A TAXONOMIC REVISION OF *HYPOGENA* (COLEOPTERA: TENEBRIONIDAE) AND A REVIEW OF ANTENNAL SENSORY STRUCTURES IN TENEBRIONIDAE

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ABSTRACT

Tenebrionidae is a diverse, worldwide family of beetles comprising approximately 20,000 species in 2,300 genera (Bousquet *et al.*, 2018). *Hypogena* Dejean 1831 is a genus of 13 species of subcortical, horned beetles in the family. This genus is primarily identified using male specific characters like the presence of cephalic horns and aedeagal structures. *Hypogena* is currently placed within the tribe Triboliini, but recent phylogenetic work indicates that the current generic composition of Triboliini is paraphyletic. Scanning electron microscopy (SEM) is used to identify cryptic characters in *Hypogena* that separate it from other Triboliini genera. Additionally, four new species of *Hypogena* are described here.

Within Tenebrionidae, as with most other insects, antennae are important chemoreceptors and are putatively under a significant amount of selection pressure. In the present study, scanning electron microscopy was used to examine stellate sensoria within the family. The presence of stellate sensoria is a highly conserved trait within Tenebrionidae. Sensoria types are mapped onto a recent phylogeny of Tenebrionidae to identify patterns in sensoria evolution and classify the patterns into distinct character states. Results indicate that stellate sensoria, presence and type, are useful for delimiting higher level taxa within Tenebrionidae. Finally, this study outlines a relatively low cost method of antenna specimen preparation for examination with a scanning electron microscope. This will allow future researchers to examine stellate sensoria in other groups of Tenebrionidae to further test hypotheses presented here.

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Chapter 1: A taxonomic review of *Hypogena* Dejean, 1831 (Coleoptera: Tenebrionidae)

Introduction

The genus *Hypogena* was first described by Dejean in 1831 and is currently in the tribe Triboliini in the family Tenebrionidae. This is a group of relatively rarely collected beetles where the females are difficult to identify. Potentially due to these reasons, this group has not had a full revision. Dejean's original publication contained eight *nomen nudem* (Spillman, 1973). Spillman (1973) resurrected the name *Hypogena* from the junior synonym *Ulosonia* Laporte, 1840, in the tribe Ulomini. *Hypogena* species are distributed from the US states of Florida, Arizona, and California to Argentina (Steiner, 2005, Blackwelder, 1945). *Hypogena* are known to come to light traps and live predominantly under loose bark of dead trees. They have a distinct dorsoventrally flattened form and range in size from 5 mm (*H. marginalis*) to 10 mm (*H. biimpressa*). The males of all known species have two or three distinct horns on their heads in various sizes, lengths and projections. The larvae and the pupa for this group have not been described.

The main identifying character for this group are the prominent cephalic horns that are present on the males of all known species. Males from most of the species in this genus have three horns: a clypeal horn and two supraorbital horns. In some species, the clypeal horn is not present. There is currently only one *Hypogena* key (Kulzer, 1962), which uses characters associated with the horns, pronotal puncturing, the overall length of the beetle, the depth of the elytral striae, and the elytral puncturing (Kulzer, 1962). Kulzer also provides images of the aedeagi for eight of the 13 species. Kulzer's key does not allow for the identification of female specimens, and it does not

include all of the currently known species. Since 1962 several species have been described (*Hypogena cat* Steiner, 2005, *Hypogena triceratops* Steiner, 2005*,* and the fossil species *Hypogena marginalis* Doyen and Poinar, 1994). In additional, four new species are described herein.

Hypogena is currently placed within the tribe Triboliini (Aalbu, 2002). However, recent phylogenetic evidence shows that this classification may not accurately represent evolutionary history. The molecular phylogeny of Kanda (2017) placed *Hypogena* as sister to a clade containing the tribes: Cerenopini, Alleculiini, Scaurini, and Tenebrionini (in part) based a relatively dense taxon sampling of Tenebrionidae for four nuclear genes. When looking at morphology, there are several structures that show a distinct difference between *Hypogena* and the type genus of Triboliini, *Tribolium*. The most distinctive difference is the presence of stellate sensoria in *Hypogena*. Within Triboliini, only *Hypogena, Mycotrogus* and *Tharsus* bear stellate sensoria on their antenna (Doyen, 1985). Stellate sensoria are distinctive structures formed by multiple sensilla that are grouped together (Medvedev, 1977, Aloquio *et al.*, 2017).

Very little is known about the life cycles of *Hypogena* species, besides that they live subcortically under the bark of dead deciduous trees (Steiner, 2005). They are thought to prefer the bark of standing dead trees.

Material

Specimens of *Hypogena* and other triboliine genera were loaned from entomological museums. Examinations of these specimens, along with the literature

(Champion 1886; Kulzer, 1962; Spillman, 1973; Steiner, 2005), was sufficient to identify the insects to species using morphological characters.

The Paris Museum of Natural History (MNHN) was contacted, but they were unable to locate the type material for *H. biimpressa* (Latreille, 1813), *H. laevicollis* (Kulzer, 1962), or *H. amazonica* (Kulzer, 1962). The University of Sao Paulo (CEAH) was contacted for a loan, but no specimens were borrowed. The Swedish Museum of Natural History (NHRS) was contacted. As per their loan policy with type material, an image of the holotype of *H. tricornis* was received. The Zoological Museum of Kiel University (ZMUK) was contacted and images of the type specimens for *H. vacca* were obtained. A list of the collections from which loans were received is below. The bolded letters is the museum code, the first set of brackets is the curator of the museum and the second is number of specimens received.

Loans were received from:

CASC The California Academy of Science (Jere Scweikert) (432)

RLAC The Rolf L. Aalbu Collection (Rolf Aalbu) (10)

USNM Smithsonian National Museum of Natural History (Warren Steiner Jr.) (374)

FMNH The Field Museum of Natural History (Corrie Moreau) (25)

TAMU Texas A&M University Insect Collection (Edward G. Riley) (50)

EMEC The Essig Museum of Entomology (David Kavanaugh) (201)

OSAC Oregon State Arthropod Collection (Chris J. Marshall) (3)

CDFA California State Collection of Arthropods (Jaqueline Airoso) (280)

UCDC The Bohart Museum of Entomology (Lynn Kimsey) (30)

NHMB Naturhistorisches Museum in Basel (Eva Sprecher) (185)

NHMUK British Museum of Natural History (Max Barclay) (204)

FSCA Florida State Collection of Arthropods (Paul Skelley) (79)

NMPC Czech Republic National Museum (Aleš Bezděk) (31)

Methods

Morphology

The present study is based on morphological characters. Specimens were identified based on comparison to type material, previously identified specimens, and characters used in the literature (Champion, 1895; Kulzer 1962), as well as novel characters codified during this research. Male specimens, once identified, were sorted based on locality. If any females shared the same collecting event information, they were examined for similarities with the males. While examining specimens, novel characters were used to further refine species concepts.

Specimens were databased and georeferenced in mx.speciesfile.org. Specimens were then given a unique identifier (TenebrionidBase number) that corresponds to their georeferenced data. If the coordinates were not given, then they were inferred with Google Maps. Geographic ranges were made for each species once all available specimens were georeferenced. Maps were made in ArcGIS version 10 (ESRI, 2011). Maps were not made for species with only one specimen.

As this group shows some variation in the genitalia, the male genitalia were dissected from representatives from each species. The wings were dissected from *Hypogena vacca* (Fabricius, 1801), *Hypogena tricornis* (Dalman, 1823) and *Hypogena depressa* (Champion, 1886) to explore variation within the genus. Ethanol washes were used to spread the wing. After the last wash, the wing was washed in HMDS to prevent

the wing collapsing before it could be board-mounted. Prepared wings were then compared to published wing structure information for *Tenebrio molitor* (Doyen, 1966). The female genitalia were also dissected from two representatives each of *H. vacca, H depressa*, and *H. marginata.* Abdomens were cleared with 10% potassium hydroxide, then dyed with Bioquip double stain. Genitalia were then preserved in glycerin. All dissections were compared to *Tenebrio molitor* using the same language as Doyen's review of *Tenebrio* skeletal anatomy (1966).

SEM

SEM Specimen Collection

Scanning electron microscopy (SEM) was used to examine the antennal sensoria on the antennae of 19 tribes in Tenebrionidae. In this chapter the sensory structures of *Hypogena tricornis*, *Tenebrio molitor, Tribolium confusum* and *Tribolium castanaeum* are examined. The remaining tribes will be discussed in the review of stellate sensoria of Tenebrionidae. It was also used to examine cryptic morphological structures on members of *Hypogena*. Specimens of *Hypogena* were collected from Guatemala in 2016 and were preserved in 95% ethanol. They were identified and databased into mx.speciesfile.org prior to examination. Specimens of *Tenebrio molitor, Tribolium confusum* and *Tribolium castaneum* were collected from lab colonies. One antenna was removed from each specimen and placed into a low humidity environment until ready to be examined with the scanning electron microscope.

Specimen Preparation – *Hypogena* morphology

The following method is modified from the methods detailed in John Kuo's Electron Microscopy (2014, p. 462-3). Specimens were stored in 95% ethanol until dehydration. As the beetles have thick cuticle, specimens were not fixed in a buffer (Kuo, 2014). To dehydrate the specimens, they were submerged in two graded alcohol baths up to 100% for ten minutes. The 100% EtOH bath was repeated three times to remove any excess water from the insect. Specimens were then critical point dried. The structures of interest were relatively large, so the specimens were coated with gold/palladium for 75 seconds.

Specimen preparation – Antenna

Dried antennae were placed onto a stub with two-sided carbon tape so that the antennal sensoria would be in clear view of the detectors. They were then sputtercoated with gold/palladium for six seconds. If the image was obscured by charging, then they were recoated for an additional six seconds. All images of the antennal sensoria are of the terminal flagellomeres.

SEM Examination

A Zeiss Supra 40VP was used to examine all specimens. Specimens were viewed with an accelerating voltage of between five and six KeV. If charging occurred that distorted the area of interest, the accelerating voltage was decreased. If the accelerating voltage was too low (1 kV), then the working distance was also decreased. Two images were taken for each structure examined. The first was an image of the

structure of interest at a close magnification (224X-7370X magnification). The second image was taken to show the general layout of the structure of interest in relation to the rest of the organism (74-150X magnification).

Phylogenetic Analysis

The key produced by Kulzer (1962) was used to identify potentially informative characters for identification. This data, along with newly identified characters, were used to construct a morphological matrix for the genus in Mesquite 3.4 (Maddison, 2018). Any characters that were predicated upon the presence of another character were either marked normally if the original character was present or with a dash if the original character was absent. This ensures that compound characters would not be included in any phylogenetic analyses with species that do not possess those characters (Brazeau, 2011). If the character was obscured or otherwise not able to be scored, then it was marked with a question mark. The matrix contained 94 adult characters for the 13 recognized species, four new species, and seven outgroup taxa. All uninformative characters were discarded in the final analysis. *Tenebrio molitor* was used to root the resulting topologies. The only fossil for this group is a relatively young Dominican amber preserved specimen: *H. marginalis*, which was included in the matrix.

Trees were inferred from a morphological matrix of 94 characters analyzed in Paup* 4.0 (Swofford, 2003). The tree was rooted with *Tenebrio molitor* from the tribe Tenebrionini. Five genera of Triboliini are present in the analyses: *Tribolium, Latheticus, Tharsus, Mycotrogus* and *Hypogena*. Bootstrap values were determined in Paup* with 1000 replications. Posterior probabilities were determined with Mr. Bayes 3.2.6 on CIPRESS 3.3. (Huelsenbeck *et al.*, 2001; Ronquist *et al.* 2003; Miller *et al.,* 2015).

Results

Morphological examination

The sensoria on the terminal antennomeres shows that *Hypogena* has stellate sensoria that can be made up of as many as 7 to 11 sensilla that are all located in one depressed pit (Figure 1.1.A). The sensoria are primarily located on the distal and lateral edges of the antennomeres. *Tribolium castaneum* has sensoria that are made up of bifurcated sensoria (Figure 1.1.B). The sensoria are located only on the distal edge of the antennomeres. In *Tribolium confusum* the sensoria are similarly bifurcated as in *Tribolium castaneum*. The sensoria are located only on the distal edge of the antennomeres. In *Tenebrio molitor* there are simple sensoria that are located in depressed pits. The sensoria are located on the distal and lateral edges of the antennomeres and point toward the apical edge of the antennomere.

Male genitalia

Kulzer (1962) showed that the male genitalia of *Hypogena* are relatively distinctive at the species level. Some characters include: whether the basal piece is the same length as the apical piece, whether the apical piece weakly or strongly tapered distally, whether there is a tuft of setae on the parameres, whether the parameres are fused, whether there is a more membranous area on the basal piece and whether the edges of the apical piece are sinuate dorsally or laterally (Figure 1.2).

Female Genitalia

Taxonomically, female genitalia were not found to be useful in distinguishing between species of *Hypogena*. According to Tschinkel and Doyen (1980), *Tenebrio molitor* has a reduced ovipositor, fourth coxite with lateral gonostyle, and a single bursa derived spermatheca. In *Hypogena*, the coxites are highly reduced with the gonostyles arising apically from the fourth coxite. The paraprocts are large and partially enclose the coxites. The bursa copulatrix has a single spermatheca and accessory gland. The spermathecal gland has an apical spermatheca (Figure 1.3).

Wings

Wings of *Hypogena* were not considered diagnostically useful. In comparison with *T. molitor*, *Hypogena* wings do not have a median vein, cubitoanal vein (cu-a), or fourth anal vein (4a). The third anal vein (3A), radiomedian cross vein (r-m) is reduced. The wedge cell is quadrate. The anterior branch of the first anal vein (1A) does not continue far into the cubital area. This usually ends near the side of the wedge cell that closest to the jugal region of the wing. The radical cross vein (r) and the recurrent radius (Rr) can be very thick, which makes the area that is produced between those areas small. No veins meet the edge of the wing (Figure 1.4).

