig. 34) with two conspicuous long setae on fused cardo/stipes; maxillary palp 2-segmented; maxillary palpifer incompletely annular. Labial palp 2-segmented; palpifer unsclerotized, indistinct. Fused submentum/mentum with several long conspicuous setae. Leg well developed, visible in dorsal view; tibiotarsus (Fig. 38) with cluster of capitate setae near apex; tarsungulus (Fig. 39) with broad base, pointed apex, bearing single short simple seta at base of concave inner side. Paired dorsal abdominal glands not evident, possibly vestigial or absent.

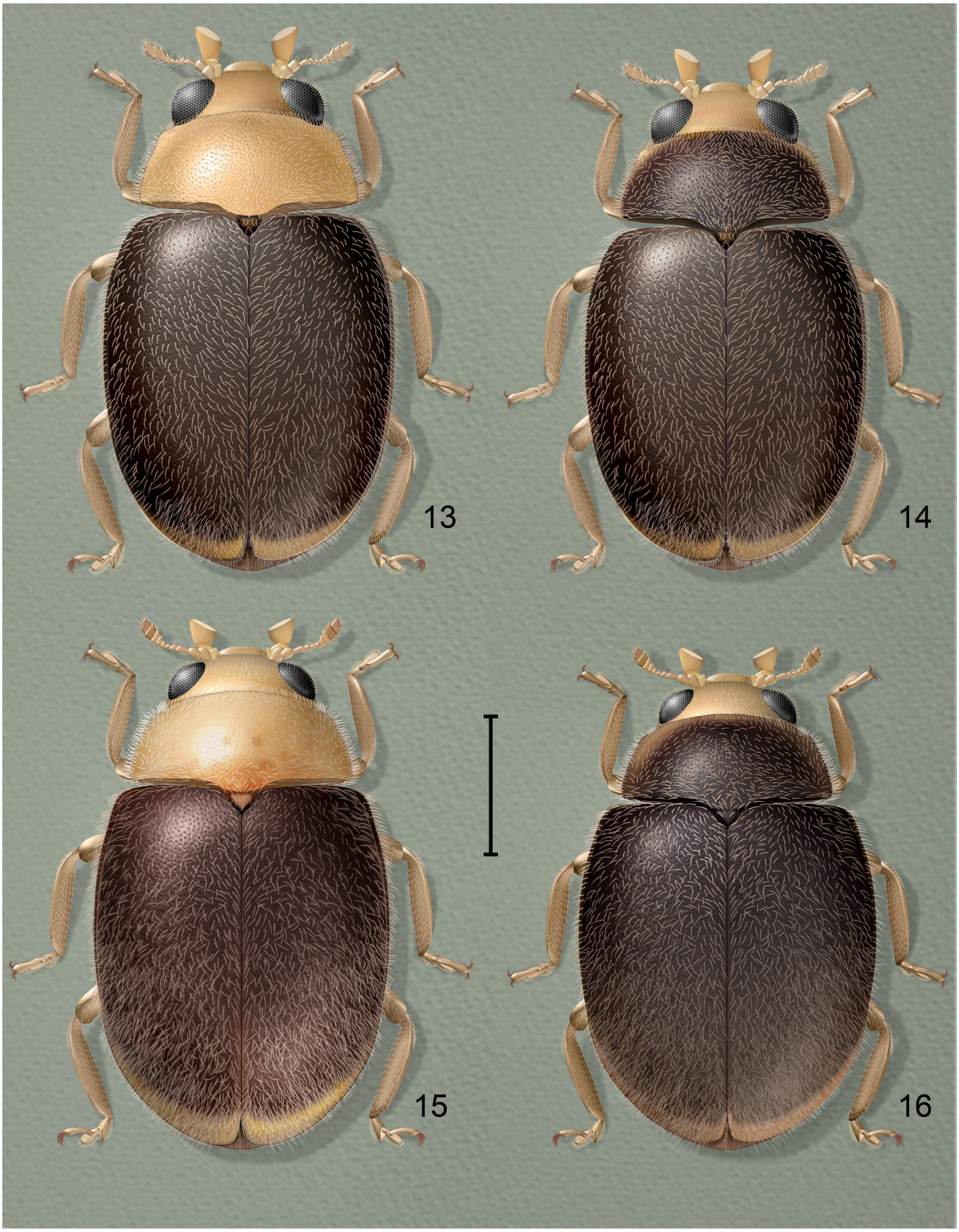
Trophic relations. Larvae develop on food bodies of *Piper* species. Although the four species described below are all from Costa Rica, the distinctive larval tents have been observed on leaves of *Piper* as far north as San Martin Tuxtla, Veracruz, Mexico, and as far south as Itacolomi State Park in Minas Gerais, Brazil.



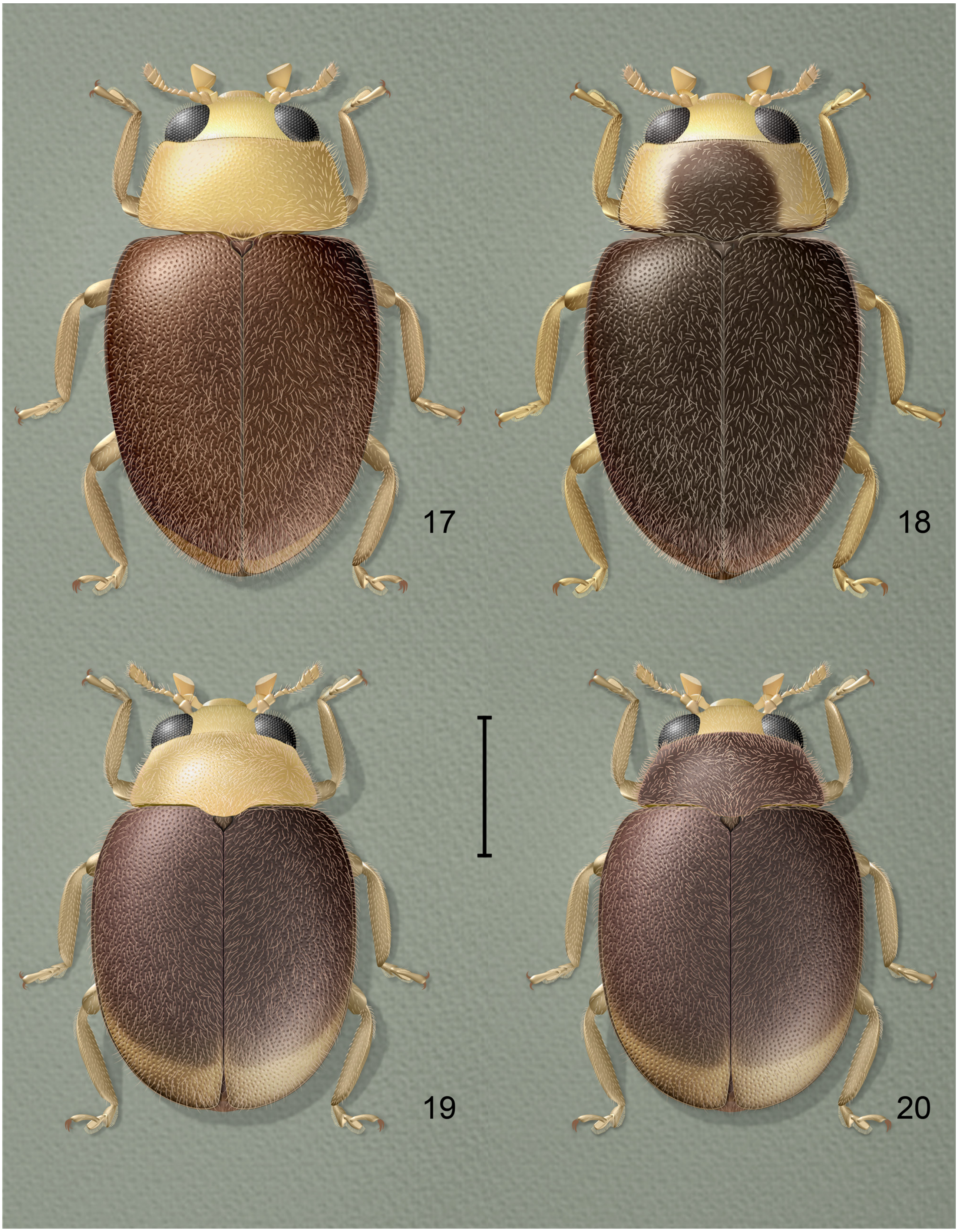
FIGURES 1–2. Diagrammatic representation of major diagnostic features of Diomini and Hyperaspidini: 1, Diomini: a, ventral view of head capsule showing position of maxillary palp when retracted; b, left antennal club from dorsal view when extended; c, apex of mesothoracic leg showing trimerous tarsus; d, left half of first abdominal ventrite showing configuration of postcoxal line. 2, Hyperaspidini: a, ventral view of head capsule showing position of maxillary palp when retracted (left side of image) or extended (right side of image); b, left antennal club from dorsal view when extended (left image), same rotated 90 degrees counter clockwise to show membranous sensory patches of last two antennomeres (right image); c, apex of mesothoracic leg showing cryptotetramerous tarsus; d, left half of first abdominal ventrite showing various configurations of the postcoxal line.



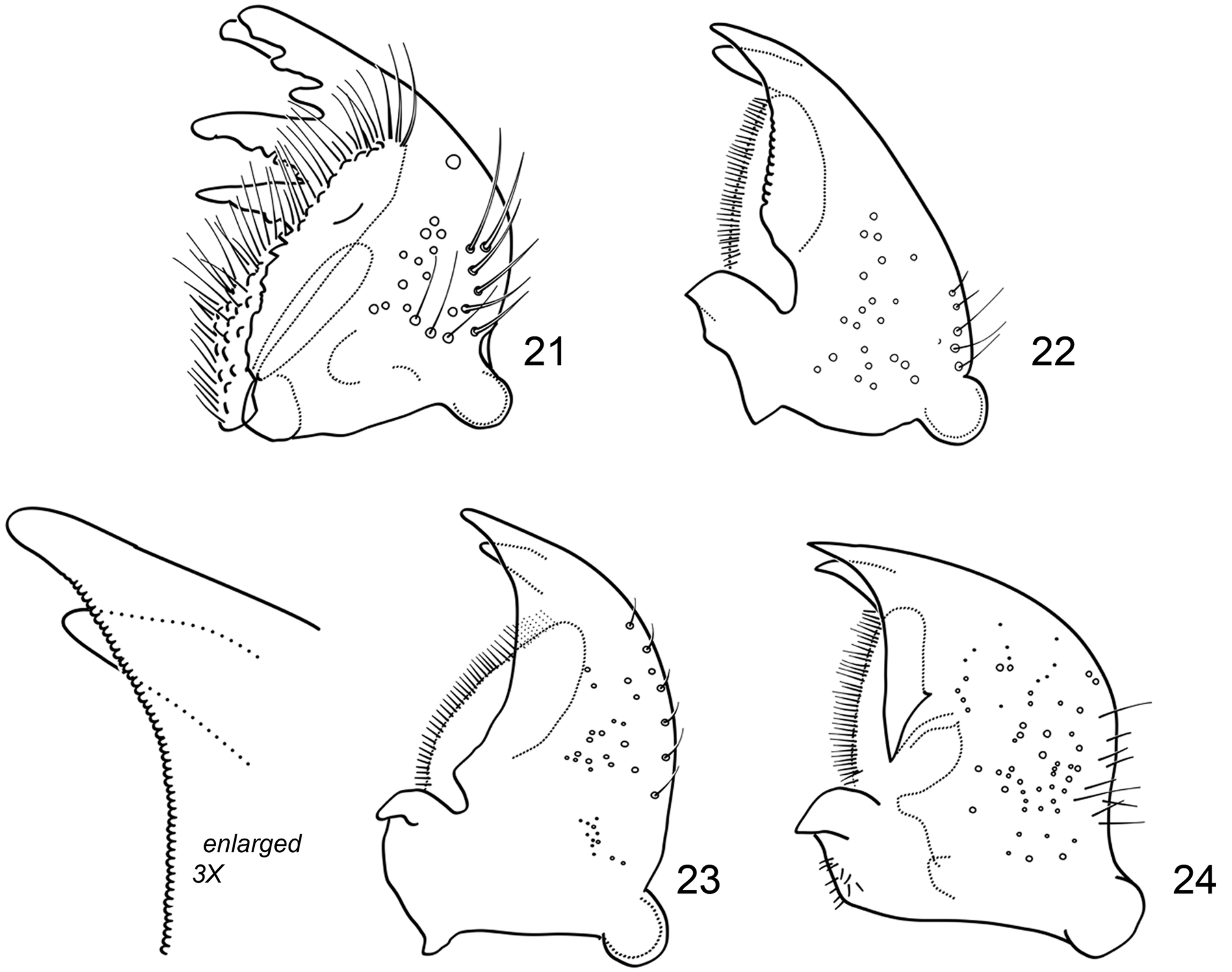
FIGURES 3–12. Genitalia of Diomini and Selvadiina (Hyperaspidini): 3–6, female genitalia, dorsal view (spermatheca shaded gray): 3, *Selvadius nunenmacheri* Gordon 1970 (Hyperaspidini: Selvadiina), showing distal end of sperm duct and spermatheca, accessory gland not shown (after Gordon 1985); 4, *Erratodiomus brindisi* Gordon 1999 (Hyperaspidini: Selvadiina), bursa through spermatheca, accessory gland not shown (after Gordon 1999); 5, *Decadiomus hughesi* Gordon & Hilburn 1990 (Diomini), bursa through spermatheca (note long convoluted sperm duct); 6, *M. lachesis* (Diomini) (*A.g.*= accessory gland); 7–12, male genitalia of Diomini, left lateral view of penis: 7, *D. hughesi*; 8, *M. lachesis*; 9, *Diomus donatus* Gordon (capsule); 10, *M. lachesis* (capsule); 11, *Decadiomus bigemmeus* (capsule); 12, *Decadiomus liebecki* (capsule)



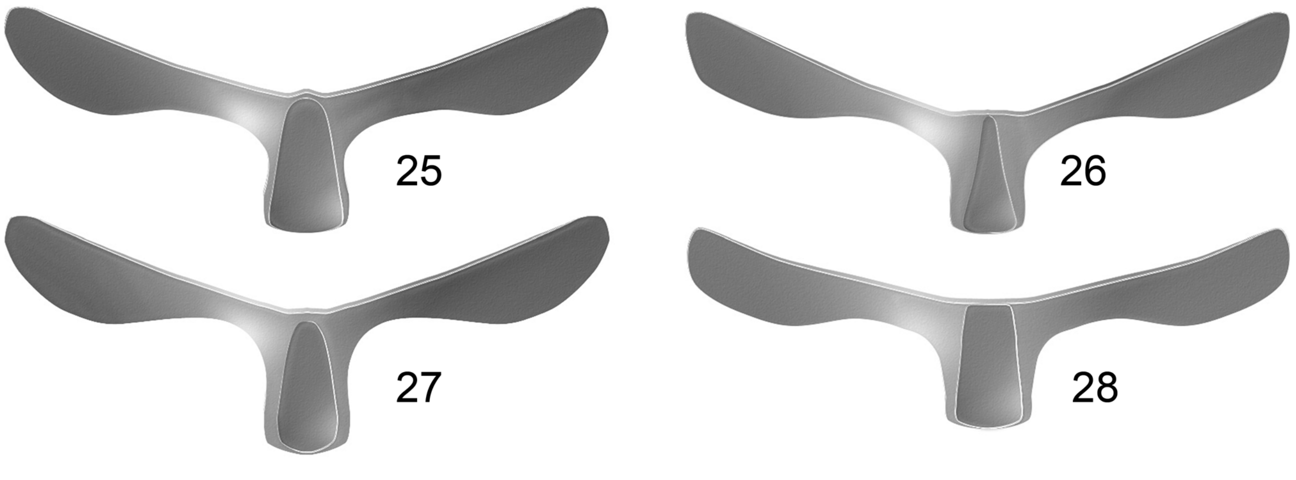
FIGURES 13–16. *Moiradiomus* species habitus illustrations. 13, *M. clotho*: holotype, male; 14, *M. clotho*: paratype, female. 15, *M. lachesis*: holotype, male; 16, *M. lachesis*: paratype, female. Scale bar = 0.5 mm.