Other Morphology

Multiple structures were observed on *Hypogena* species and closely related genera that cannot be viewed clearly using conventional light microscopy. The first such structures are outgrowths of the cuticle on the protarsi (Figure 1.5). These structures appear on

the first two protarsomeres in *Hypogena*. The second structure is a “gearing” on the posterior edge of the metasternite in all species of *Hypogena* that is made up of cuticular processes that extend above the metacoxa (Figure1.6.A). These processes are also symmetrical and are made up of multiple smaller processes to form the gearing (Figure 1.6.B).

Species Redescriptions

***Hypogena* Dejean, 1831**

Type Species *Hypogena biimpressa* Latreille, 1833: 199

Diagnosis

The males of the genus *Hypogena* are easily recognizable by a combination of the following characters: two supraocular horns are present and produced between the eyes, one horn produced on the clypeus, antennae bearing stellate sensoria, first two protarsomeres with cuticular outgrowth to form spines, gearing on posterior edge of metasternum, body distinctly dorsoventrally flattened. The females of this genus are similar in most respects, except they do not have produced horns. Females also have more prominent punctures on the vertex, frons and clypeus than the males.

Redescription

General: length: 5 – 10 mm; width: 2 – 4 mm; color black to reddish brown. Body dorsoventrally flattened.

Head: distance between cardo and eye less than width of cardo. Males with two or three cephalic horns. Mandibles with groove extending to connection point. Labrum

fully setose. Gena not extending laterally past widest point of eye. Antennae 11 segmented; not forming distinct club. Apical six antennomeres bearing stellate sensoria. Mentum trapezoidal, punctate; eye large, reniform.

Thorax: pronotum always punctate with punctures smaller than eye facet; many coarsely punctate with punctures larger than eye facet; posterior margin of pronotum bisinuate. Prothorax laterally explanate; anterior apices of prothorax produced anteriorly, sometimes reaching middle of eye. Elytra bearing striate, striae punctate. Epipleuron tapering posteriorly; epipleural carina explanate. Prosternum punctate. Mesepisternum coarsely punctate, unless otherwise indicated. Posterior edge of metasternum with cuticular gearing.

Legs: tarsal formula: 5-5-4. Protibia with first two tarsomeres expanded to form spines. Lateral side of protibia with socketed spines. All tibiae with two apical spurs.

Abdomen: all abdominal segments punctate; punctures on last two ventrites finer than on previous segments. Aedeagus with parameres fused. Female genitalia with coxites highly reduced; Spermathecal gland with single apical spematheca.

Distribution: US states of AZ, CA, TX and FL south to Argentina. (Figure 1.7)

Hypogena marginalis* Doyen & Poinar*, 1994

Hypogena marginalis Doyen & Poinar, 1994: 35.

This species was described from Dominican amber in 1994 and the description found therein is sufficient for this species (See Figure 8 for images of holotype).

***Hypogena cat* Steiner, 2005**

Hypogena cat Steiner, 2005: 573.

This species was recently described and the original description is sufficient to identify specimens to species (Steiner, 2005). (See Figure 9 for images of holotype and figure 1.10 for distribution).

***Hypogena triceratops* Steiner, 2005**

Hypogena triceratops Steiner, 2005: 571.

This species was recently described and the original description is sufficient to identify specimens to species (Steiner, 2005). (See Figure 1.11 for images of holotype)

***Hypogena tricornis* (Dalman, 1823)**

Phaleria tricornis Dalman, 1823: 59.

Ulosonia tricornis Laporte, 1840: 220. Synonymy: Spilman (1973:42).

Type Specimen: HOLOTYPE (male) labeled: (a) “Jamaica/ Wellfelt?”; (b) “♂”; (c) “NHRS-JLKB 000027279” (NHRS). PARALECTOTYPE (female) labeled: (a) “Jamaica/ Wellfelt?”; (b) “♀”; (c) “NHRS-JLKB 000027280” (NHRS). (See figure 1.12).

Diagnosis: The male of this species can be readily identified by the three long, thin, erect horns that are placed between the eyes and on the clypeus. The horns are equal in length and thickness. This species is also distinctive in the coarse punctures on the pronotum are always closely concentrated in the center of the disc. The female is similar in all respects, except that the horns are not present and the frons is more punctate.

Redescription

General: 7 – 8 mm long; 2 – 3 mm wide.

Head: clypeal horn long, thin and not emarginate; clypeal horn equal in thickness to supraorbital horns. Clypeal horn equal in size to supraorbital horns; supraorbital

horns bend slightly inwards. Both supraorbital horns and clypeal horns produced perpendicular to head and do not curve forward; clypeal and supraorbital horn finely punctate; punctures scattered over horn surface. Antennae at least as long as pronotum; antennae with stellate sensoria; third antennomere same size and fourth and more than 1.5 times size of second. Vertex and frons of male almost smooth. Dorsally, eye curved forming arch. Anterior edge of clypeus flat with corners rounded. Mentum trapezoidal, flat, punctate and lightly setose. Labrum fully setose.

Thorax: pronotum with puncturing of two sizes; coarse punctures concentrated primarily on disc. Hypomeron laterally rugulose. Short setae on prosternum arising from punctures; puncturing on prosternum smaller than one eye facet; prosternal punctures separated by less than one diameter. Elytral striae present, punctate; strial punctures separated by less than one diameter. Elytral interstices convex and punctate; punctures larger than one fourth of strial puncture size; interstitial punctures separated by more than one diameter. Mesepisternum punctate; punctures smaller than eye facets; mesepisternal punctures separated by more than one diameter; mesepisternum not setose. Lateral margins of pronotum subparallel. Marginal edges of pronotum expanded more than one coarse puncture's diameter. Posterior metasternal gearing present. Anterior edge of pronotum reaching middle of eye, but not past middle of eye.

Legs: tarsi pubescent. On lateral edge of protibia, seven or more socketed spines are produced and continue up one third of protibia. On medial edge of protibia spines are produced that continue for length of protibial. Distal edge of protibia bearing brush of setae. First two tarsomeres forming spines on planter edge of tarsi.

Abdomen: first three visible abdominal segment laterally rugulose; fourth and fifth abdominal sternites punctate. Abdomen setose; setae arising from punctures.

Female: intraocular space raised and extending transversely inwards; intraocular space impinging on eye. Punctures of vertex and frons smaller than eye facet. Clypeal punctures smaller than one eye facet; punctures on clypeus spread evenly across clypeus. Clypeus upraised.

Distribution: Cuba, Trinidad, Mexico (Chiapas, Nuevo León, Yucatan, San Luis Potosi, Tamaulipas, Veracruz, Sonora, Puebla, Baja California Sur, Oaxaca, Nayarit), Belize, Panama (Panama), Venezuela (Bolivar, Zulia), Columbia, Ecuador (Guayas), Cayman Islands, Costa Rica (Guanacaste, Heredia), El Salvador (San Salvador), USA (Texas, Florida), Guatemala (Escuintla, Petén). (Figure 1.13). The type material is from Jamaica.

Hypogena biimpressa (Latreille, 1813)

Hypogena biimpressa (Latreille, 1813)

Tenebrio biimpressus Latreille, 1813: 17.

Type Specimen: NEOTYPE (female) labeled: (a) “Bogotâ”; (b) “F. Bates Coll. / 81 – 19.”; (c) “Tenebrionid Base / Aaron D. Smith / Catalog # 21233”; (BMNH). Designated here. NEOTYPE (male) labeled (a) “Espirilo Tanlo”; (b) “6442”; (c) “Descourtils”; (d) “Fry Coll. / 1905.100.”; (BMNH). Designated here. (See figure 1.14).

Diagnosis: The supraorbital horns of this species long, project perpendicular to head and bend slightly inwards. The clypeal horn is short, conical and projects forward. The punctures on the pronotum are of two sizes and the coarse punctures are mostly

concentrated on the lateral portions of the pronotum. The ventral side of the thorax bears golden setae. The female is similar in most characters, except for the presence of the horns. The mesepisternal punctures often intersect and form a scalloped appearance.

Redescription

General: 10 – 11 mm long; 3.5 – 4 mm wide.

Head: clypeal horn present, short and conical; clypeal horn not emarginate; clypeal horn two times width of one supraorbital horn at base; clypeal horn projected forward. Supraorbital horns long, thin and slightly bent inwards toward each other; supraorbital horns produced perpendicular to head; supraorbital horns slightly bent forward. Supraorbital and clypeal horns finely punctate. Antennae at least as long as pronotum; third antennomere more than 1.5 times length of both second and fourth antennomere; antennae with stellate sensoria. Puncturing on vertex and frons smaller than one eye facet. Gena not extending laterally past eye. In dorsal view, eyes forming arch. Anterior corners of clypeus rounded. Mentum trapezoidal and setose. Labrum fully setose. Mandibles with groove continuing to connection point of mandible.

Thorax: pronotum with puncturing of two sizes; few coarse punctures that are concentrated on lateral portions of pronotum. Pronotal hypomeron rugulose. Prosternum and hypomeron setose; setae long, dense and yellow to gold in color. Prosternal puncturing smaller than facets of eye; prosternal puncturing separated by less than one diameter. Elytral striae present with punctate; strial punctures separated by less than one diameter. Elytral interstices convex; interstices with punctures smaller than one fourth of strial puncture size; interstices punctate; punctures numerous and

separated by more than one. Mesepisternum with punctures larger than one eye facet; punctures intersecting. In lateral view, pronotum arched. Lateral margins of pronotum not parallel. Margins of pronotum expanded wider that one coarse puncture. Pronotum narrowest anteriorly. Posterior metasternal gearing present. Anterior edge of pronotum reaching to middle of eye, but not past middle of eye.

Legs: tarsi pubescent. Tibia with two apical spurs. Protibia with more than seven laterally socketed spines that continue up one third of protibia. On protibia, line of medial spines present. On protarsi, first two tarsomeres with cuticular spines. Distal portion of tibia with brush of setae.

Abdomen: first two abdominal sternites laterally rugulose; first three abdominal sternites setose; first three abdominal sternites coarsely punctate; last two abdominal segments finely punctate.

Female: cuticle on intraocular space narrowly raised near eye; intraocular space impinging on eye. Clypeus with punctures smaller than eye facets, which are spread evenly across clypeus. Clypeus upraised from surrounding cuticle.

Distribution: Honduras (El Paraiso, Atlántida), Mexico (Jalisco, Sinaloa, Chiapas, Tabasco, Yucatán, México, Hidalgo, Veracruz, Tamaulipas, Merelos, Colima, Nayarit, Guerruro), Peru, Panama (Panama, Colón), Brazil (Pará, Rondônia, Espirito Santo, Mato Grosso, Sao Paulo, Santa Catarina, Rio de Janeiro, Bahia), Paraguay (Alto Paraná), Venezuela (Aragua), Haiti, Nicaragua (Chontales), Colombia, Ecuador (Los Rios), Dominican Republic, El Salvador (La Unión), Costa Rica (Alajuela, Guanacaste, Heredia), Guatemala (Escuintla). (Figure 1.15).

***Hypogena marginata* (LeConte, 1851)**

Hypogena marginata (LeConte, 1851)

Uloma marginata LeConte, 1851: 149.

Type Specimen: HOLOTYPE (male) labeled: (a) Gold circular paper (Refers to collection location: California); (b) On red paper “Type 4672”; (c) “Ulosonia marginata Lec” (MCZ). (See figure 1.16).

Diagnosis: The male of this species has two short conical horns that arise from between the eyes and a very short clypeal horn, that looks like clypeus is more pointed than in the female. These horns project forward, parallel to the body. The clypeal horn may be absent or simply a tubercle projected forward at the anterior edge of the clypeus. The pronotal punctures for this species are of two sizes and the coarse punctures are scattered throughout the pronotum. The prosternum of this species does not bear setae. The female for this species is similar in most regards, except for the presence of the horns.

Redescription

General: 6 – 7 mm long; 2 – 3 mm wide

Head: clypeal horn small, slightly more produced area of clypeus. Clypeal horn of similar thickness to supraorbital horns. Clypeal horn projected forward. Supraorbital horns short, barely reaching past eye. Supraorbital horns projected forward; not bent after initial production. Supraorbital horns finely punctate. Antennae at least as long as pronotum. Antennae bearing stellate sensoria. Third antennomere of same size as fourth and more then 1.5 times size of second. Punctures of vertex and frons smaller than eye facets. Gena not extending laterally past eye. Eyes curved, forming arch.

Clypeus pointed from production of clypeal horn. Mentum trapezoidal, flat and lightly setose. Labrum fully setose.

Thorax: pronotal puncturing of two sizes. Coarse punctures numerous and scattered throughout pronotum. Hypomeron laterally rugulose. Prosternum punctate; punctures smaller than eye facet. Prosternal punctures separated by less than one diameter. Elytral striae present; striae punctate. Strial punctures separated by more than one diameter. Elytral interstices convex with punctures larger than one fourth strial puncture size. Interstitial punctures separated by less than one diameter. Mesepisternum punctate with punctures smaller than eye facet; puncturing separated by more than one diameter. From lateral view, pronotum not arched. Lateral margins of pronotum subparallel. Margin of pronotum expanded more than diameter of one coarse puncture. Posterior metasternal gearing present. Anterior edge of pronotum reaching middle of eye but not past eye.

Legs: tibia pubescent. Tibiae with two apical spurs. Lateral edge of protibia with seven or more socketed spines that continue halfway up tibia. Distal portion of tibiae with brush of setae. Cuticular outgrowths present on first two protarsomeres.

Abdomen: first three visible abdominal segments weakly laterally rugulose. All abdominal sternites punctate. Punctures on first four abdominal segments coarsely punctate; Last abdominal sternite finely punctate. All abdominal sternites with setae arising from punctures; setae longer on first abdominal segment than on last.

Female: cuticle on intraocular space narrowly raised near eye; Intraocular space impinging on eye. Clypeus with punctures smaller than eye facets and spread evenly

across clypeus. Anterior corners of clypeus rounded, but otherwise flat. Clypeus upraised.

Distribution: Peru (Lima), Guatemala, USA (Texas, California, Arizona), Costa Rica, Mexico (Sonora, Colima, Baja California Norte, Veracruz, Tamaulipas, Nuevo León, Baja California Sur) (Figure 1.17).

***Hypogena depressa* (Champion, 1886)**

Hypogena depressa (Champion, 1886)

Ulosonia depressa Champion 1886: 164.