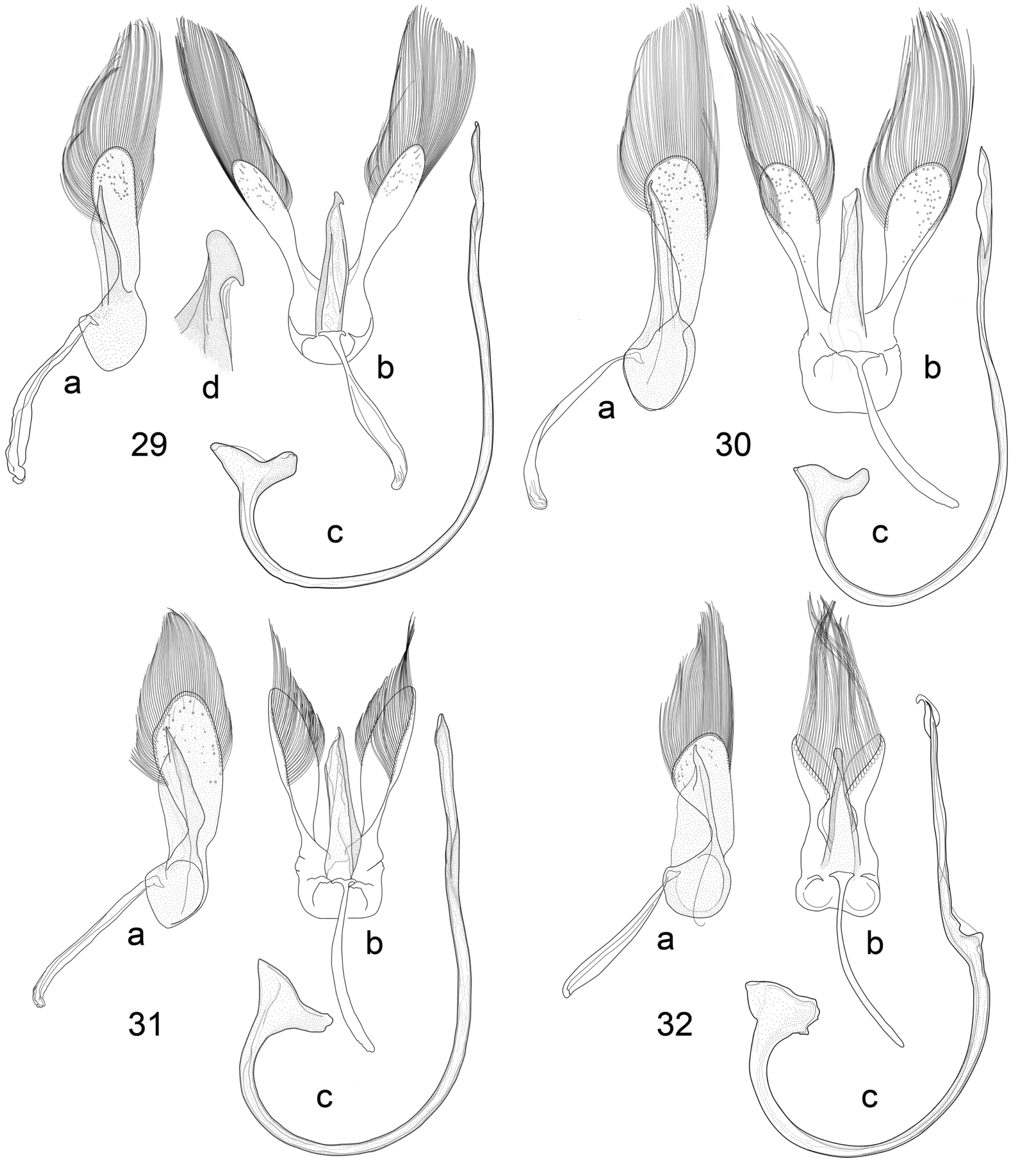
FIGURES 17–20. *Moiradiomus* species habitus illustrations. 17, *M. atropos*: holotype, male; 18, *M. atropos*: paratype, female. 19, *M. nanita*: holotype, male; 20, *M. nanita*: paratype, female. Scale bar = 0.5 mm.



FIGURES 21–24. Dorsal view of right mandible: 21, *Subcoccinella vigintiquatuorpunctata* (L.) (folivorous) (after Kovář 1996); 22, *Bulaea* sp. (omnivorous with emphasis on pollinivory/phytophagy); 23, *Moiradiomus lachesis* (enlarged detail of apical portion of incisor blade shown to left of main structure) (specialized on *Piper* food bodies); 24, *Adalia bipunctata* (entomophagous with emphasis on aphids) (after Kovář 1996).



FIGURES 25–28. Diagrammatic ventral view of *Moiradiomus* prosterna (setae, color patterns, and surface punctation not indicated): 25, *M. clotho*; 26, *M. lachesis*; 27, *M. atopos*; 28, *M. nanita.*



FIGURES 29–32. Male genitalia of *Moiradiomus* species (a, left lateral view of phallobase; b, ventral view of phallobase; c, left lateral view of penis; d, apex of basal lobe, enlarged): 29, *M. clotho*; 30, *M. lachesis*; 31, *M. atopos*; 32, *M. nanita.*

Etymology. *Moiradiomus* (gender Masculine) formed from a combination of Moira (=fate) + *Diomus* (a genus of lady beetle, possibly in reference to Greek mythology where Diomus was an Athenian hero, son of Colyttus, and a companion of Heracles). Moira is an Ancient Greek word (μοῖρα) meaning a portion or lot of the whole. In Greek mythology the Moirae are the three fates, daughters of Zeus and Themis, who spin, measure, and cut the thread of life.

Remarks. The relationships between the new genus and other genera of Diomini (sens. nov.) remains a mystery. Adult members of *Moiradiomus* key to *Decadiomus* in Gordon (1999) because the antenna is composed of 10 antennomeres. However, individuals with only 10 antennomeres were also noted to randomly occur in certain Australian *Diomus* species (Pang & Ślipiński 2009). The female genitalia of *Moiradiomus* are quite different from members of *Decadiomus* and instead match those of *Heterodiomus* spp. (Gordon 1999; Gordon & González 2003). The larva of the new genus differs greatly from the unusual onisciform larva of two myrmecophilous species, *Diomus thoracicus* (type species of *Diomus*) and *Diomus lupusapudoves* Vandenberg *et al*. (Vandenberg *et al*. 2018), but is similar to the setiferous, spindle-shaped forms found in *Diomus terminatus* (Say, 1835) (Hentz & Nuessly 2002, Akbar *et al*. 2009) and *D. roseicollis* (Mulsant, 1853) (Rees *et al*. 1994), as well as *Decadiomus pictus* Chapin, 1933 (Böving 1933). *Moiradiomus* larvae also appear to lack the dorsal intersegmental glands reported in *Diomus* and *Decadiomus* larvae (Rees *et al.* 1994; Vandenberg *et al*. 2018). These glands have been shown to have a repellent effect on ants or play a role in chemical mimicry and are identified by Seago *et al*. (2011) as an important step in the transition to feeding on ant-protected prey. Presumably they have been rendered obsolete by the enclosed environment provided by the woven larval tent of *Moiradiomus*.

Moiradiomus clotho **sp. nov.**

(Figs. 13, 14, 25, 29)

Diagnosis. Most readily distinguished from its congeners by the male genitalia (Fig. 29) with basal lobe terminating in a hook-shaped process (Fig. 29d) resembling a vulture's head, and parameres relatively slender, weakly expanded distally, with longest setae subequal in length to paramere. The adult can be distinguished by the elongated terminal maxillary palpomere (Fig. 13, 14). It differs from *M. lachesis* in possessing a larger head and eyes, and narrower frons. It is also distinguished by its larval host plant: *P. holdridgeianum* W. C. Burger, 1971.

Description of holotype (male) (Fig. 13). Length 1.9 mm, width 1.0 mm. Form elongate, oval, weakly convex. Metathoracic wing present. Dorsal surfaces feebly shining, distinctly punctate, pubescent with fimbriate borders. Head, pronotum, appendages including mouthparts, straw yellow, with meso- metacoxae slightly darkened; head slightly darker and oranger than pronotum; scutellar shield medium brown; elytron medium brown with apex narrowly yellow, epipleuron yellow brown; pubescence shiny, off white. Venter predominantly brown, darkest on meso-, metaventrite; prosternum pale yellow; mesepimeron paler than surrounding sclerites with margins narrowly darkened; abdomen pale brown, lighter, yellower toward apex; tarsal claw, mandibular apex dark reddish amber. Dorsal punctation moderately coarse; punctures separated by approximately 1× diameter, on elytron equal in width to eye facet, finer on head, pronotum. Dorsal pubescence semi erect, moderately dense, evenly distributed, lacking distinct setal pattern; individual setae equal to about 2/3 to 1× length of scutellar shield, arcuate; elytral setae mostly directed posteriorly except directed outwardly at sides of body, posterolaterally near suture. Head large, 0.70× width of pronotum; eye large, finely facetted, with interfacetal setae, weakly notched near antennal insertion by small rounded ocular canthus; inner orbits arcuate, strongly diverging toward vertex, weakly diverging toward clypeus, with minimum separation at slightly below midlength; interocular distance 1.5× width of eye in frontal view. Antenna composed of 10 antennomeres; antennomere 3 elongate, about 2.3× length of antennomere 4; last 4 antennomeres forming gradual club expanding apically from antennomere 7–9; antennomere 10 subrhomboidal, slightly narrower, slightly longer than 9. Maxillary palp with terminal palpomere elongate, moderately expanded distally; with oblique apex. Pronotum transverse, width 2.0× length, weakly, evenly convex. Elytron in dorsal view with lateral margin weakly arcuate; elytral apices dehiscent. Ventral surfaces pubescent, distinctly punctate, except glabrous, impunctate in posterior 4/5ths of metacoxal plate; punctation coarser, denser on abdomen. Prosternum (Fig. 25) with carinae of intercoxal process extending nearly to apex, weakly convergent, framing subtriangular depression with broadly rounded apex. Suture between abdominal ventrites 1 and 2 distinct, linear; 5th , 6th ventrite with apex shallowly, roundly emarginate in median ½. Tarsal claw with broad scythe-like inner tooth extending from base to apical 1/3rd or beyond.

Male genitalia (Fig. 29). Basal lobe in ventral view (Fig. 29b) subparallel in basal half, strongly tapered toward apex in distal half, terminating in small hook-shaped swelling resembling vulture's head (Fig. 29d), distinctly shorter than paramere; in lateral view weakly sinuous (Fig. 29a), with apex nearly flat; paramere elongate, gradually expanded, apically rounded, about 3.0× as long as wide, subequal in length to longest setae. Penis (Fig. 29c) lacking apical flagellum, slender with wedge-shaped capsule.

Female (Fig. 14). Similar to male except slightly smaller on average with more extensive brown pigmentation; base of head orange brown; pronotum brown with anterolateral margins yellowish; posterolateral angle of hypomeron, submentum medium brown; prosternum dark brown. 5th abdominal ventrite with posterior margin linear; 6th ventrite with posterior margin arcuate. Tarsal claw with short triangular tooth near base, not extending beyond apical ½.

Variation. Length 1.5–2.0 mm. Individuals vary slightly in the extent and intensity of dark pigmentation on dorsal and ventral surfaces.

Trophic relations. Larvae develop on food bodies of *P. holdridgeianum.*

Etymology. Clotho, proper noun in apposition, Classical Latin from Greek κλώθω *(klotho)*, to spin. In Greek mythology, the youngest of the three Fates or Moirae; the spinner of the thread of life.

Type material. Holotype (male) with labels: "COSTA RICA: San José: Zurqui de Moravia, 1600m, II–III.2014, P. Hanson / ex. *Piper holdridgeiana*" (USNM) and 5 paratypes (2 males, 3 females) with same labels as holotype (2, USNM; 3 MZUCR).

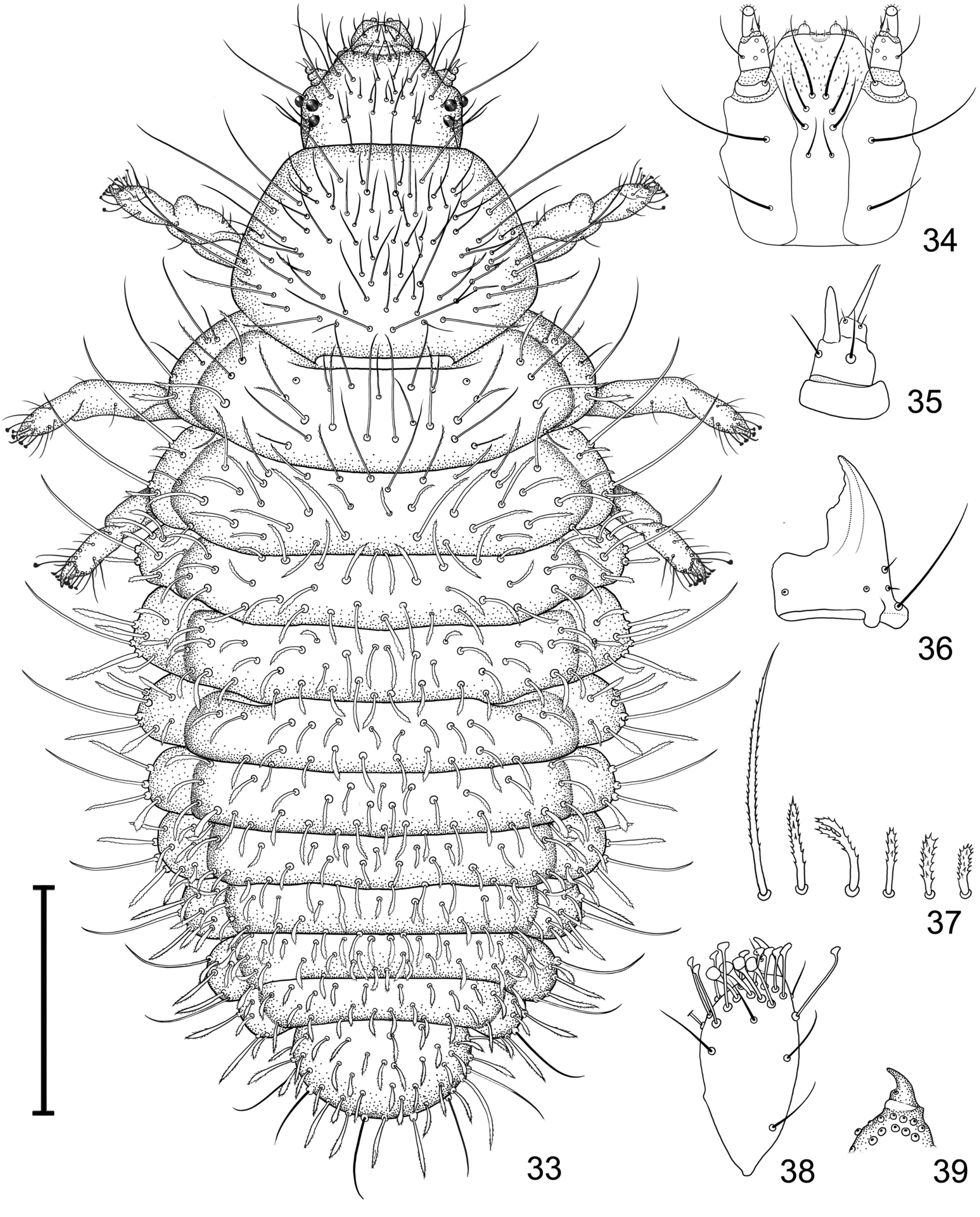
***Moiradiomus lachesis* sp. nov.**

(Figs. 15, 16, 26, 30, 40)