Type Specimen: LECTOTYPE (male) labeled: (a) Cuernavaca (b) “Mexico / Salle Coll.”; (c) “Godman-Salvin / Coll. Biol. / Centr.-Amer.”; (d) on grey paper “1899”; (e) “Ulosonia ♂ / depressa Ch.”; (f) on blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 19609” (BMNH). PARALECTOTYPE (female) labeled: (a) “Cuernavaca”; (b) “Mexico / Salle Coll.”; (c) Godman-Salvin / Coll., Biol. / Centr.-Amer”; (d) “Ulosonia ♀ / depressa Ch”; (e) on blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 19608”; (BMNH). CUM TYPO COMPARATUM (male) labeled: (a) “Bilimek / Mexico / 188”; (b) “CUM TYPO / COMPARATUM / 14.X.61.Kulzer”; (c) “Ulosonia / depressa Champ. / det.H.Kulzer 1961”; (d) on blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 19653” (NHMB). (See figure 1.18).

Diagnosis: This species is very similar to *H. tricornis* in size and form. The horns, while similar to those of *H. tricornis* but not as long. The puncturing on the pronotum in both the male and female are of two sizes. The coarse punctures are not concentrated only on the disc and can be found throughout the pronotum. The lateral portions of this species are shallowly raised to form the disc. The hypomeron is laterally rugulose, but

not punctate. Most of the character states are the same in the female, except the presence of the horns.

Redescription

General: 8 – 9 mm long; 2 – 3 mm wide.

Head: clypeal horn long; twice as thick as supraorbital horn. Supraorbital horn long, thin, bending slightly inwards; Clypeal and supraorbital horns produced perpendicularly to head and produced forward. Clypeal and supraorbital horns finely punctate. Anterior corners of clypeus rounded. Antennae at least as long as pronotum; puncturing on vertex and frons smaller than eye facet. Third antennomere same size as fourth and more than 1.5 times size of second. Antennae with stellate sensoria. Gena not extending laterally past eye. Mentum trapezoidal and lightly setose. Labrum fully setose. Groove on mandible present, continuing to connection point of mandible.

Thorax: pronotal puncturing of two sizes, with numerous coarse punctures scattered across pronotum. Lateral portions of pronotum weakly raised to form disc; Hypomeron laterally rugulose and not punctate. Prosternum punctate; punctures smaller than eye facets. Prosternum punctures not bearing setae. Prosternal punctures separated by more than one diameter. Elytral striae present; punctate; strial punctures farther than one diameter from each other. Elytral interstices convex; Interstitial punctures larger than one fourth of strial puncture size. Interstices numerous punctures that are more than one diameter from each other. Mesepisternum punctate; punctures smaller than eye facets; punctures less than one diameter from each other. From lateral view, pronotum not arched. Lateral margins of pronotum subparallel. Lateral edge of pronotum expanded wider than diameter of one coarse puncture. Pronotum

narrowest anteriorly. Anterior portion of pronotum reaching middle of eye, but not past middle of eye. Posterior metasternal gearing present.

Legs: tarsi pubescent. Tibia bearing two apical spurs. More than seven socketed spines present and continuing halfway up lateral edge of protibia. Medial spines on tibia absent. Distal portion of tibiae bearing brush of setae. Protarsal outgrowths present on first two tarsomeres.

Abdomen: first three abdominal sternites laterally rugulose. First three abdominal sternites coarsely punctate with setae arising from punctures; remaining two abdominal sternites finely punctate.

Female: cuticle of intraocular space raised and extending transversely inwards; intraocular space impinging on eye. Puncturing on vertex and frons as large or larger than eye facet. Punctures on clypeus smaller than eye facet and spread evenly across clypeus. Clypeus upraised.

Distribution: Brazil (Pará), Guatemala (Zacapa), Honduras (Comayagua), USA (Texas, New Mexico, Arizona), Costa Rica (San José, Guanacaste), Jamaica, Bahamas, Cuba, Mexico (Baja California Norte, Nayarit, Veracruz, Sinaloa, Oaxaca, Puebla). (Figure 1.19).

***Hypogena canaliculata* (Champion, 1886)**

Hypogena canaliculata (Champion, 1886)

Ulosonia canaliculata Champion, 1886: 164.

Type Specimen: LECTOTYPE (male) labeled: (a) “V. de Chiriqui, / 2-3000ft / Champion”; (b) “Godman-Salvin / Coll., Ciol. / Centr.-Amer.”; (c) “Ulosonia / canaliculata / ♂ Ch”; (BMNH). PARALECTOTYPE (female) labeled: (a) “Cache. / Costa Rica / H.

Rogers"; (b) Godman-Salvin / Coll., Biol. Centr.-Amer."; (c) "Ulosonia / canaliculata / ♀ Ch"; (BMNH). (See figure 1.20).

Diagnosis: This species is similar to *H. tricornis* in size and form. The type specimen for this species has poorly developed horns, but in other specimens, they can be as long as those seen in *H. tricornis*. The puncturing on the pronotum is primarily of one size. Most punctures are fine, but on the lateral portions of the pronotum, there may be at most one or two larger punctures. The hypomeron is smooth and does not have any punctures. The female is similar in most character states except the presence of the horns.

Redescription

General: 9.5 – 11 mm long; 3 – 4 mm wide.

Head: clypeal horn long, not emarginate and twice as wide at base as one supraorbital horn; clypeal horn projected forward. Supraorbital horns long, thin and continuing straight without curving; projecting perpendicular to head. Clypeal and supraorbital horns almost smooth. Antennae at least as long as pronotum. Third antennomere less than 1.5 times size of fourth and more than 1.5 times size of second. Texture of vertex and frons almost smooth. Anterior corners of clypeus rounded. Gena not extending laterally past eye. In dorsal view, eyes curved forming a complete arch. Mentum trapezoidal and lightly setose; mentum medially and longitudinally raised. Groove on mandible present, continuing to connection point of mandible. Labrum fully setose.

Thorax: pronotal puncturing of one size; coarse punctures, if present (at most 3), are located on lateral portions of pronotum. Pronotal hypomeron and prosternum

smooth, not punctate; prosternum and hypomeron not setose. Elytral striae present and punctate. Strial punctures separated by more than one diameter. Elytral interstices convex. Elytral interstices punctate; punctures larger than one fourth of strial puncture size; interstitial punctures separated by more than one diameter. Mesepisternum finely punctate; punctures smaller than eye facet. Mesepisternal punctures separated by more than one diameter. Mesepisternum not setose. From lateral view, pronotum not arched. Lateral edges of pronotum subparallel. Marginal edge of pronotum widely expanded. posterior metasternal gearing present. Anterior edge of pronotum reaching middle of eye but not past it.

Legs: tarsi pubescent. Apical spurs on tibia present. Less than seven socketed spines on lateral edge of protibia; socketed spines continuing up one third of protibia. Spines on medial edge of protibia present and continue for length of protibia. On distal portion of tibiae, brush of setae present. Cuticular outgrowth present of first two protarsomeres.

Abdomen: first three visible abdominal sternites laterally rugulose. All abdominal sternites finely punctate and not setose.

Female: cuticle next to eye on intraocular space raised and extending transversely inwards; intraocular space impinging on eye. Puncturing on vertex and frons smaller than one eye facet. Clypeus finely punctate and punctures concentrated in center; Clypeus upraised from surrounding cuticle.

Distribution Brazil (Santa Catarina), Guatemala (Petén), Costa Rica (Alajuela, Limón, Guanacaste), Panama (Coclé), Cuba, Mexico (Tamaulipas, Tabasco), Nicaragua (Chontales), (Figure 1.21).

***Hypogena dejeani* (Champion, 1886)**

Hypogena dejeani (Champion, 1886)

Hypogena dejeani Champion, 1886: 165.

Type Specimen: LECTOTYPE (male) labeled: “Las Mercedes, / 3000 ft. / Champion”; (b) “Ulosonia ♂ / dejeani Ch.”; (c) on blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 19606”; (BMNH). Designated here. PARALECTOTYPE (male) labeled: (a) “Las Mercedes / 3000 ft / Champion.”; (b) Godman-Salvin / Coll., Biol. / Centr.-Amer.”; (c) “Type.”; (d) “Sp. figured.”; (e) “Ulosonia ♂ / dejeani, Ch.”; (f) on blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 19607” (BMNH). Designated here. (See figure 1.22).

Diagnosis: The male of this species has distinctive armature. The clypeal horn for this species is long and wide at the base, becoming thinner until the anterior third, where it becomes wider. The end of the horn is emarginate. The supraorbital horns are also long, and produced perpendicular to the head. The horns then curve forward to point anteriorly. The punctures are of one size with no coarse punctures present. This species is very similar to *H. cat* but can be differentiated by the lack of coarse punctures. There are very few female specimens, but most characters are similar to those in the male except the presence of the horns.

Redescription

General: 7 – 9 mm long; 2 – 3 mm wide.

Head: clypeal horn long, thinner in middle and widening apically; horn flattened; twice as thick at base than one supraorbital horn. Clypeal horn projected forward.

Supraorbital horns long, and from dorsal view, bent inwards toward each other; produced perpendicularly to head. After initial production, supraorbital horns are strongly bent forward to point anteriorly. Clypeal and supraorbital horns not punctate. Antennae at least as long as pronotum. Antennae with stellate sensoria. Third antennomere less than 1.5 times longer than fourth and more than 1.5 times length of second. Vertex and frons almost smooth. Gena not extending laterally past eye. Anterior margin of clypeus interrupted by clypeal horn, not forming circular arch. Mentum trapezoidal, punctate and not pubescent. Labrum fully setose.

Thorax: pronotal punctures of one sizes; coarse punctures not present. Hypomeron rugulose and finely punctate. Prosternum finely punctate. Prosternal punctures separated by less than one diameter. Elytral striae present and punctate. Strial punctures separated by less than one diameter. Elytral interstices flat to weakly convex. Elytral interstices with punctures with punctures larger than one fourth strial puncture size. Interstitial punctures separated by more than one diameter. Mesepisternum with punctures smaller than eye facets. Mesepisternal punctures separated by less than one diameter. From lateral view, pronotum not arched. Lateral margins of pronotum subparallel. Margins of pronotum narrowly expanded. Anterior margin of pronotum reaching middle of eye but not past eye. Posterior metasternal gearing present. Prosternal process not continuing past posterior margin of pronotum.

Legs: tarsi pubescent. Two apical spurs present on tibiae. On lateral edge of pronotum, more than seven socketed spines present and continuing for one third of protibia. Spines present on marginal edge of protibia and continuing for length of tibia.

Distal portion of tibiae bearing brush of setae. Cuticular outgrowths present of first two protarsomeres.

Abdomen: first two visible abdominal segments laterally rugulose. Third visible abdominal sternites laterally rugulose on anterior fourth. All abdominal segments punctate; first three coarsely punctate and remaining two finely punctate. All visible abdominal segments not setose.

Female: intraocular space raised and extending transversely inwards to meet in middle of head. Intraocular space impinging on eye. Vertex and frons with puncturing smaller than eye facets. Clypeus with punctures smaller than eye facets and concentrated in center of clypeus. Anterior margin of clypeus flat, but with rounded corners. Clypeus not distinctly upraised from surrounding cuticle.

Distribution: Mexico (Veracruz), Costa Rica (Puntarenas) (Figure 1.23).

***Hypogena vacca* (Fabricius, 1801)**

Hypogena vacca (Fabricius, 1801)

Ulosonia vacca (Fabricius, 1801).

Trogosita vacca Fabricius, 1801: 153.

Ulosonia parvicornis Fairmaire, 1892: 250. Synonymy: Kulzer (1962: 93).

Type Specimen: LECTOTYPE (male) labeled: (a) “Amer. Mer. / Schmidt”; (b) “Mus de Sehestedt”; (c) “*Trogosita vacca* Fabr.”; (d) on red paper “Type.”; (ZMUK). Designated here. SYNTYPE (female) labeled: (a) “Amer. Mer. / Schmidt”; (b) “Mus de Sehestedt”; (c) “*Trogosita vacca* Fabr.”; (d) on red paper “Type.”; (ZMUK). (See figure 1.24).

Diagnosis: The male of this species has two large supraorbital horns and a small tuberculate clypeal horn. The supraorbital horns are usually very thick, perpendicular to

the head, and often diverge away from each other. The clypeal horn is variable, sometimes appearing very short, or sometimes larger with the middle portion of the horn being somewhat thinner than the final portion. The punctures on this species is of two sizes and the coarse punctures are primarily located on the lateral portions of the pronotum and are widely spaced away from one another. The posterior edge of the pronotum is raised. This species is small, usually between 5 - 7 mm long. The female is similar is every aspect except the presence of the horns.

Redescription

General: 7 – 8 mm long; 2.5 – 3 mm wide.

Head: clypeal horn short and similar in thickness at base to one supraorbital horn. Clypeal horn may be tuberculate or thinner in middle and widen slightly apically. Clypeal horn projected forward. Clypeal horn almost smooth. Supraorbital horn long and thick. Supraorbital horns, from dorsal view, may not bend or may bend outwards, away from each other. Supraorbital horns produced perpendicularly to head and bent slightly forward. Supraorbital finely punctate. Antennae at least as long at pronotum. Antennae with stellate sensoria. Third antennomere similar size as fourth and more than 1.5 times size of second. Vertex and frons not punctate, almost smooth. Gena not extending laterally past eye. Eyes curved, forming arch. Clypeus not forming circular arch due to clypeal horn. Mentum trapezoidal, punctate and setose. Labrum fully setose.

Thorax: pronotal puncturing of two sizes. Coarse punctures numerous and concentrated on lateral portions of pronotum. Coarse punctures separated by more than one diameter. Posterior edge of pronotum with raised edge. Hypomeron laterally rugulose, not punctate. Prosternum finely punctate. Short setae arising from punctures.

Prosternal punctures separated by less than one diameter. Elytral striae present and punctate. Strial punctures separated by less than one diameter. Elytral interstices convex. Interstices with punctures as large or larger than one fourth size of strial puncture size. Interstitial punctures separated by more than one diameter. Mesepisternum with punctures as large as or larger than eye facets. Mesepisternal punctures separated by less than one diameter. From lateral view, pronotum not arched. Lateral margins of pronotum subparallel. Margins of pronotum expanded wider than diameter of one coarse puncture. Posterior metasternal gearing present. Anterior edge of pronotum extending to middle of eye but not past eye. Prosternal process not continuing past posterior margin of pronotum.

Legs: tarsi pubescent. Tibiae bearing two apical spurs. Lateral edge of protibia more than seven socketed spines that continue halfway up protibia. Spines on medial edge of protibia present and continuing for length of tibia. Cuticular outgrowths present of first two protarsomeres.

Abdomen: first three visible abdominal segments are laterally rugulose. All abdominal segments are finely punctate. First three abdominal segments setose; setae arising from punctures.

Female: cuticle on intraocular space raised near eye and extending transversely inwards. Intraocular space impinging on eye. Vertex and frons with punctures as large or larger than facets of eye. Clypeus with punctures smaller than eye facets and spread evenly across clypeal surface. Anterior margin of clypeus flat, but with corners rounded. Clypeus upraised from surrounding cuticle.

Distribution: Paraguay, Brazil (Minas Gerais, Sao Paulo, Espirito Santo, Rio Grande do Sul, Santa Caterina) Bolivia, Argentina (Tucumán, Jujuy, Salta, Buenos Aires, Chaco, Mendoza) (Figure 1.25).

***Hypogena laevicollis* (Kulzer, 1962)**

Hypogena laevicollis (Kulzer, 1962)

Ulosonia laevicollis Kulzer, 1962: 95.

Type Specimen: HOLOTYPE (male) labeled: (a) “Hansa Humboldt / Sta. Satharina / Brazilien, Reitter”; (b) on red bordered paper “HOLOTYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961”; (c) On blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 20144” (NHMB). ALLOTYPE (female) labeled: (a) “Hansa Humboldt / Sta. Satharina / Brazilien, Reitter”; (b) on red bordered paper “ALLOTYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961”; (c) On blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 20145” (NHMB). PARATYPE (female) labeled: (a) “Hansa Humboldt / Sta. Satharina / Brazilien, Reitter”; (b) on red bordered paper “PARATYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961”; (c) On blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 20143” (NHMB).PARATYPE (female) labeled: (a) “Hansa Humboldt / Sta. Satharina / Brazilien, Reitter”; (b) on red bordered paper “PARATYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961”; (c) On blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 20137” (NHMB). PARATYPE (male) labeled: (a) “Hansa Humboldt / Sta. Satharina / Brazilien, Reitter”; (b) on red bordered paper “PARATYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961”; (c) On blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 20138” (NHMB). PARATYPE (male) labeled: (a) “Hansa Humboldt / Sta. Satharina / Brazilien, Reitter”; (b) on red bordered paper “PARATYPUS / Ulosonia laevicollis n. Sp.

/ det H. Kulzer 1961"; (c) On blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20139" (NHMB). PARATYPE (male) labeled: (a) "Hansa Humboldt / Sta. Satharina / Brazilien, Reitter"; (b) on red bordered paper "PARATYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961"; (c) On blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20140" (NHMB). PARATYPE (male) labeled: (a) "Hansa Humboldt / Sta. Satharina / Brazilien, Reitter"; (b) on red bordered paper "PARATYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961"; (c) On blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20141" (NHMB). PARATYPE (female) labeled: (a) "Hansa Humboldt / Sta. Satharina / Brazilien, Reitter"; (b) on red bordered paper "PARATYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961"; (c) On blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20142" (NHMB). PARATYPE (male) labeled: (a) "Vila Oliva / 19 - 2 - 52"; (b) Rio Grande do Sul / 3886 / Pe Buck Leg." (c) "PARATYPUS / Ulosonia laevicollis n. Sp. / det H. Kulzer 1961"; (d) on blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20146"; (NHMB). PARATYPE (male) labeled (a) on green paper "S Catharina / Nova Teutonia"; (b) on green paper "F. Plaumann / leg 8 1935" (c) "PARATYPUS / Ulosonia / laevicollis n. sp. / det H. Kulzer 1961"; (d) on blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20147"; (NHMB). PARATYPE (female) labeled (a) on green paper "S Catharina / Nova Teutonia"; (b) on green paper "F. Plaumann / leg 8.5.1935" (c) "PARATYPUS / Ulosonia / laevicollis n. sp. / det H. Kulzer 1961"; (d) on blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20148"; (NHMB). PARATYPE (female) labeled (a) on green paper "S Catharina / Nova Teutonia"; (b) on green paper "F. Plaumann / leg 8.5.1935" (c) "PARATYPUS / Ulosonia / laevicollis n. sp. / det H. Kulzer 1961"; (d) on blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 20149";

(NHMB). PARATYPE (male) labeled: (a) on yellow bordered paper “Paratype”; (b) “Hansa Humboldt / Sta. Catharina / Brasilien Reitter”; (c) “Paratypus / Ulosonia / laevicollis / det H.Kulzer 1961”; (d) “Brit. Mus. / 1961-329”; (e) Tenebrionid Base / Aaron D. Smith / Catalog # 20150”; (BMNH). PARATYPE (female) labeled: (a) on yellow bordered paper “Paratype”; (b) “Hansa Humboldt / Sta. Catharina / Brasilien Reitter”; (c) “Paratypus / Ulosonia / laevicollis / det H.Kulzer 1961”; (d) “Brit. Mus. / 1961-329”; (e) Tenebrionid Base / Aaron D. Smith / Catalog # 20151”; (BMNH). PARATYPE (male) labeled: “Nova Teutonia 11.XI.1955, Leg. F. Plaumann (Ardoin Collection). PARATYPE (female) labeled: “Nova Teutonia 11.XI.1955, Leg. F. Plaumann”; two specimens. (Ardoin Collection). PARATYPE (male) labeled: “Brazil” no locality information. Two specimens. (ZSM). PARATYPE (female) labeled: “Brazil” no locality information. Two specimens. (ZSM). PARATYPE (female) labeled: “Brèsil, Prov. Sta Catarina, Hansa Humboldt. Leg. Ant. Maller, 1934”; three specimens. (MNHN). The types from the Paris museum, Ardoin collection, and Münich are described in Kulzer 1962. I have not seen these types. (See figure 1.26 for Holotype and Allotype).

Diagnosis: The clypeal horn of this species is short, conical and projects forward. The supraorbital horns are long, projecting initially perpendicularly and then bending to point anteriorly. The supraorbital horns are also thinnest at the base and become more thick away from the head. The punctures on the pronotum are almost exclusively fine. The head of the male is smooth, whereas the head of the female has larger punctures, but not larger than one eye facet. This species is larger than others of this genus (9-10 mm). The female has similar characters as the male, except with the presence of the horns.

Redescription

General: 9 – 11 mm long; 3 – 4 mm wide.

Head: clypeal horn short and of similar thickness to supraorbital horns. Clypeal horn produced forward. Supraorbital horns long, thick and bent inwards toward each other. Supraorbital horns thicker apically and thinner at base. Supraorbital horn produced perpendicular to head and are strongly bent to point anteriorly. Clypeal and supraorbital horns finely punctate. Antennae at least as long as pronotum. Antennae with stellate sensoria. Third antennomere less than 1.5 times size of fourth and more than 1.5 times size of second. Vertex and frons not punctate. Gena not extending laterally past eye. Eyes forming complete arch. Anterior margin of clypeus flat except corners of clypeus rounded,

Mentum trapezoidal, flat, finely punctate and not setose. Labrum fully setose.

Thorax: pronotal puncturing not of two sizes. Only fine punctures present on pronotum. From lateral view, pronotum slightly arched. Lateral margins of pronotum not parallel. Margins of pronotum narrowly expanded. Pronotum narrowest anteriorly. Anterior edge of pronotum reaching piddle of eye but not past eye. Pronotal hypomeron laterally rugulose. Hypomeron setose; setae arising from punctures. Prosternum finely punctate and not pubescent. Prosternal punctures separated by more than one diameter. Elytral striae present and punctate. Strial punctures separated by less than one diameter. Elytral interstices flat with punctures smaller than one fourth size of strial punctures. Interstitial punctures separated by more than one diameter. Mesepisternum with punctures smaller than eye facet. Mesepisternal punctures separated by more than one diameter.

Legs: tarsi pubescent. Tibiae with two apical spurs. Protibiae with more than 7 socketed spines on lateral edge that continue one third up tibia. Distal portion of tibiae with brush of setae. Cuticular outgrowths present on first two tarsomeres.

Abdomen: first three abdominal segments laterally rugulose on anterior fourth of sclerite. First three abdominal segments coarsely punctate; last two abdominal segments finely punctate. Punctures of first three abdominal segments bearing setae.

Female: cuticle on intraocular space narrowly raised near eye. Intraocular space impinging on eye. Punctures on vertex and frons smaller than eye facet. Clypeus with fine punctures that are spread evenly across surface of clypeus. Clypeus upraised.

Distribution: Brazil (Rondônia, Rio de Janeiro, Rio Grande do Sul) (Figure 1.27).

***Hypogena amazonica* (Kulzer, 1962)**

Hypogena amazonica (Kulzer, 1962)

Ulosonia amazonica Kulzer, 1962: 97.

Type Specimen: HOLOYPE (male) labeled: “Teffé (Ega) Amazones, M. de Mathan, 3. Trimestre, 1878” (MNHN). ALLOTYPE (female) labeled: “Teffé (Ega) Amazones, M. de Mathan, 3. Trimestre, 1878” (MNHN). PARATYPE (male) labeled: “Teffé (Ega) Amazones, M. de Mathan, 3. Trimestre, 1878” (MNHN). PARATYPE (female) labeled: “Teffé (Ega) Amazones, M. de Mathan, 3. Trimestre, 1878” (MNHN). PARATYPE (male) labeled: (a) Teffé (Ega) / Amazonés / M. de Mathan / 3e Trimestre 1878”; (b) “PARATYPUS / Ulosonia / amazonica / n sp. / det. H. Kulzer 1961”; (c) on blue paper “Tenebrionid Base / Aaron D. Smith / Catalog # 20135” (NHMB). PARATYPE (female) labeled: (a) Teffé (Ega) / Amazonés / M. de Mathan / 3e Trimestre 1878”; (b) “PARATYPUS / Ulosonia / amazonica / n. sp. / det. H. Kulzer 1961”; (c) on blue paper

“Tenebrionid Base / Aaron D. Smith / Catalog # 20136” (NHMB). PARATYPE (male) labeled: “Amazones, Fontebao, Dr. Hahnel”; two specimens (MNHN). PARATYPE (female) labeled: “Amazones, Fontebao, Dr. Hahnel”; two specimens (MNHN). PARATYPE (male) labeled: “Macicore, Amazones” (Ardoin collection). PARATYPE (female) labeled: “Macicore, Amazones” (Ardoin collection). PARATYPE (male) labeled: “Teffé (Ega) Amazones” (Ardoin collection). PARATYPE (female) labeled: “Amazones” no exact location; two specimens. (HNHM). The specimens in Budapest, Paris and the Ardoin Collection are described in Kulzer (1962). These types have not been examined. (See figure 1.28).

Diagnosis: The supraorbital horns are thicker than those seen in *H. biimpressa*, and arise perpendicularly from the head and then curve forward slightly, not as distinctly as in *H. triceratops* or *H laevicollis*. The clypeal horn in this species is short, producing a conical, forward projecting horn. The males of this species also bear a distinctive pointed process on the medial side of the proximal portion of the profemur. This is the only species with this process. The punctures are of two sizes and the coarse punctures are scattered over the pronotum. The female of this species is similar in most respects except the presence of the horns and the profemoral process.

Redescription

General: 7 – 8 mm long, 2.5 – 3 mm wide.

Head: clypeus with short conical horn; base of clypeal horn twice as thick as one supraorbital horn. Supraorbital horns long; produced perpendicular to head; not bent inward; curving forward slightly after initial production. Clypeal horn and supraorbital horns finely punctate. Antennae at least as long as pronotum; third antennomere 1.5x

longer than 2nd or 4th antennomere; antennae with stellate sensoria. Puncturing on vertex and frons smaller than eye facet. Gena not extending laterally past eye; eyes curved, forming arch. Anterior edge of clypeus mostly flat with corners rounded. Mentum trapezoidal flat, punctate, and lightly setose; Labrum fully setose. Groove on mandible extending to connection point of mandible.

Thorax: pronotal puncturing of two sizes; coarse punctures numerous and scattered throughout pronotum. Hypomeron laterally rugulose. Prosternum punctate; prosternal punctures bearing short setae. Prosternal punctures separated by more than one diameter. Elytral striae present and punctate; strial punctures separated by less than one diameter. Elytral interstices convex and bearing punctures greater than one fourth of strial puncture size; interstitial punctures separated by more than one diameter. Mesepisternum with punctures smaller than one eye facet; mesepisternal punctures separated by less than one diameter. In lateral view, pronotum slightly arched. Lateral margins of pronotum subparallel. Edge of pronotum expanded less than diameter of one coarse puncture. Metasternal posterior gearing present. Anterior edge of pronotum reaching past middle of eye.

Legs: tarsi setose. Tibia with two apical spurs. On lateral edge protibia bearing more than 7 socketed spines that extend up one third of tibia. No medial spines on protibia. Protarsi bearing cuticular spines on first two tarsomeres. Medial edge of femur bearing cuticular process.

Abdomen: first three visible abdominal sternites are laterally rugulose. All abdominal sternites punctate with larger puncture on first three sternites. First three abdominal sternites setose; setae arising from punctures.

Female: intraocular space extending transversely inwards; intraocular space impinging on eye. Puncturing on vertex smaller than eye facet. Puncturing on frons smaller than eye facet. Clypeus finely but clearly punctured and punctures spread evenly across clypeus. Front edge of clypeus mostly flat except anterior corners, which are rounded; clypeus upraised from surrounding cuticle. No cuticular process on medial edge of profemur.

Distribution: Brazil (Pará, Rondônia, Amazonas, Rio de Janeiro), Peru (Amazonas) (Figure 1.29).

***Hypogena brasiliensis* (Kulzer, 1962)**

Hypogena brasiliensis (Kulzer, 1962)

Hypogena brasiliensis Kulzer, 1962: 94.