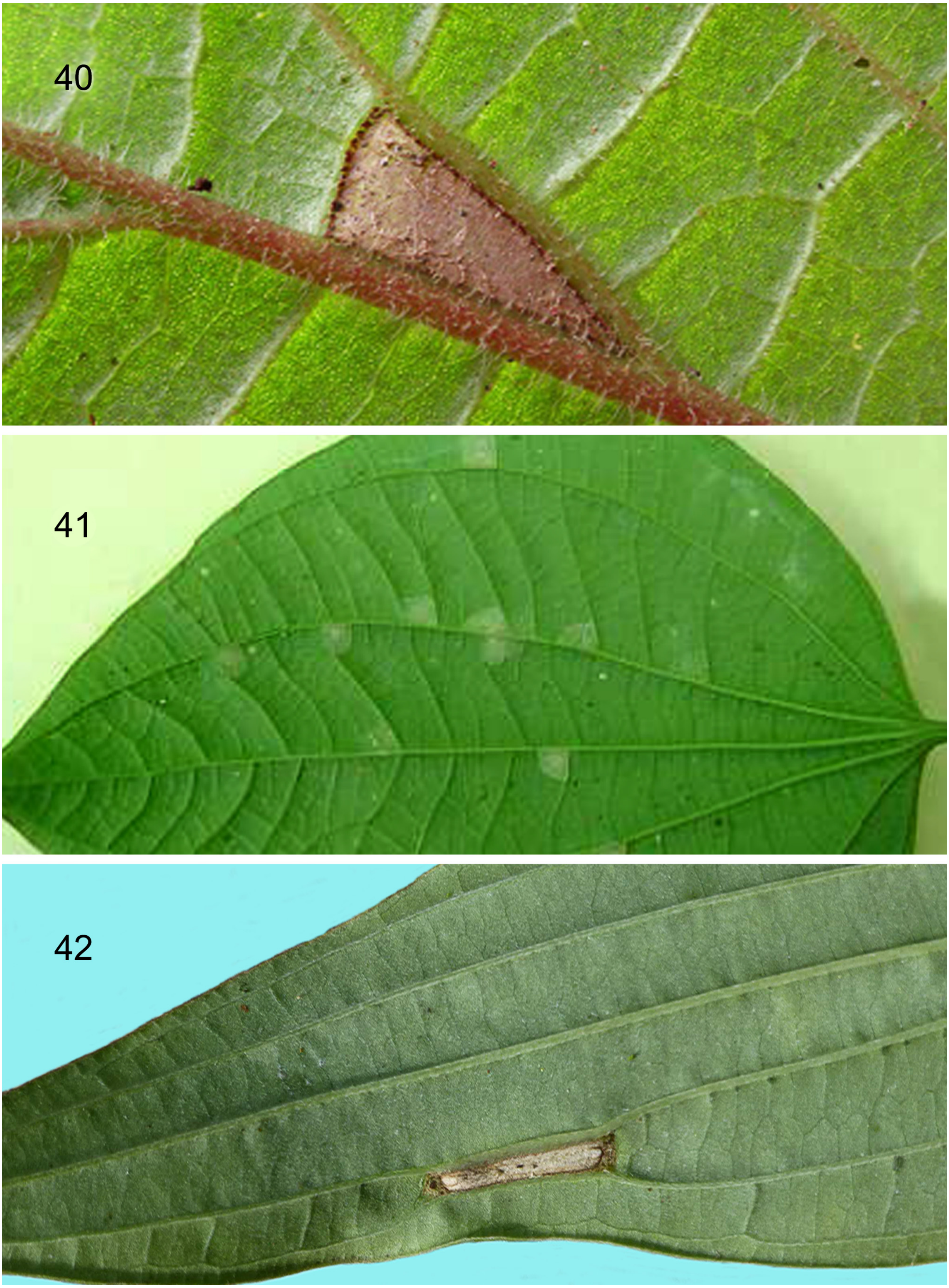
Diagnosis. This species is readily distinguished from its congeners by the male genitalia (Fig. 30) which are most similar to those of *M. atropos* except the basal lobe is nearly flat in lateral view with apex weakly sinuous and parameres apically rounded. In addition, the adult head is smaller relative to the pronotum (Fig. 15, 16) than in the other known species. The prosternal carinae (Fig. 26) are more strongly convergent, framing a subtriangular depression with attenuate, narrowly rounded apex. It is also distinguished by its larval host plant: *P. lanosibracteum* Trelease, 1929.

Description of holotype (male) (Fig. 15). Length 1.9 mm, width 1.1 mm. Form elongate, oval, weakly convex. Metathoracic wing present. Dorsal surfaces feebly shining, distinctly punctate, pubescent with fimbriate borders. Head, pronotum, appendages including mouthparts, straw yellow, with meso- metacoxae slightly darkened; pronotum with indistinct darker dapples in median area near base; elytron medium brown with apex narrowly yellow; scutellar shield paler yellow brown with margins narrowly darkened; elytral epipleuron yellow brown; pubescence shiny, off white. Venter predominantly brown, darkest on meso-, metaventrite; prosternum pale yellow; mesepimeron, mesepisternum paler than surrounding sclerites with margins narrowly darkened; abdominal ventrite 3 pale yellow brown, ventrites 4–6 yellow; tarsal claw, mandibular apex dark reddish amber. Dorsal punctation moderately coarse; punctures separated by approximately 1× diameter, on elytron equal in width to eye facet, finer on head, pronotum. Dorsal pubescence semi erect, moderately dense, evenly distributed, lacking distinct setal pattern; individual setae equal to about 2/3 to 1× length of scutellar shield, arcuate; elytral setae mostly directed posteriorly except directed outwardly at sides of body, posterolaterally near suture. Head moderate sized, 0.62× width of pronotum; eye large, finely facetted, with interfacetal setae, weakly notched near antennal insertion by small rounded ocular canthus; inner orbits arcuate, strongly diverging toward vertex, weakly diverging toward clypeus, with minimum separation at slightly below midlength; interocular distance 1.6× width of eye in frontal view. Antenna composed of 10 antennomeres; antennomere 3 elongate, about 2.0× length of antennomere 4; last 4 antennomeres forming gradual club expanding apically from antennomere 7–9; antennomere 10 subrhomboidal, slightly narrower, slightly longer than 9. Maxillary palp with terminal palpomere short, strongly expanded distally; with oblique apex. Pronotum transverse, width 2.4× length, weakly, evenly convex. Elytron in dorsal view with lateral margin weakly arcuate; elytral apices dehiscent. Ventral surfaces pubescent, distinctly punctate, except glabrous, impunctate in posterior 4/5ths of metacoxal plate; punctation coarser, denser on abdomen. Prosternum (Fig. 26) with carinae of intercoxal process extending nearly to apex, strongly convergent, framing subtriangular depression with attenuate, narrowly rounded apex. Suture between abdominal ventrites 1 and 2 distinct, linear; 5th , 6th ventrite with apex shallowly, roundly emarginate in median ½. Tarsal claw with broad scythe-like inner tooth extending from base to apical 1/3rd or beyond

Male genitalia (Fig. 30). Basal lobe (Fig. 30b) in ventral view weakly, evenly tapered toward oblique apex, with small thorn-like process at distal most point, distinctly shorter than paramere; in lateral view (Fig. 30a) weakly sinuous, with apex curving upwards; paramere elongate, gradually expanded, apically rounded, about 3.0× as long as wide, distinctly longer than longest setae. Penis (Fig. 30c) lacking apical flagellum, slender with wedge-shaped capsule.



FIGURES 33–39. Fourth instar larva of *Moiradiomus lachesis*: 33, dorsal habitus view, scale bar = 0.5 mm; 34, ventral view of mouthparts, enlarged; 35, right antenna, enlarged; 36, dorsal view of right mandible, enlarged; 37, diverse dorsal setae, enlarged; 38, tibiotarsus showing distribution of clavate setae, enlarged; 39, apex of tibiotarsus (setae removed) showing shape of tarsal claw, enlarged.



FIGURES 40–42. Tents of *Moiradiomus* spp.: 40, *M. lachesis* on *Piper lanosibracteum*; 41, *M. nanita* on *P. reticulatum*; 42, *M. atropos* on *P. friedrichsthalii*.

Female (Fig. 16). Similar to male except less elongate, slightly smaller on average, moderately convex; brown areas darker brown, more extensive than in male; scutellar shield same color as elytron; elytral epipleuron dark brown, pronotum dark brown with anterior, anterolateral margins diffusely lighter, yellowish; prosternum, mesepimeron, mesepisternum medium brown. 5th abdominal ventrite with posterior margin truncate; 6th ventrite with posterior margin arcuate. Tarsal claw with short triangular tooth near base, not extending beyond apical ½.

Variation. Length 1.5–2.0 mm. Individuals vary slightly in the extent and degree of dark pigmentation on dorsal and ventral surfaces. Scutellar shield may be same color as elytron or distinctly paler.

Trophic relations. Larvae develop on food bodies of *P. lanosibracteum* (Fig. 40).

Etymology. Lachesis, proper noun in apposition. Classical Latin from Ancient Greek Λάχεσις (Lakhesis), literally, lot; from lanchanein, to obtain by lot or fate, happen. In Greek mythology, one of the three Fates, or Moirae, who determines the length of the thread of life and a person's allotment of misery and suffering.

Type material. Holotype (male) with labels: "COSTA RICA: San José: Zurqui de Moravia, 1600m 28.III.2014, P. Hanson / ex. *Piper lanosibracteum*" (USNM) and 5 paratypes (2 males, 3 females) with same labels as holotype (2, USNM; 3, MZUCR).

Moiradiomus atropos sp. nov.

(Figs. 17, 18, 27, 31, 42)

Diagnosis. This species is readily distinguished from its congeners by the male genitalia which have the basal lobe distinctly humped in lateral view and apex of parameres obliquely truncate. In addition, the adult form is more slender and apically tapered and the prosternal carinae are weakly convergent, framing an elongate ovoid depression with broadly rounded apex. It is also distinguished by its larval host plant: *P. friedrichsthalii* Casimir de Condolle, 1869.

Description of holotype (male) (Fig. 17). Length 1.7 mm, width 1.0 mm. Form elongate, oval, tapered apically, weakly convex. Metathoracic wing present. Dorsal surfaces feebly shining, distinctly punctate, pubescent with fimbriate borders. Head, pronotum, appendages including mouthparts, straw yellow, with meso- metacoxae slightly darkened; base of pronotum in front of scutellar shield with light brown transverse mark; scutellar shield light brown; elytron light brown with apex narrowly yellow brown, epipleuron yellow brown, nearly transparent; pubescence shiny, off white. Venter predominantly light brown; prosternum pale yellow; mesepimeron, mesepisternum paler than surrounding sclerites except posterior margin of mesepimeron narrowly darkened; abdomen light brown, lighter, yellower toward apex; tarsal claw, mandibular apex dark reddish amber. Dorsal punctation moderately coarse; punctures separated by approximately 1× diameter, on elytron equal in width to eye facet, finer on head, pronotum. Dorsal pubescence semi erect, moderately dense, evenly distributed, lacking distinct setal pattern; individual setae equal to about 2/3 to 1× length of scutellar shield, arcuate; elytral setae mostly directed posteriorly except directed outwardly at sides of body, posterolaterally near suture. Head large, 0.80× width of pronotum; eye large, finely facetted, with interfacetal setae, weakly notched near antennal insertion by small rounded ocular canthus; inner orbits arcuate, strongly diverging toward vertex, weakly diverging toward clypeus, with minimum separation at slightly below midlength; interocular distance 1.5× width of eye in frontal view. Antenna composed of 10 antennomeres; antennomere 3 elongate, about 2.3× length of antennomere 4; last 4 antennomeres forming gradual club expanding apically from antennomere 7–9; antennomere 10 subrhomboidal, slightly narrower, slightly longer than 9. Maxillary palp with terminal palpomere short, strongly expanded distally; with oblique apex. Pronotum transverse, width 2.0× length, weakly, evenly convex. Elytron in dorsal view with lateral margin weakly arcuate; elytral apices dehiscent. Ventral surfaces pubescent, distinctly punctate, except glabrous, impunctate in posterior 4/5ths of metacoxal plate; punctation coarser, denser on abdomen. Prosternum (Fig. 12) with carinae of intercoxal process extending nearly to apex, weakly convergent, framing elongate ovoid depression with broadly rounded apex. Suture between abdominal ventrites 1 and 2 distinct, linear; 5th, 6th ventrite with apex shallowly, roundly emarginate in median ½. Tarsal claw with broad scythe-like inner tooth extending from base to apical 1/3rd or beyond.

Male genitalia (Fig. 31). Basal lobe in ventral view (Fig. 31b) weakly, unevenly tapered toward oblique apex, with small thorn-like process at distal most point, distinctly shorter than paramere; in lateral view (Fig. 31a) with strong hump, apex flat; paramere elongate, strongly expanded toward obliquely truncated apex, about 2.5× as long as wide, about 2× longer than longest setae. Penis (Fig. 31c) lacking apical flagellum, slender with wedge-shaped capsule.

Female (Fig. 18). Similar to male except pronotum with brown blotch occupying median 2/3; pronotal base with narrow brown margin. 5th abdominal ventrite with posterior margin truncate; 6th ventrite with posterior margin arcuate. Tarsal claw with short triangular tooth near base, not extending beyond apical ½.

Variation. Length 1.5–1.7 mm. Individuals vary in the intensity of brown pigmentation on dorsal and ventral surfaces.

Trophic relations. Larvae develop on food bodies of *P. friedrichsthalii* (Fig. 42).

Etymology. Atropos, proper noun in apposition. Ancient Greek Ἄτροπος (Atropos), literally meaning inflexible or not turning, from the Greek a-, (not) + tropos, (to turn). In Greek mythology, one of the three Fates, or Moirae; the cutter of the thread of life, depicted as an old woman.

Type material. Holotype (male) with labels: "COSTA RICA: Alajuela: Res. Biol. A. Brenes (San Ramon), 900m 16.IV.2014, P. Hanson / ex. *Piper friedrichsthalii*" (USNM) and 5 paratypes (4 males, 1 female): 1 with same labels as holotype; 4 with labels: "COSTA RICA: Alajuela: Res. Biol. A.Brenes, ex. *Piper friedrichsthalii*, V.2017, E. Chacon" (3, USNM; 2, MZUCR).

Moiradiomus nanita sp. nov.

(Figs. 19, 20, 28, 32, 41)

Diagnosis. This species is readily distinguished from its congeners by the male genitalia (Fig. 32) with its short, broad paramere (length only 2× width), basal lobe in ventral view strongly tapered toward apex with rounded apical knob, and penis tube with slight angulation and irregular swelling near distal ½. In addition, the adult form (Figs. 19, 20) is smaller and relatively shorter than in the other species, and the prosternal carinae (Fig. 28) are nearly parallel, framing a subtrapezoidal depression. It is also distinguished by its larval host plant: *P. reticulatum* L., 1753.

Description of holotype (male) (Fig. 19). Length 1.3 mm, width 0.9 mm. Form shortened, oval weakly convex. Metathoracic wing present. Dorsal surfaces feebly shining, distinctly punctate, pubescent with fimbriate borders. Head, pronotum, appendages including mouthparts, straw yellow, with meso- metacoxae slightly darkened; base of pronotum in front of scutellar shield with light brown smudge; scutellar shield light brown; elytron light brown with apex narrowly yellow brown, epipleuron yellow brown, nearly transparent; pubescence shiny, off white. Venter predominantly light brown; prosternum pale yellow; mesepimeron, mesepisternum paler than surrounding sclerites except posterior margin of mesepimeron narrowly darkened; abdomen light brown, lighter, yellower toward apex; tarsal claw, mandibular apex dark reddish amber. Dorsal punctation moderately coarse; punctures separated by approximately 1× diameter, on elytron equal in width to eye facet, finer on head, pronotum. Dorsal pubescence semi erect, moderately dense, evenly distributed, lacking distinct setal pattern; individual setae equal to about 2/3 to 1× length of scutellar shield, arcuate; elytral setae mostly directed posteriorly except directed outwardly at sides of body, posterolaterally near suture. Head large, 0.80× width of pronotum; eye large, finely facetted, with interfacetal setae, weakly notched near antennal insertion by small rounded ocular canthus; inner orbits arcuate, strongly diverging toward vertex, weakly diverging toward clypeus, with minimum separation at slightly below midlength; interocular distance 1.2× width of eye in frontal view. Antenna composed of 10 antennomeres; antennomere 3 elongate, about 1.8× length of antennomere 4; last 4 antennomeres forming gradual club expanding apically from antennomere 7–9; antennomere 10 subrhomboidal, slightly narrower, slightly longer than 9. Maxillary palp with terminal palpomere short, strongly expanded distally; with oblique apex. Pronotum transverse, width 2.0× length, weakly, evenly convex. Elytron in dorsal view with lateral margin weakly arcuate; elytral apices dehiscent. Ventral surfaces pubescent, distinctly punctate, except glabrous, impunctate in posterior 4/5ths of metacoxal plate; punctation coarser, denser on abdomen. Prosternum (Fig. 28) with carinae of intercoxal process extending to apex, subparallel, framing subtrapezoidal depression. Suture between abdominal ventrites 1 and 2 distinct, linear; 5th ventrite with apex truncate; 6th ventrite with apex shallowly, roundly emarginate in median ½. Tarsal claw with broad scythe-like inner tooth extending from base to apical 1/3rd or beyond.

Male genitalia (Fig. 32). Basal lobe in ventral view (Fig. 32b) strongly, unevenly tapered toward apex, with small knob at distal most point, slightly shorter than paramere; in lateral view (Fig. 32a) nearly flat in basal 2/3rds sinuous in apical third with upturned apex; paramere short and broad, strongly expanded toward obliquely rounded apex, about 3.0× as long as wide, slightly longer than longest setae. Penis (Fig. 32c) lacking apical flagellum, slender with irregular swelling at apical ½; capsule wedge shaped.

Female (Fig. 20). Similar to male except pronotum light brown; prosternum, mesepimeron, mesepisternum medium brown. 5th abdominal ventrite with posterior margin truncate; 6th ventrite with posterior margin arcuate. Tarsal claw with short triangular tooth near base, not extending beyond apical ½.