Type Specimen: HOLOTYPE (male) labeled: (a) on green paper “Brazil / S Leopoldo”; (b) on red bordered paper “HOLOTYPUS / Ulosonia brasiliensis / det. H. Kulzer 1962”; (c) Tenebrionid Base / Aaron D. Smith / Catalog # 20134” (NHMB). PARATYPE (male) labeled: “Brasilien, S. Leopoldo”. (NHMB). This paratype has not been examined. (See figure 1.30).

Diagnosis: The hind horns of this species are similar to those of *H. biimpressa*, but do not curve inwards and are thicker than it that species. The clypeal horn is much thicker (three times as thick) than one supraorbital horn. All the horns are produced perpendicular to the head and continue without bending. The pronotum has punctures of two sizes. The coarse punctures are much larger and more distinct than in other species in this genus. The coarse punctures are scattered throughout the pronotum.

Presently there is no identified female for this species. But it is assumed that, similar to other members of this genus, that the female with me similar in most characters except for the presence of the horns.

Redescription

General: 8 – 9 mm long; 3 – 4 mm wide

Head: distance between eye and cardo less than width of cardo. Clypeal horn long, thick, somewhat flattened; three times thickness, at base, than one supraorbital horn. Supraorbital horns long, thin and are not curved laterally; not bent forward. Clypeal and Supraorbital horn produced perpendicularly to head. Clypeal and supraorbital horns finely punctate. Antennae at least as long as pronotum. Antennae bearing stellate sensoria. Third antennomere less than 1.5 times size of fourth but more than 1.5 times size of second. Vertex and frons punctate; punctures smaller than eye facet. Anterior margin of clypeus forming arch. Gena not extending laterally past eye. Eye forming complete arch. Labrum fully setose.

Thorax: pronotal puncturing of two sizes; coarse punctures numerous and scattered throughout pronotum; coarse punctures more than two times size of fine punctures. Pronotal hypomeron laterally rugulose; not punctate; not pubescent. Elytral striae present and punctate. Strial punctures separated by less than one diameter. Elytral interstices convex, and punctate. Interstitial puncture size smaller than one fourth strial puncture size; punctures separated by more than one diameter. Mesepisternum with punctures larger than eye facet. Mesepisternal punctures separated by less than one diameter. In lateral view, pronotum not arched. Lateral margins of pronotum subparallel. Margins of pronotum expanded less than size of one coarse puncture.

Anterior edge of pronotum not reaching middle of eye. Prosternal process not continuing past posterior edge of pronotum.

Legs: tarsi pubescent. Apical spurs present on tibiae. More than seven socketed spines present on lateral edge of protibia. Brush of setae present on distal portion of tibiae. Outgrowth of cuticle present on first two protarsomeres.

Abdomen: abdominal sternites punctate, first three abdominal sternites setose.

Distribution: Brazil (Rio Grande do Sul), Columbia. A second male specimen was identified from comparison with the Holotype, despite being collected 3000 miles away from the holotype. (Figure 1.30).

New Species Descriptions

Hypogena cryptica

Type material: HOLOTYPE (male) labeled: (a) “MEX: Baja Norte / 9 mi S Rosarito / X-5-1983 / D. Faulkner & / F. Andrews”; (b) “Under leaves on / stalk of dead / Agave shawii”; (CSCA). Designated here. ALLOTYPE (female) labeled: (a) “MEX: Baja Norte / 7.7 mi. NNW Rosarito / X-4-1983 / D. Faulkner & F.Andrews”; (b) “Under leaves on stalk of dead Agave shawii”; (CSCA). Designated here. PARATYPE (male) labeled: (a) “MEX. San Felipe / Baja Calif. / III-26-63”; (EMEC). Designated here. PARATYPE (female) labeled: (a) “MEX: Baja Calif. Sur / 3.6 mi. NNE Cabo San / Lucas IX-29-1981 / F.Andrews & D.Faulkner”; (b) “Collected under / bark of standing dead “Torote” / Bursera microphylla”; (CSCA). Designated here. (See figure 1.32).

Diagnosis: This species is similar in size and shape to *H. biimpressa*. The horns are similar to *H. biimpressa* by having a short clypeal horn and long supraorbital horns that point inward toward each other. The hypomeron and prosternum not having long,

gold/yellow setae is what distinguishes this species from *H. biimpressa*. The mesepisternum is also not scalloped as in *H. biimpressa*. Finally, in this species the coarse punctures are not primarily concentrated on the lateral portions of the pronotum, rather they are spread out across the pronotum.

Description

General: 8 – 11 mm long; 3 – 4 mm wide.

Head: distance between cardo and eye less than width of cardo. Clypeal horn short, conical. Clypeal horn twice as wide, at base, as one supraorbital horn. Clypeal horn produced forward from clypeus. Supraorbital horns long, thin and slightly bent towards each other; produced perpendicular to head; not bent in lateral view. Clypeal and supraorbital horns finely punctate. Antennae approximately equal in length to length of pronotum. Antennae not forming club. Antennae with stellate sensoria. Third antennomere equal in size to fourth and more than 1.5 times size of second. Vertex in male and frons in both sexes with punctures smaller than eye facets. Gena not extending laterally past eye. Eyes curved forming complete arch. Due to production of clypeal horn, clypeus is pointed in middle. Mentum trapezoidal and densely setose. Groove on mandible present and continuing to connection point of mandible. Labrum fully setose.

Thorax: pronotum punctate with punctures of two sizes. Coarse punctures numerous and spread evenly across pronotum. Hypomeron laterally rugulose. Prosternum not pubescent; prosternum punctate with punctures smaller than eye facets. Prosternal puncturing separated by less than one diameter. Elytral striae present and punctate. Strial punctures shallow; separated by less than one diameter. Elytral

interstices convex with punctures equal to or smaller than one fourth size of strial punctures. Interstitial punctures separated by more than one diameter. Mesepisternum punctate; punctures smaller than eye facets. Mesepisternal punctures separated by one or less than one diameter. Mesepisternum not pubescent. From lateral view, pronotum not arched. From anterior view, pronotum not forming complete arch, disc flat. Anterior edge of pronotum reaching middle of eye, but not past eye. Lateral margins of pronotum subparallel. Margins of pronotum expanded wider than diameter of one coarse puncture. Prosternal process not continuing past posterior edge of pronotum.

Abdomen: all abdominal segments densely punctate; first three visible abdominal segments bearing very large punctures; fourth and fifth visible abdominal segments have finer punctures. Punctures on abdominal sternites separated by less than one diameter. Abdominal sternites not setose.

Legs: tarsi pubescent. Tibiae with two apical spurs. On lateral edge of protibia, seven or more socketed spines are present and continue up one third of tibia. All tibiae and femurs setose along entire length. Cuticular outgrowths present on first two tarsomeres.

Female: cuticle on intraocular space narrowly raised near eye. Intraocular space impinging on eye. Puncturing on vertex as large as or larger than eye facets. Clypeus with punctures smaller than eye facets and spread evenly across clypeus. Anterior edge of clypeus flat but corners are rounded. Clypeus upraised.

Distribution: Mexico (Baja California Norte, San Luis Potosi, Veracruz, Tamaulipas, Baja California Sur), USA (Arizona, California), Guatemala (Figure 1.33).

Etymology: The specific epithet *cryptica* is a reference to the similarity that this species bears to *H. biimpressa*.

Hypogena hirsuta

Type Material: HOLOTYPE (male) labeled: (a) “ECUADOR / Puna Is / XI-9-1950”; (b) “Ross and Michelbacher Collectors”; (CASC). Designated here. ALLOTYPE (female) labeled: (a) “ECUADOR / Puna Is / XI-9-1950”; (b) “Ross and Michelbacher Collectors”; (CASC). Designated here. PARATYPE (male) labeled: (a) “Costa Rica: Guanacaste / Prov. Finca La Pacifica / 5 km NW Canas / VII-19-1973 / J.Doyen and P.Opler”; (EMEC). Designated here. PARATYPE (male) labeled: (a) “Brasil: Mato Grosso, / Sinop (12°32’S, 55°37’W) / x-1974 M. Alvarenga”; (b) green-blue circular paper. (ADSC). Designated here. (See figure 1.34).

Diagnosis: This species has horns similar to those of *H. marginata*, which are short tubercles that point slightly inwards and a clypeal horn that is very weakly produced, resembling a pointed forward projected clypeus. This species is different in the presence of distinctive golden setae on the prosternum and hypomeron. It also has a mesepisternum that is setose and punctate in such a way that it resembles rows of scalloping. The female is similar except without the horns.

Description

General: 8 – 10 mm long; 3 – 4 mm wide.

Head: distance between eye and cardo less than width of cardo. Clypeal horn short; with anterior edge produced, pointed. Width of clypeal horn, at base, twice size of one supraorbital horn. Clypeal horn produced forward. Supraorbital horns short, thin,

conical and not bent. Supraorbital horns produced forward. Clypeal and supraorbital horns finely punctate. Antennae at least as long as pronotum. Third antennomere same size and fourth and more than 1.5 times size of second. Puncturing on vertex as large as or larger than eye facets. Gena not extending laterally past eye. Eyes curved, forming arch. Clypeus not forming arch due to production of clypeal horn. Mentum trapezoidal and lightly setose. Labrum fully setose.

Thorax: pronotal puncturing of two sizes. Coarse punctures not numerous and scattered across pronotum. Hypomeron laterally rugulose. Prosternum finely punctate; puncturing smaller than eye facets. Prosternal puncturing separated by less than one diameter. Prosternum and hypomeron setose; setae white to golden. Elytral striae present and punctate. Strial punctures separated by less than one diameter. Elytral interstices convex and punctate. Interstitial puncture size as large or larger than one fourth of strial punctures. Interstitial punctures separated by one diameter. Mesepisternum punctate; punctures that are elongated anteriorly. Punctures larger than one eye facet. Mesepisternum setose. Puncturing of mesepisternum separated by less than one diameter. From lateral view, pronotum not arched. Lateral edges of pronotum subparallel. Margins of pronotum expanded wider than one coarse puncture. Pronotum narrowest anteriorly. Posterior metasternal gearing present. Anterior edge of pronotum reaching middle of eye. Prosternal process not extending past posterior portion of pronotum.

Abdomen: first three abdominal sternites laterally rugulose. All visible sternites punctate and setose; setae arising from punctures. First four visible abdominal sternites with coarsely punctate. Fifth visible abdominal sternite with finely punctate.

Genitalia: basal piece arched ventrally, widest near base. Lateral edges of basal piece sclerotized, inner area membranous. Apical piece slightly wider at base than distal end. Sides sinuate and coming to rounded end. Parameres not divided. From lateral view, apical piece sinuate.

Legs: tarsi pubescent. Two apical spurs present on tibiae. On lateral edge of protibia, more than seven socketed spines are present and continue up one third of protibia. Distal end of tibia without brush of setae. Cuticular outgrowths present on first two tarsomeres.

Female: cuticle on intraocular space narrowly raised near eye. Intraocular space impinging on eye. Puncturing on frons smaller than facets of eye. Clypeus with puncturing smaller than eye facets and spread evenly across surface of clypeus. Anterior edge of clypeus flat, but with anterior corners rounded. Clypeus upraised from surrounding cuticle.

Distribution: Brazil (Mato Grosso), Guatemala (Escuintla), Honduras (Atlántida), Costa Rica (Guanacaste), Panama (Panama), Mexico (Colima, Nayarit, México, Veracruz, Chiapas), Venezuela (Aragua) (Figure 1.35)

Etymology: The specific epithet *hirsuta* is a reference to the distinctive golden setae that is present on the prosternum and hypomeron of this species.

Hypogena reburra

Type material HOLOTYPE: (female) labeled: (a) Columbia; (b) 46-20; (c) Hypogena topino (BMNH). Designated here. This specimen is in poor condition, so no internal structures were examined. (See figure 1.36).

Diagnosis: This species can be readily identified by the long erect hairs that arise from punctures on the pronotum and the elytral striae. This species is also more elongate than other *Hypogena*. The type for this species in a female and does not have distinctive horns. It is assumed that as all other species in this genus have horns, this species also has a horned male. However, since most other characters are preserved between males and females of this genus, this species is distinct enough that the male could be correctly identified.

Description

General: 9 – 10 mm long, 2 – 3 mm wide. Body bearing erect hairs arising from large punctures on pronotum, abdomen and in elytral striae.

Head: cuticle on intraocular space raised near and continuing transversely inwards; intraocular space not impinging on eye. Antennae at least as long as pronotum. Puncturing on vertex and frons at least as large as eye facets. Punctures on clypeus smaller than eye facets; punctures evenly distributed across area of clypeus. Gena does not extend laterally past eye. In dorsal view, eyes curved, forming arch. Eyes curve to bottom of head. Antennae not form club. Third antennomere more than 1.5 times second but same size as fourth. Anterior edge of clypeus flat, with anterior corners rounded. Mentum trapezoidal, punctate and setose; setae long. Labrum fully setose. Mandible with distinct groove continuing to attachment point of sclerite.

Thorax: pronotal punctures of two sizes; coarse punctures concentrated on lateral portions of pronotum. Hypomeron and prosternum smooth with coarse punctures separated by about one diameter apart from each other. Setae not present on prosternum. Elytral striae present and shallowly punctate. Strial punctures separated by

more than one diameter. Long porrect hairs arising from strial puncture. Elytral interstices convex and punctate; punctures that are more than one fourth size of strial punctures. Mesepisternum coarsely punctate, punctures separated by one diameter. In lateral view, pronotum is not arched. Lateral edges of pronotum not parallel. Margin of pronotum narrowly expanded less than size of coarse puncture. In anterior view, pronotum forms shallow, complete arch. Anterior edge of pronotum not reaching eye.

Abdomen: first three visible abdominal segment rugulose and coarsely punctate; punctures with hairs arising from them. Hairs that arise from abdominal punctures more than five times size of puncture. Last two visible abdominal segments finely punctate. No abdominal segments bear setae shorter than five times size of abdominal punctures.

Legs: tarsi setose. Tibiae with two apical spurs. Lateral edge of protibia with more than seven socketed spines continuing for two thirds of protibia. Spines present on medial edge of protibial, continuing for length of tibia. On first two protarsomeres cuticular outgrowth present.

Distribution: Columbia.

Etymology: The specific epithet *reburra* is a Latin root meaning “one with bristling hair.” This is a reference the long erect hairs that cover the body of this species.

Hypogena akuma

Type material: HOLOTYPE (Male) labeled: (a) Brazil: (b) Rondonia/ 62 km SW Ariguemes/ nr. Fdza Rancho Grande / 8-20-XI-1994; (c) J. Eger, C.O. Brien; (d) black light (FSCA). Designated here. (See figure 1.37).

Diagnosis: This species can be easily distinguished from all other species by the presence of a dense line of setae on the proximal side of the medial edge of each femur. It also has horns similar to those of *H. marginata* but are shorter and straighter than in the type for that species. As many species of *Hypogena* have both major and minor males, it is unclear whether this is a major male or a minor male. If it is a minor male, then there should be other specimens with more produced horns. There is no female for this specimen, but as other members of this genus, most characters, besides the horns, are preserved across sexes.

Description

General: 8 – 9 mm long and 2 – 3 mm wide.

Head: distance between eye and cardo is much smaller than width of cardo; cardo directly adjacent to eye. Clypeal horn weakly produced and not emarginate. Supraorbital horns similar to *H. marginata*, but not bent inwards. Antennae at least as long as pronotum. Punctures on vertex and frons smaller than eye facets. Clypeal horn projecting forward from clypeus. Supraorbital horns project perpendicularly from eye. Horn doesn't bend forward after initial production. Both clypeal and supraorbital horns finely punctate. Gena not extending laterally past eye. Eyes form arch. Eyes continue from top of head to bottom. Antennae do not form club. Length of third antennomere less than 1.5 times size of fourth antennomere and is more than 1.5x size of second. Anterior edge of clypeus is flat with corners rounded. Mentum trapezoidal, flat, punctate and setose. Labrum fully setose. Groove on mandible present, continuing to attachment point of sclerite.

Thorax: puncturing on pronotum of two sizes; Coarse punctures approximately size eye facets; coarse punctures scattered across pronotum. Hypomeron almost smooth; not punctate. Prosternum and hypomeron not setose. Puncturing on prosternum smaller than eye facets; prosternal puncturing separated by less than one diameter. Elytral striae present; striae shallowly punctate; strial punctures separated by less than one diameter. Elytral interstices convex, punctate; interstitial punctures smaller than one fourth of size of one strial puncture; interstitial punctures separated by more than one diameter. Mesepisternum punctate with punctures equal to size of eye facets; mesepisternal punctures separated by less than one diameter; mesepisternum not setose. From lateral view, pronotum flat. Lateral margins of pronotum not parallel. Margins of pronotum expanded larger than size of one coarse puncture. Pronotum narrowest anteriorly. Anterior edge of pronotum extending to middle of eye, but not past it middle of eye. Metasternal gearing present on posterior edge. Mesocoxa not closed by mesepisternum and metepisternum. Prosternal process extends past posterior margin of pronotum.

Abdomen: anterior fourth of first three visible abdominal sternites laterally rugulose. All abdominal sternites punctate. No abdominal sternites setose.

Legs: tarsi pubescent. Tibiae with two apical spurs. Lateral edge of protibia with less than 6 socketed spines on distal fourth of tibia. Spines present on medial edge of protibia. Brush of setae present on distally on medial edge of tibiae. Cuticular outgrowths present on first two protarsomeres. Medial edge of femurs with distinct line of setae.

Distribution: Brazil (Rondônia).

Etymology: The specific epithet of this species of a reference to the Japanese name for a devil or demon. This is a reference the horns of the male, which are similar to those in popular portrayals of demons.

Key to *Hypogena* species

1) Mesepisternum setose; prosternum and hypomeron setose with white to golden setae; coarse pronotal punctures scattered across pronotal surface; clypeal horn short, pointed anteriorly from clypeus; supraorbital horns short, tuberculate, and pointed anteriorly; Ecuador, Brazil, Costa Rica, Honduras, Panama, Venezuela, Mexico, Cuba, Guatemala…… …….. *H. hirsute* **n.sp.**

– Mesepisternum not setose; hypomeron may be setose; pronotal punctures variable; horns variable, may be short and tuberculate or long……. 2

2) Line of setae present on all femurs; coarse punctures scattered across pronotum; clypeal horn short, tuberculate; supraorbital horns short, tuberculate, not pointing inwards as in *H. marginata*; Brazil …….. *H. akuma* **n.sp**.

– Line of setae not present on any femur; pronotal punctures varable; horns variable ……. 3

3) Pronotum and elytra with long distinct setae arising from coarse punctures; body elongate; coarse pronotal punctures concentrated on lateral portions of pronotum; male specific characters unknown; Columbia ……. *H. reburra* **n.sp.**

– Not bearing long porrect hairs; body usually not as elongate; pronotal punctures variable ……... 4

4) Pronotal punctures of one size or at most 4 larger punctures…….. 5

– Pronotal punctures of two sizes with numerous coarse punctures …..……..……..... 8

5) Mentum medially and longitudinally raised; Hypomeron without punctures, smooth; horns long thin, subequal in length; horns usually not as well developed as those of *H. tricornis*; Brazil, Costa Rica, Cuba, Guatemala, Nicaragua, Mexico, Panama …….

6) ……...*H. canaliculata* **Champion**

– Mentum not raised; hypomeron usually punctate; horns variable ……..…… 6

7) (5) Mentum medially depressed; hind femur weakly bent; clypeal horn long, and arising perpendicular to head; clypeal horn thinnest at base and widening apically and flat on top; supraorbital horn strongly bent both inwards and forward; Peru …….. *H. triceratops* **Steiner**

– Mentum not depressed, hind femur not bent; horns variable ……..… 7

8) Anterior fourth of first two abdominal segments laterally rugulose; size large: 9 – 10 mm; clypeal horn conical, projecting forward from clypeus; supraorbital horns large, thinnest basally and widening apically; supraorbital horns strongly bent to point anteriorly; Brazil, Peru ……..…….. *H. laevicollis* **Kulzer**

– First two abdominal segment completely laterally rugulose; clypeal horn long, flat, widening apically and flat to emarginate on top; supraorbital horns long, produced perpendicular to head and strongly curved forward; Mexico, Costa Rica, …… *H. dejeani* **Champion**

9) Coarse punctures densely concentrated on the disc; clypeal and supraorbital horns long, thin and arising perpendicularly to head; all horns subequal in length; supraorbital horns bending slightly toward each other; USA, Mexico, Guatemala, Belize, El Salvador, Honduras, Costa Rica, Panama, Columbia, Venezuela, Ecuador, Cayman Islands, Cuba, Jamaica……..……... *H. tricornis* **Dalman**

– Coarse pronotal punctures not concentrated primarily on disc; horns usually not equal in length or as thin as in *H. tricornis* …….. 9

10) Coarse pronotal punctures concentrated on lateral portions of pronotum ……..…….. 10

– Coarse pronotal punctures scattered throughout pronotum ……..…….. 12

11) Hypomeron and prosternum setose with distinct golden setae; clypeal horn short, conical and arising forward from clypeus; supraorbital horns long, bending slightly inward toward each other; supraorbital horns projecting perpendicularly from head; Nicaragua, Mexico, Peru, Columbia, Panama, Haiti, Brazil, Ecuador, Honduras, Guatemala, Dominican Republic, Costa Rica, El Salvador……. *H. biimpressa* **Latreille**

– Hypomeron and prosternum without distinct setae; horns variable ……...…… 11

12) Posterior edge of pronotum with raised edge; supraorbital horns thick and either not bending laterally or bending away from each other; clypeal horn short, tuberculate; clypeal horn often conical but may be thinner in the middle and widening apically; Brazil, Bolivia, Paraguay, Argentina. …..……..……..……..……..……..……..……... *H. vacca* **Fabricius**

– Posterior edge of pronotum without raised edge; clypeal horn long, flattened and truncated; clypeal horn widening apically and then becoming flat to slightly emarginate on top; supraorbital horns strongly curved forward to point anteriorly. Peru, Colombia, Panama, Mexico ……..…….. *H. cat* **Steiner**

13) Coarse pronotal punctures more than twice the size of fine punctures; male with three long horns; clypeal horn three times the size, at base, of supraorbital horns. Hind horns perpendicular, not bending; Brazil, Colombia ……..……... *H. brasiliensis* **Kulzer**

– Coarse pronotal punctures two times the size or less of fine punctures; clypeal horn not three times the size of one supraorbital horn; ……..……13

14) Lateral edges of pronotum gradually raised, weakly sloping upwards from margins of pronotum; clypeal horn not short, of similar size to supraorbital horns; horns similar to *H. tricornis* but not as long; Honduras, Mexico, Bahamas, Costa Rica, Guatemala, Brazil , Cuba, USA, Jamaica……. *H. depressa* **Champion**

– Lateral edges of pronotum not as depressed as above; after flat margin, lateral edges of prontum steeply raised and flattens out near disc; clypeal horn usually short; supraorbital horns variable ……..……. 14

15) Male with cuticular spike on profemur; clypeal horn short, conical and produced forward; supraorbital horns long, not curved toward each other, but slightly curved forward Brazil, Peru ……..……... *H. amazonica* **Kulzer**

– Male without cuticular spike on profemur; clypeal horn short; supraorbital horns variable…… …….. 15

16) (14) Supraorbital horns short tubercles, projected forward from head; Mexico, Costa Rica, Guatemala, Peru, USA. ……...…….....…….....…….....…….....…... *H. marginata* **LeConte**

– Supraorbital horns long, projected perpendicularly from head; USA, Mexico, Guatemala..… ...……...…….....…….....…….....…….....……..…... *H. cryptica* **n.sp**

Phylogenetic analyses

The illustrated phylogeny (Figure 1.38) is a strict consensus Maximum Parsimony tree, based on three most parsimonious trees of length 361, *Mycotrogus* is recovered as basal to *Hypogena*. *Hypogena, Mycotrogus*, *and Tharsus* are recovered

outside of Triboliini within a clade sister to *Argoporis* (Cerenopini). Comparison of morphology of *Hypogena* shows that *Hypogena* is more similar to this clade than it is with other Triboliini genera, excluding *Mycotrogus* and *Tharsus*. The most conspicuous similarity is the presence and type of sensoria on the antennae.

Within *Hypogena*, the fossil species *Hypogena marginalis* was recovered as basal to the rest of *Hypogena*. Some well-resolved groups within *Hypogena* were also recovered that species that share some synapomorphies (orange and purple boxes).

Discussion

Morphology of Hypogena

The tarsal outgrowths on *Hypogena* are cuticular and extend from the underside of the tarsi (Figure 1.5). The tarsal outgrowths are only present on the first two tarsomeres. This structure is present in the protarsi of both sexes. As little is known about the lifecycle of *Hypogena,* besides their living under the bark of standing dead trees, it is difficult to determine the function of this structure. In various families of Coleoptera, tarsal structures seen in one sex are used during mating (Bilton *et al.*, 2008). However, in *Hypogena* the structures occur in both sexes and there are no grooves on the females for reception of the tarsal outgrowths.

The “gearing” is also cuticular and arises from the posterior of the metasternite. This structure is not true gearing as there is no equivalent corresponding structure on the anterior surface of the metacoxa (Figure 1.6). The function for these structures is unknown; however, it is speculated that they may be a gin trap, or used for stridulation

along with the protarsal outgrowths. Biomechanically, it is implausible that this structure would be used for stridulation with the protarsal outgrowths.

Tribal Placement of Hypogena

Looking at the sensory structures on *Hypogena*, *Tribolium confusum*, *Tribolium castaneum*, and *Tenbrio molitor,* a vast difference is shown between these genera and *Hypogena*. In *Tribolium* there are simple sensoria that have been bifurcated, and are in a slight depression. This may be a diagnostic character for the genus *Tribolium*. In *Tenebrio*, there are simple sensoria that are not bifurcated, and are in a shallow depression. The sensoria are also directed more towards the distal portion of the antennomere. In *Hypogena*, there are stellate sensoria. The simple sensoria that compose the stellate sensoria are directed outwards and are located in a deep depression. This shows that morphologically *Hypogena* is distinct from the type material of Triboliini, which supports the phylogenetic data (Kanda, 2017). Examinations of specimens under a light microscope show that *Tharsus spp.* and *Mycotrogus spp.* also have stellate sensoria, as well as other morphological characteristics shared with *Hypogena*, but not the other genera currently included in Triboliini.

According to Figure 1.38, Triboliini is currently polyphyletic with *Tharsus, Mycotrocus* and *Hypogena* being recovered outside of Triboliini. These genera are likely grouped by the synapomorphic character of stellate sensoria in all three genera. The metasternal cuticular gearing and the presence of sexually dimorphic horn-like processes are shared between *Mycotrogus* and *Hypogena.* This figure also shows that *Argoporis* is recovered as sister to the clade containing *Hypogena*, which reflects where

it was placed with genetic data (Kanda, 2017). The character driving this relationship is likely the presence of compound sensoria in all genera in that clade. Within *Hypogena*, *H. marginata, H. hirsuta, H. cryptica* and *H. vacca* (orange box) all are similar in size and horn type. They all have a very weakly produced clypeal horn and distinctly larger supraorbital horns. All the species in the clade of *H. cat, H. triceratops, H. laevicollis, H.dejeani and H. canaliculata* (purple box), are similar with a lack of coarse punctures on pronotal puncturing, except *H. cat*. *H. dejeani, H. cat,* and *H. triceratops* all have a truncated clypeal horn.

According to Kanda (2017), *Hypogena* is recovered sister to a clade containing the tribes: Scotobini, Cerenopini, Alleculini and Eulabini (Kanda, 2017). The sensoria in Scotobini are stellate sensoria, similar to those seen in *Hypogena*, but with the component sensoria greatly reduced. The sensory structures in the tribe Eulabini are also similar to the stellate sensoria seen in *Hypogena*, but with the simple sensoria not as diverged as they are in *Hypogena.* In the tribe Cerenopini there are placcoid sensoria, which are unlike those seen in *Hypogena*, but are still present in a depression. Examination of the morphology of the stellate sensoria across these four tribes show that *Hypogena* is closer related to the clade containing Scotobini, Cerenopini, Alleculini and Eulabini than its current placement indicates, which also reflects the phylogenetic data (Kanda, 2017).