Variation. Length 1.1–1.5 mm. Individuals vary slightly in the extent and degree of dark pigmentation on dorsal and ventral surfaces.

Trophic relations. Larvae develop on food bodies of *P. reticulatum* (Fig. 41).

Etymology. Nanita, proper noun in apposition, from Nan (a version of Ann) + ita (diminutive). A reference to an old nursery rhyme or cantrip used to encourage a coccinellid to fly from your fingertip: *Ladybird, ladybird, fly away home. Your house is on fire. Your children all roam, except little Nan, who sits in a pan, weaving gold laces as fast as she can.*

Type material. Holotype (male) with labels: "COSTA RICA: Heredia: OTS-La Selva, 100m II.2013, P. Hanson / ex. *Piper reticulatum*" (USNM); 9 paratypes (4 males, 5 females): 8 with same labels as holotype; 1 with labels: "COSTA RICA: Puntarenas: Rincon de la Osa, I.2017, P. Hanson / ex. *Piper reticulatum*" (5, USNM; 4, MZUCR).

Key to species of *Moiradiomus*

The species of *Moiradiomus* can be readily separated by characteristics of the male genitalia and the species of larval host plant. Additional morphological and color differences are added to the key as confidence characters, but we project that these will prove insufficient for identification purposes, particularly considering our small sample sizes and the potentially large number of undescribed species in the genus.

1. Male genitalia with short, broad paramere (length only 2× width) (Fig. 32a); basal lobe in ventral view (Fig. 32b) strongly tapered toward apex with rounded apical knob. Penis tube (Fig. 32c) with slight angulation and irregular swelling near distal ½. Larvae develop on food bodies of *P. reticulatum*. Adults proportionally shorter (Figs. 19, 20) than other known species, with prosternal carinae (Fig. 28) nearly parallel, framing subtrapezoidal depression . . . . *M. nanita,* **n. sp.**

1'. Male genitalia with paramere longer (length approximately 2.5–3.0× width) (Figs. 29a, 30a, 31a); basal lobe not as above. Penis tube without angulation and swelling near distal ½ (Figs. 29c, 30c, 31c). Larvae develop on other *Piper* hosts. Adult form elongate oval (Figs. 13–18), prosternal carinae more or less distinctly converging toward apex, framing subtriangular to ovoid depression (Figs. 25–27) 2

2. Male genitalia with basal lobe strongly unevenly tapered in apical half (Fig. 29b), terminating in hook-shaped process resembling a vulture's head (Fig. 29d). Larvae develop on food bodies of *Piper holdridgeianum*. Adult with terminal maxillary palpomere elongate, moderately expanded distally (Figs. 13, 14). . . . . *M. clotho*, **n. sp.**

2.' Male genitalia with basal lobe nearly parallel-sided in apical half, terminating in oblique apex (Figs. 30b, 31b). Larvae develop on other *Piper* hosts. Adult with terminal maxillary palpomere short, strongly expanded distally (Figs. 15–18) 3

3. Basal lobe of male genitalia with pronounced dorsal hump at basal 1/3, forming a conspicuous subangulation in lateral view (Fig. 31a). Prosternum with strongly convergent carinae framing subtriangular depression with attenuate, narrowly rounded apex (Fig. 27). Larvae develop on food bodies of *Piper friedrichsthalii*. Adult form narrow, tapered toward apex; male with scutellar shield same color as elytron, and base of pronotum in front of shield with light brown transverse mark (Fig. 17) . . . . *M. atropos*, **n. sp.**

3'. Basal lobe of male genitalia with dorsal surface nearly flat, weakly sinuous in lateral view (Fig. 30a). Prosternum with weakly convergent carinae framing elongate ovoid depression (Fig. 26). Larvae develop on food bodies of *Piper lanosibracteum*. Adult form less narrow, oval with lateral margins nearly parallel-sided, then rounded off in apical 2/5; male scutellar shield may be paler than elytron and base of pronotum in front of shield without brown transverse mark (Fig. 15). . . . . *M. lachesis.,* **n. sp.**

Biology of *Moiradiomus* species

The larvae of all four species of *Moiradiomus* described above construct small tents on the leaves of *Piper* and inside these shelters they induce the production of food bodies. The larval tents contain fibers that resemble silk in that they are very thin, shiny white and are secreted by the mouthparts of the larva. When approximately 30 tents were removed from *P. reticulatum* and incinerated, the odor resembled that of burned hair and resulted in dry particulate ash, which is consistent with this material being silk. Although we use the term "silk", further research is required to verify that this is indeed the material secreted by the larvae.

The tents are always situated on the underside of the leaf and the silk is usually attached to leaf veins, which serve as walls for their shelter. There was never more than one larva inside a tent. Eggs were not observed but on a few occasions very young, apparently recently eclosed larvae were observed in the initial stages of tent construction. Based on these limited observations it appears that the young larvae begin by constructing a smaller tent, but they soon expand it to its final size. Very small larvae (probably first instars) were frequently observed in full-sized tents.

Larvae of *M. lachesis* on *P. lanosibracteum* usually construct a triangular-shaped tent at the intersection of a secondary vein with the primary (central) vein, and the apical end of the tent is attached to a small tertiary vein joining the other two veins (Fig. 40). There was nearly always a thin, brown, necrotic line on the periphery, where the tent was attached to the leaf veins, which is possibly a result of chewing by the larva. Most tents of *M. lachesis* were located in the basal half of the leaf, probably due to the absence of secondary veins originating in the apical part of the leaf. The tents are 3–8 mm in length, with an apical width of 2–5 mm, the most common size being 4–5 mm long and 3 mm wide (42% of 62 tents measured). The number of tents per leaf varied from one to eight. From a total of 88 affected leaves collected on three separate dates at Zurquí de Moravia, 65% had just one per leaf, 26% had two per leaf, 7% had three per leaf, and the remaining 2% had four to eight.

The shape and placement of the tents of *M. clotho* on *P. holdridgeianum* are similar to those of *M. lachesis* described above, but the tents of the other two species are slightly different, possibly due to differences in the leaf venation of their host plants. The leaves of *P. reticulatum* lack a prominent central vein and instead have five primary veins radiating from the base of the leaf. On this plant *M. nanita* constructs either a triangular tent at the extreme base of the leaf, between two primary veins, or a more quadrate-shaped tent beween a primary vein and two secondary veins (Fig. 41). For reasons that remain unclear, the vast majority of tents observed at the La Selva Biological Station in northeastern Costa Rica were located in the latter position (often in high numbers), while the majority of those at Rincón de la Osa in southwestern Costa Rica were located at the base of the leaf.

The tents of *M. atropos* on *P. friedrichsthalii* are elongate, rectangular in form and are usually located between two secondary veins, sometimes at the base where these two veins meet, but often more apically (Fig. 42). It appears that larval chewing along the edges of the veins (where the tent is attached) results in a thickening of the veins and the upper surface of the leaf becoming slightly convex; moreover, the two secondary veins become drawn closer together in the area containing the tent.

All larval instars appear to contribute to the construction of the tent, and the latter changes over time as the larva develops. Tents with very young larvae are white, soft, and have relatively few fibers, allowing one to see the larva inside. The fibers form a fine, net-like pattern as opposed to the linear threads produced by many spiders. Over time the tents become light brown, more parchment-like, and opaque, making it impossible to see the larva inside without cutting open the tent; however, mature quadrate tents of *M. nanita* are usually less opaque. In *M. lachesis* the absence of trichomes from the floor and walls of the chamber (i.e. the leaf blade and sides of the veins, respectively), and their presence in the tent, strongly suggest that the young larva cuts trichomes and incorporates them into the initial silken threads. In all four species the inner surface of older tents contains numerous amorphous patches that consist of membranes from collapsed food bodies, presumably after the larva has sucked out the contents. On one occasion an older larva was observed lifting a collapsed food body toward a small hole in the tent that was created with forceps in the laboratory. The gradual accumulation of collapsed food bodies and natural aging of the materials probably account for the older tents becoming more opaque.

On four occasions forceps were used to make a small hole in a young tent of *M. lachesis* on a recently collected leaf and after a couple hours one or two very thin, silken threads were observed across the hole. Apparently the larva attempted to repair the damage, although in none of these cases was the hole completely covered. In one case the larva was observed secreting silken fibers from its mouthparts across the hole.