Phylogenetically and morphologically, *Hypogena* and other closely related genera do not appear to belong in Triboliini. The recovery of *Hypogena* as sister to the clade containing multiple tribes and that only *Mycotrogus* and *Tharsus* were recovered closer to *Hypogena* indicates that a new tribe should be erected for these genera.

Potential new species

A single adult female specimen (CASC) from 4.5 miles northeast of Los Planes in Baja California, Mexico cannot currently be classified within the known species of *Hypogena*. Due to the importance of male characters in identification of members of this genus, a male needs to be found before a new species is described. Due to the relatively limited sampling and restricted ranges of some *Hypogena* species, it is likely that more species are yet to be collected and described.

Notes on other species

Fairmaire (1891) described the species *Ulosonia caratodera,* citing the similarity of the head horns but also the presence of horns on the pronotum. Kulzer (1962) stated that it was likely that the species occurred in a separate genus, citing the presence of the thoracic horns, which are not present in any other member of *Hypogena*. Having not examined this species, it is not possible to determine where it belongs phylogenetically.

References

Aalbuu, R. L., Triplehorn, C. A., Campbell, J. M., Brown, K. W., Somerby, R. E., & Thomas, D. B. (2002). Tenebrionidae Latreille 1802. In *American Beetles* (Arnett, R. H., M. C. Thomas, P. E. Skelley and J. H. Fran, Vol. 2, pp. 463–509). Boca Raton, Florida: CRC Press.

Berry, R. L. (1973). The Cerenopini and Eulabini, two tribes previously included in the Scaurini (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of America*, *66*(1), 70–77. https://doi.org/10.1093/aesa/66.1.70

Bilton, D. T., Thompson, A., & Foster, G. N. (2008). Inter- and intrasexual dimorphism in the diving beetle *Hydroporus memnonius* Nicolai (Coleoptera: Dytiscidae). *Biological Journal of the Linnean Society*, *94*(4), 685–697. https://doi.org/10.1111/j.1095-8312.2008.01029.x

Blackwelder, R. E. (1945). Checklist of the Coleopterous insects of Mexico, Central America, the West Indies, and South America. *United States National Museum Bulletin*, *185*, 343–550. https://doi.org/10.5479/si.03629236.185.3

Bousquet, Y., Thomas, D. B., Bouchard, P., Smith, A. D., Aalbu, R. L., Johnston, M. A., & Steiner Jr., W. E. (2018). Catalogue of Tenebrionidae (Coleoptera) of North America. *ZooKeys*, *1*, 1–455. https://doi.org/10.3897/zookeys.728.20602

Brazeau, M. D. (2011). Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnaean Society*, *104*, 489–498.

Champion, George C. (n.d.). *Biologia Centrali-Americana: zoology, botany and archaeology* (Vol. 4). R. H. Porter. Retrieved from https://www.biodiversitylibrary.org/bibliography/730

Champion, George Charles. (1895). *A list of Tenebrionidae supplementary to the "Munich" Catalogue*. Société Entomologique de Belgique.

Dalman, J. W. (1823). *Analecta entomologica.* Typis Lindhianis. Retrieved from https://www.biodiversitylibrary.org/bibliography/66069

deArmas, L. F., & Garrido, O. H. (2012). Primer registro de Hypogena biimpressa (Coleoptera: Tenebrionidae) para La Española, Antillas Mayores. *Solenodon*, *10*, 107–109.

Doyen, J T. (1985). Reconstitution of the tribes Ulomini and Triboliini for North America and Central America (Tenebrionidae, Coleoptera). *Proceedings of the Entomological Society of Washington.*, *87*, 512–524.

Doyen, J. T. (1988). Tenebrionidae and Zopheridae of the Chamela biological station and vicinity, Jalisco, Mexico (Coleoptera). *Folia Entomológica Mexicana*, (No. 77), 211–276.

Doyen, J. T. (1966). The skeletal anatomy of *Tenebrio molitor* (Coleoptera: Tenebrionodae), *5*(3), 103–150.

Doyen, J. T. & Poinar, G. (1994). Tenebrionidae from Dominican amber (Coleoptera). *Insect Systematics & Evolution*, *25*, 27–51. https://doi.org/10.1163/187631294X00027

ESRI (2011). ArcGIS Desktop. Version 10. Environmental Systems Research Institute, Redlands, California.

Fabricius, J. C. (1801). *Systema elevtheratorvm secvndvm ordines, genera, species, adiectis synonymis, locis, observationibvs, descriptionibus* (Vol. 1). Kiliae

(Bibliopoli academici.

Fairmaire, L. (1891). Coléopteres Hétéromeres. *Annales de La Société Entomologique de France*, *61*, 77–98.

Fairmaire, M. L. (1892). Descriptions de quelques Coléoteres Argentins. *Annales de La Sociéte Entomologiqu de Belgique*, *36*, 242–253.

Giraldo, A. E., & Flores, G. E. (2016). Peruvian Tenebrionidae: A review of present knowledge and biodiversity. *Annales Zoologici*, *66*(4), 499–513. https://doi.org/10.3161/00034541ANZ2016.66.4.002

Harrison, J. du G. (2012). Cleaning and preparing adult beetles (Coleoptera) for light and scanning electron microscopy. *African Entomology*, *20*(2), 395–401. https://doi.org/10.4001/003.020.0209

Huelsenbeck, J. P., & Ronquist, F. (2001). MRBAYES: Bayesian Inference of phylogeny. *Bioinformatics*, *17*, 754–755.

Humboldt, A. von, Bonpland, A., Cuvier, G., Latreille, P. A., Schoell, F., Stone, J. H., & Valenciennes. (1811). *Recueil d'observations de zoologie et d'anatomie compar : faites dans l'ocn atlantique, dans l'intieur du nouveau continent et dans la mer du sud pendant les anns 1799, 1800, 1801, 1802 et 1803 /*. A Paris : Retrieved from https://www.biodiversitylibrary.org/bibliography/43770

Jacquelin du Val, C. (1857). *Histoire physique, politique et naturelle de l'Ile de Cuba par Ramon de la Sagra* (Vol. Tome septième). Paris: Arthus Bertrand. Retrieved from https://www.biodiversitylibrary.org/bibliography/51128#/summary

Kuo, J. (2014). *Electron Microscopy: Methods and Protocols* (3rd ed.). New York City: Humana press. Retrieved from https://www.amazon.com/Electron-Microscopy-

Methods-Protocols-Molecular/dp/1627037756

Kang, G.-J., Zhu, Z.-R., Cheng, J.-A., & Way, M. (2012). Antennal sensilla of parthenogenetic and bisexual *Lissorhoptrus oryzophilus* (Coleoptera: Curculionidae). *The Florida Entomologist*, *95*, 8–15. https://doi.org/10.2307/23140744

Kulzer, H. (1962). Neue Tenebrioniden aus Südamerika (Col.). *Entomologische Arbeiten Museum G. Frey*, *13*, 79–100.

LeConte, J. (1852). *Descriptions of new species of Coleoptera from California.* (Vol. v 5 (1852)). New-York : Lyceum of Natural History (New York). Retrieved from https://www.biodiversitylibrary.org/item/55134

Maddison, W. P. and D.R. Maddison. 2018. Mesquite: a modular system for evolutionary analysis. Version 3.40 http://mesquiteproject.org

Medvedev, G. S. (1977). The taxonomic significance of the antennal sensillae of the darkling beetles (Coleoptera: Tenebrionidae). *Trudi Vsesoyuz - Novo Entomologicheskovo*, *58*, 61–86.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2015) A RESTful API for Access to Phylogenetic Tools via the CIPRES Science Gateway. *Evolutionary Bioinformatics* 11, 43-48.DOI: 10.4137/EBO.S21501

Peck, S. B. (2005). A checklist of the beetles of Cuba with data on distributions and bionomics: (Insecta: Coleoptera). *Arthropods of Florida and Neighboring Land Areas*, *18*, 1–241.

Ronquist, F. & J. P. Huelsenbeck. (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572-1574.

Schulz, W. A. (1901). Biologishe, zoogeographische und synonymische Notizen aus der Käferfauna des unteren Amazonenstroms. *Berliner Entomologishe Zeitschrift*, *46*, 321–338.

Spillman, T. J. (1963). The American genus *Mycotrogus*: A synopsis, a new species for Cuba, and a note on a larva. *Proceedings of the Entomological Society of Washington*, *65*(1), 21–30.

Spillman, T. J. (1973). Nomenclatural problems in six genera of Tenebrionidae (Coleoptera). *Proceedings of the Entomological Society of Washington*, *75*(1), 39–44.

Steiner Jr, W. E. (2005). Two new species of three-horned Hypogena from Peru (Coleoptera: Tenebrionidae). *Annales Zoologici*, *55*(4), 571–574.

Steiner Jr, W. E. (2011). Progress on the survey of the darkling beetles (Coleoptera: Tenebrionidae) of New Providence Island, Bahamas, and new records for two species on San Salvador. In *Proceedings of the Thirteenth Symposium on the Natural History of the Bahamas. Gerace Research Center, San Salvador, Bahamas* (pp. 114–118).

Suliman, A. I., Diakite, M. M., Ali, S., & Wang, M.-Q. (2016). Effects of the antennal sensilla distribution pattern on the behavioral responses of *Tribolium castaneum* (Coleoptera: Tenebrionidae) | Florida Entomologist. *Florida Entomolgist*, *99*(1), 52–59.

Swofford, D. (2003). *PAUP: Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tschinkel, W. R., & Doyen, J. T. (1980). Comparative anatomy of the defensive glands, ovipositors and female genital tubes of tenebrionid beetles (Coleoptera). *International Journal of Insect Morphology and Embryology*, *9*(5), 321–368. https://doi.org/10.1016/0020-7322(80)90009-4

Figures

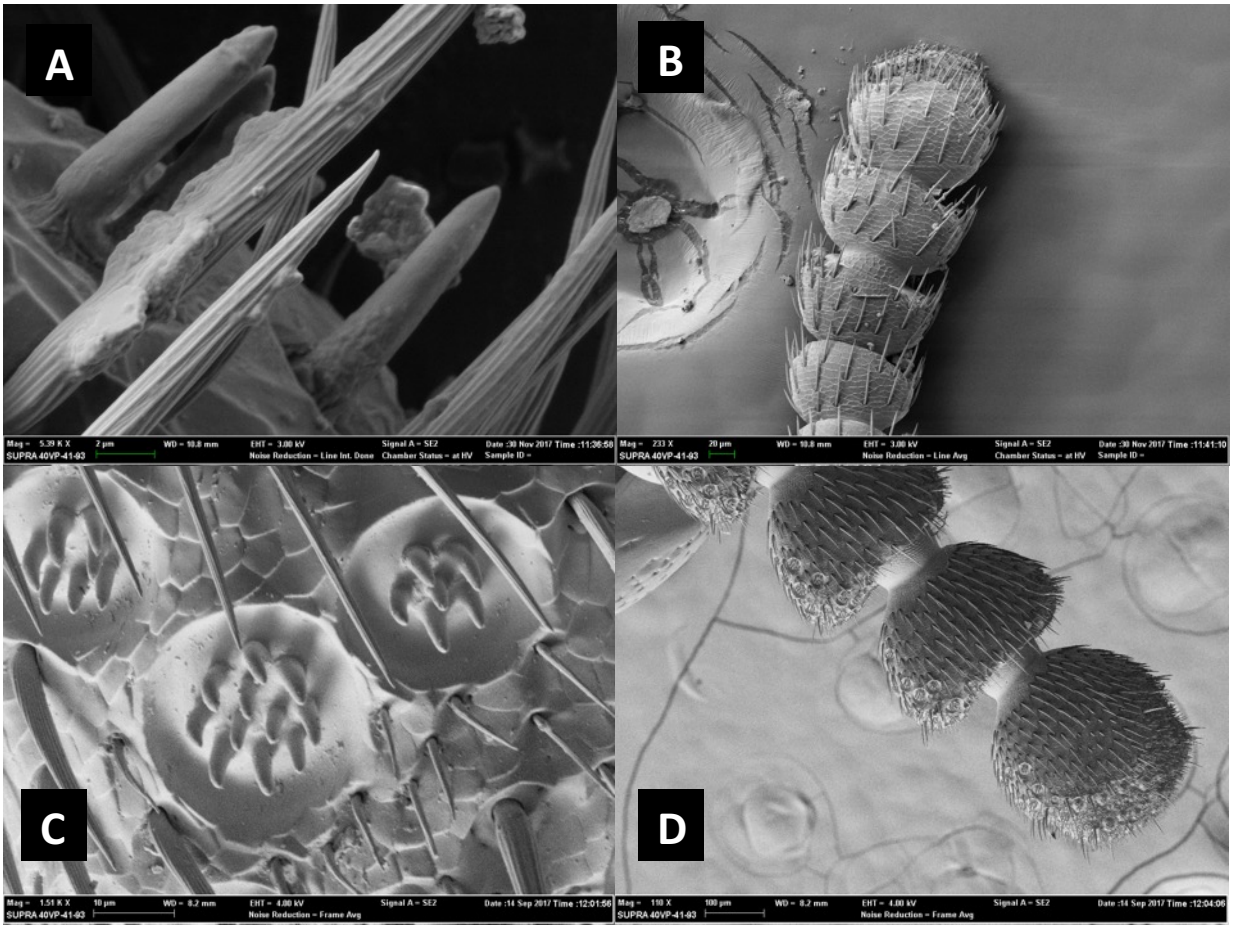

Figure 1.1: Comparison of antennal sensoria between *Hypogena* and *Tribolium*. 1.1.A. Sensoria of *Tribolium confusum* at 5390X magnification with an accelerating voltage of 3 kV. 1.1.B. Terminal segments of antennae of *Tribolium confusum* at 233X magnification with an accelerating voltage of 3kV. 1.1.C. Sensoria of *Hypogena tricornis* at 1510X magnification with an accelerating voltage of 4kV. 1.1.D. Terminal segments of antennae of *Hypogena tricornis* at 110X magnification with an accelerating voltage of 4 kV.