Larvae were never observed outside the tents, nor were any larval exit holes ever observed. Moreover, there appears to be no need for the larvae to leave their tents since the quantities of food bodies found inside can be quite astounding, often 50–100 (of variable size), representing a combined volume greater than that of the young larva. The food bodies occur on the floor of the chamber (the leaf lamina) as well as the walls (the sides of the leaf veins). On a couple of occasions a larva was observed feeding on a food body, during which time it remained very still, except for minor movements of its legs. Larvae maintained in undisturbed tents on detached leaves in the laboratory remained alive for up to three weeks, presumably feeding on the accumulated food bodies.

The larvae of all four species are white colored, although very young larvae are sometimes light yellowish, at least in *M. nanita*. The pupae are obtect as in other coccinellids, but white in color. Unlike many other coccinellids the pupae are not attached to the leaf, probably because they are enclosed in the tent. There is no cocoon. Adult emergence of *M. lachesis* at Zurqui de Moravia (1600 m) appears to occur primarily from March through May. On the other hand, preliminary observations suggest that the life cycle of *M. nanita* in La Selva (100 m) is less synchronized (both young larvae and pupae were found in January). Teneral adults are yellowish, becoming darker with time, and they often remain inside the tent for some time before chewing a hole in the roof and emerging. Adult emergence holes are larger (about 1.5 mm across) and more oval shaped than the smaller more circular holes of parasitoids.

On April 20, 2010, 49 tents of *M. lachesis* were collected at Zurquí de Moravia and dissected in the laboratory. Of these, 32% were parasitized (as evidenced by a parasitoid larva, pupa, or emergence hole), 24% were torn open (probably by predators), 20% had live beetle larvae, 16% showed successful emergence by adult beetles, and 6% had decomposing beetle larvae. In some cases the tent was completely absent rather than merely torn open, but the previous presence of a larva was indicated by brown necrotic lines on the veins where the tent had been attached. The vast majority of parasitoids reared from *M. lachesis* over a period of four years were *Galeopsomyia* sp. (Eulophidae: Tetrastichinae).

Newly emerged (< 24 hours) adults of *M. lachesis* reared in the laboratory were used to observe adult feeding habits. Three adult beetles were placed individually in glass vials closed with cotton and provided with one of the following: whitefly eggs with first instar nymphs, first instar ortheziid nymphs, or sooty mold on a citrus leaf. During periodic observations over a two-hour period the beetles did nothing but walk around the vial, occasionally attempting to fly. After 24 hours the number of potential prey items in the vials had not changed. Two adults were then provided with cut pieces of *Piper umbellatum* L., 1753 leaves containing food bodies (larval tents have never been observed on this species). Upon encountering a food body the rapid walking ceased immediately and the contents of the food body were consumed. Over a two hour period one of the adults consumed 14 food bodies. Although these results are based on a very limited sample size, they strongly suggest that the adult beetles, like the larvae, feed on food bodies. Preliminary observations suggest that, before they emerge from the tent, adults do not induce food body production, but rather utilize food bodies that were not consumed in the larval stage, but this requires confirmation. After emergence it is possible that the adults fly from plant to plant (including non-host species of *Piper*) in search of scattered food bodies that occur naturally on *Piper*. Adult behavior in the field, however, is difficult to observe since they are very active and readily drop from the plant.

Concluding remarks

The four species of *Moiradiomus* described here share at least two unusual characteristics with respect to other Coccinellidae, and indeed with respect to other Coleoptera. First, the larvae produce silk, or a silk-like substance, the identity of which requires confirmation. This “silk” appears to be extruded from the mouthparts, presumably from mandibular glands since Coleoptera are said to lack maxillary and labial glands (Chapman 1998), though this merits further investigation. Coleopteran larvae generally produce silk in the Malpighian tubules and it is most commonly produced only by the last instar to form a cocoon (Sutherland *et al.* 2010). The larvae of *Moiradiomus* are therefore unusual with regard to the origin of the silk, the way they use it (in constructing tents), and the production of silk by early and possibly all instars. Our literature search turned up a single reference (Meyerdirk 1983) to silk production in another diomine, *Diomus pumilio* [as *D. flavifrons* (Blackburn, 1889)]. This species was described as having a “loosely woven silk pupal case.” However, the photograph purportedly showing this structure (Meyerdirk 1983:1276, fig. 4) gives a dorsal and ventral view of a pupa covered with erect setae and with a shed larval skin attached to the caudal end that partially covers some of the abdominal sternites. These features occur in other diomine pupae such as *D. lupusapudoves*, and since no separate silk pupal case or cocoon was evident, we suspect the author may have misinterpreted what he saw. No reference specimens were available for examination, but the author indicated (Meyerdirk, pers. com.) that he did not recall actually observing silk spinning in the larva.

The second unusual feature of *Moiradiomus* species is their food source, namely food bodies on *Piper*. This represents the first known occurrence of completely phytophagous lady beetles outside of the tribe Epilachnini (sens. Ślipiński 2007). However, the type of phytophagy exhibited by *Moiradiomus* differs from that of the folivorous Epilachnini whose mandibles (Fig. 21) are adapted for biting-off and roughly processing plant tissue (Kovář 1996).

We examined the mandible of *Moiradiomus* adults for any signs of special adaptations for feeding on food bodies, and were initially excited to discover the secondary dentition along the incisor blade of the adult (Fig. 23, left), which is similar to that found in *Bulaea* spp. (Fig. 22). However, this same dentition was found in all other adult Diomini that we subsequently dissected, including exemplars of *Decadiomus* and *Diomus* (representing coccidophagous and aphidophagous species).

The larval mandible of *Moiradiomus* has a unidentate apex and shallow incisor groove, as found in *Diomus* (Rees *et al*. 1994; Ślipiński 2007; Akbar *et al*. 2009) and *Decadiomus* (Böving 1933). These features appear to be common in taxa that practice extraoral digestion (Samways *et al.* 1997) which involves injecting their prey with hydrolytic enzymes and then sucking out the liquified body contents (Giorgi *et al*. 2009). Larvae of *Diomus terminatus* and *D. notescens* Blackburn, 1889 have been observed to suck out the liquid contents of their aphid prey and discard the collapsed husk (Hopkinson *et al.* 2016; Akbar *et al*. 2009). We observed a similar process in *Moiradiomus* larvae, which feed on the liquid contents of food bodies and then use the collapsed food bodies to reinforce their tents.

It appears, then, that the primary features of the adult and larval mandible of *Moiradiomus* have not undergone modification to reflect a change of dietary habits. This observation corresponds to that of Samways *et al*. (1997) who report that mandible shape in Coccinellidae "does not appear to be especially restricting for changes in diet either in the ecological sense or over evolutionary time," and a related observation about Erotylidae by Leschen and Buckley (2007) that "Shifts among saprophagy, pollen, and microfungal diets do not necessarily require changes in mouthpart morphology" in contrast to other shifts to diets that are physically very different in form and texture.

We do not know the function or the homology of the median angulation on the incisor blade of the *Moiradiomus* larva, but we speculate that it may be utilized in scarring *Piper* leaf tissue, producing the necrotic lines on veins where the silk is attached, and perhaps used to induce food body production. Species of *Diomus* and *Decadiomus* sometimes exhibit molar projections of various sorts, but no median angulation has thus far been reported (Böving 1933; Rees *et al*. 1994; Ślipiński 2007; Akbar *et al*. 2009). The ability of *Moiradiomus* larvae to induce the production of food bodies is unusual, although this habit is known to occur in a clerid beetle and at least one ant species (see "Piper *food bodies and their insect associates*," above). Species of *Moiradiomus* appear to be restricted to *Piper* since their distinctive larval tents have never been observed on any other plants, at least in Costa Rica, but obviously it has not been possible to systematically examine the entire flora of the country.

With regard to their host plant associations, two questions require further investigation in order to estimate the potential species richness of *Moiradiomus*. First, how host specific are the species? The four species described here appear to be very host specific. Second, what proportion of *Piper* species harbor *Moiradiomus* larvae? Non-host plants are very difficult and laborious to document, but at least two Costa Rican *Piper* species that have been extensively examined in numerous sites never had larval tents. On the other hand, tents have been observed on at least five *Piper* species from which adult beetles have not yet been reared and potentially represent five additional new species. However, field sampling in Costa Rica has been haphazard rather than systematic and so the answers to these questions remain unknown. Nonetheless, even if less than half the *Piper* species harbor *Moiradiomus*, but the species are as host specific as our evidence suggests, the tent-weaving lady beetles could potentially comprise a large number of species, given the species richness of *Piper*. A recent taxonomic revision of the Costa Rican *Piper* species resulted in an increase from 93 to 331 described species (Callejas 2014). Further research on these lady beetles will obviously require collaboration with courageous botanists.

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