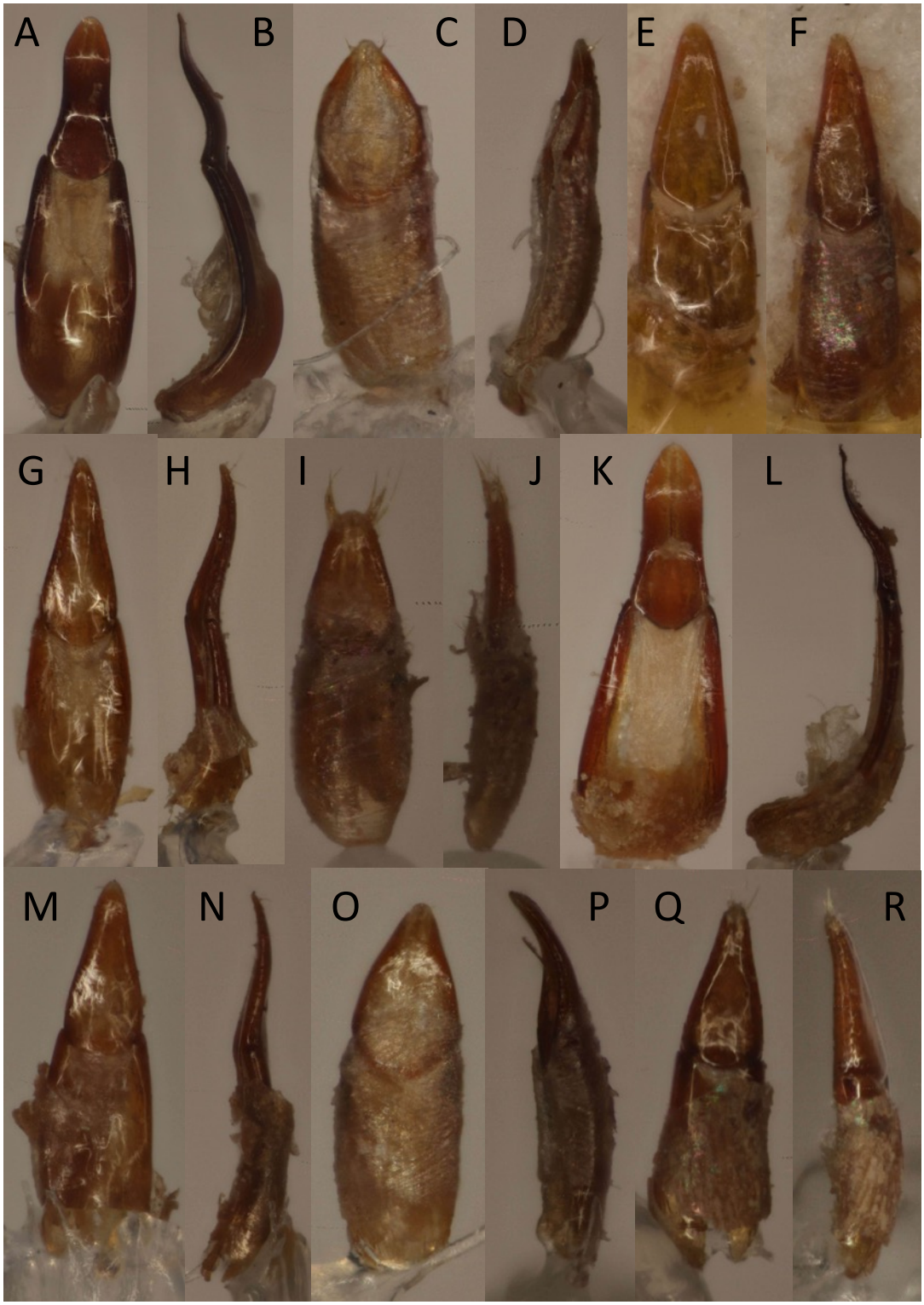

Figure 1.2: Male genitalia in *Hypogena*. 1.1.A. *H. biimpressa* dorsal. 1.1.B. *H. biimpressa* lateral. 1.1.C. *H. canaliculata* dorsal. 1.1.D. *H. canaliculata* lateral. 1.1.E. *H. brasiliensis* dorsal. 1.1.F. *H. laevicollis* dorsal. 1.1.G. *H. cryptica* dorsal. 1.1.H. *H. cryptica* lateral. 1.1.I. *H. depressa* dorsal. 1.1.J. *H. depressa* lateral. 1.1.K. *H. hirsuta* dorsal. 1.1.L. *H. hirsuta* lateral. 1.1.M. *H. marginata* dorsal. 1.1.N. *H. marginata* lateral. 1.1.O. *H. tricornis* dorsal. 1.1.P. *H. tricornis* lateral. 1.1.Q. *H. vacca* dorsal. 1.1.R. *H. vacca* lateral

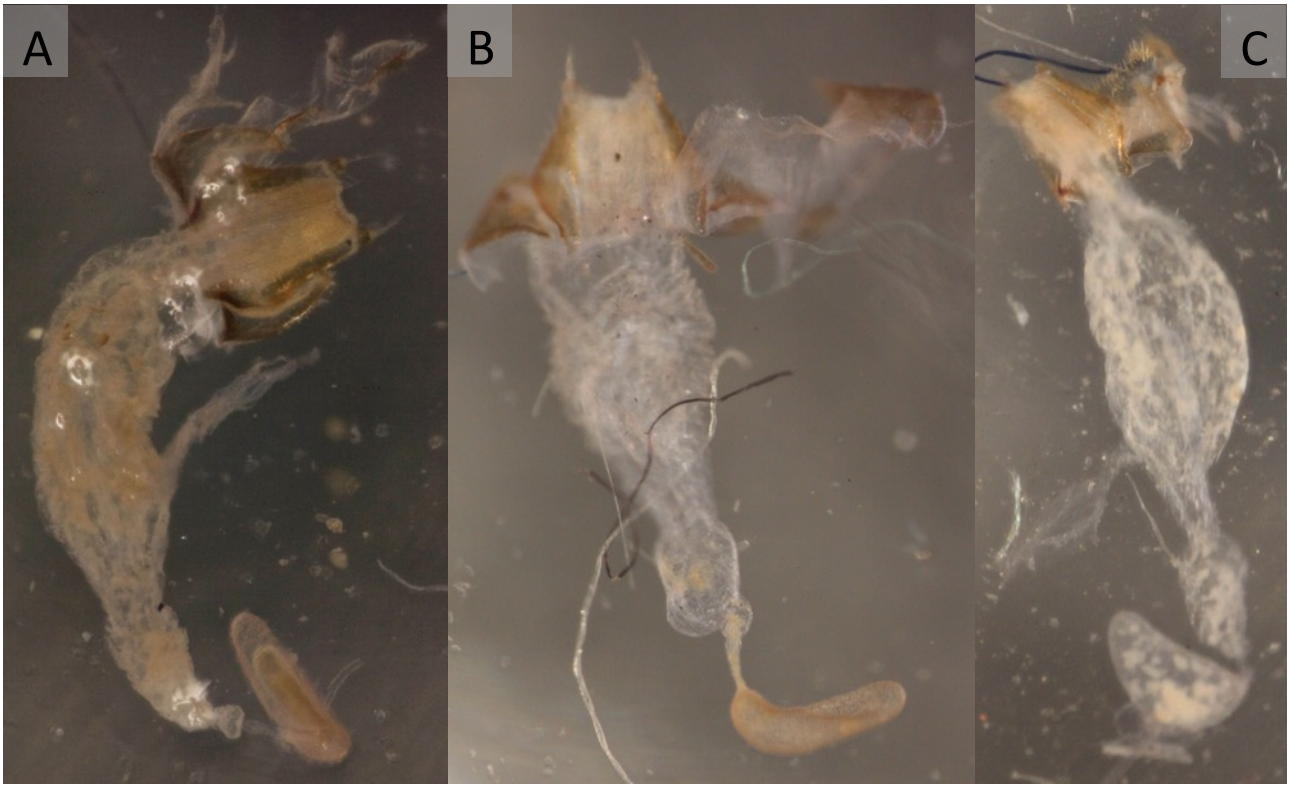

Figure 1.3: Female genitalia of *Hypogena.* 1.1.A. *H. depressa.* 1.1.B. *H. marginata.* 1.1.C. *H. vacca.*

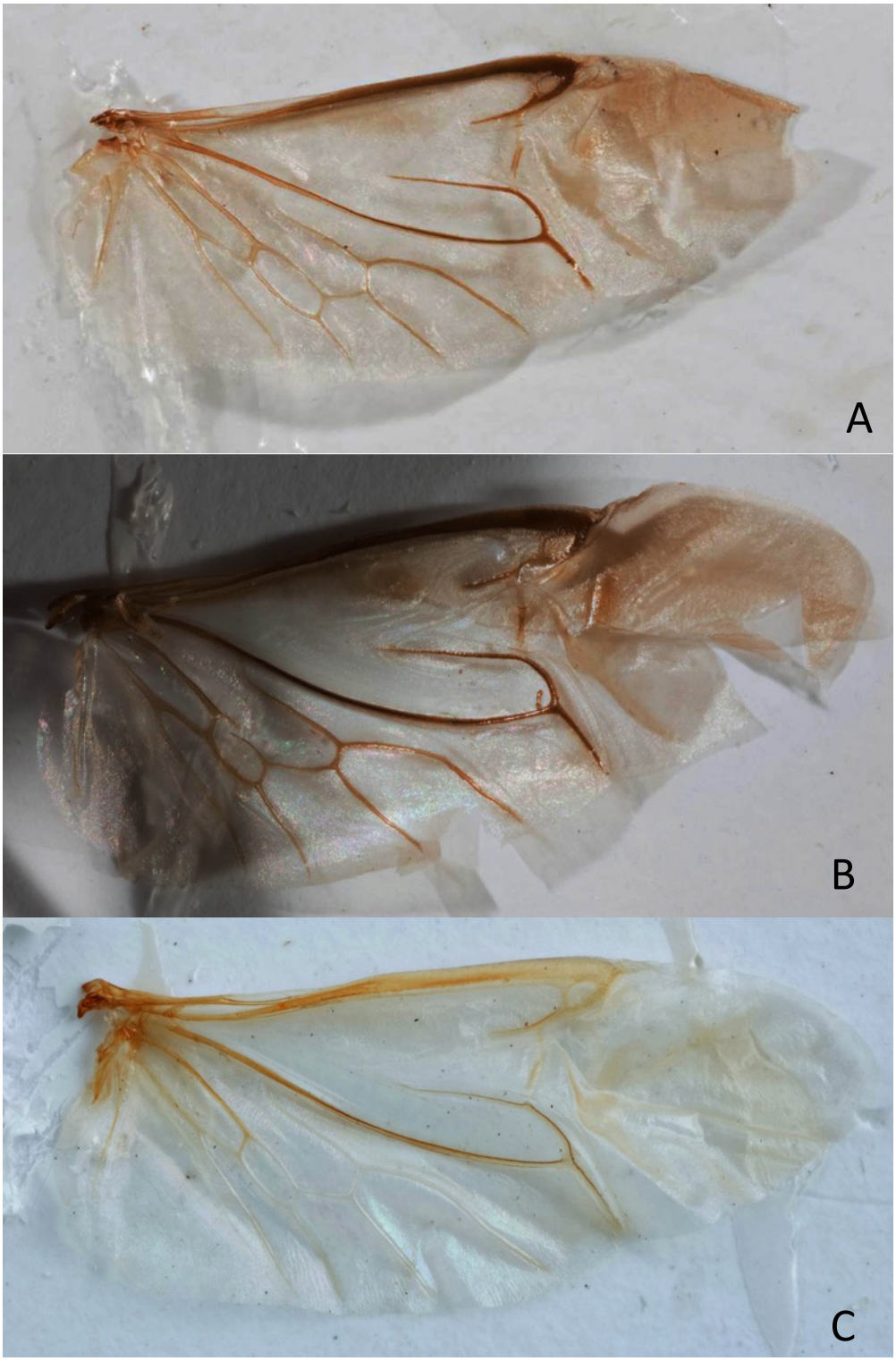

Figure 1.4: Dissected hind wing of *Hypogena species*. 1.4.A. Wing of *H. vacca*. 1.4.B. Wing of *H. depressa*. 1.4.C. Wing of *H. tricornis*.

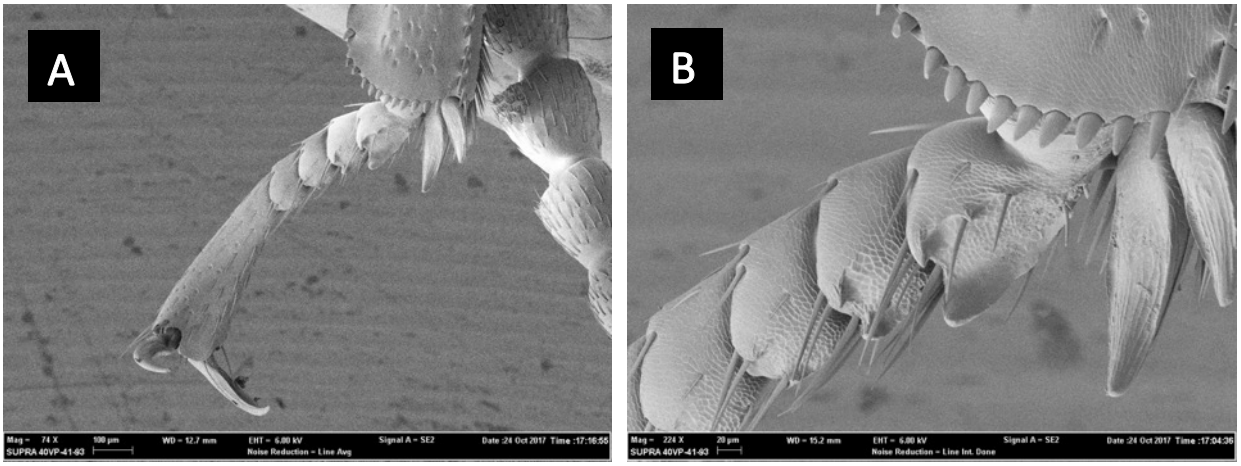

Figure 1.5: High and low magnification of tarsal outgrowths on *Hypogena tricornis*. 1.5.A: The tarsal outgrowths at 74X magnification with an accelerating voltage of 6 kV. 1.5.B: The tarsal outgrowths at 224X magnification with an accelerating voltage of 6 kV.

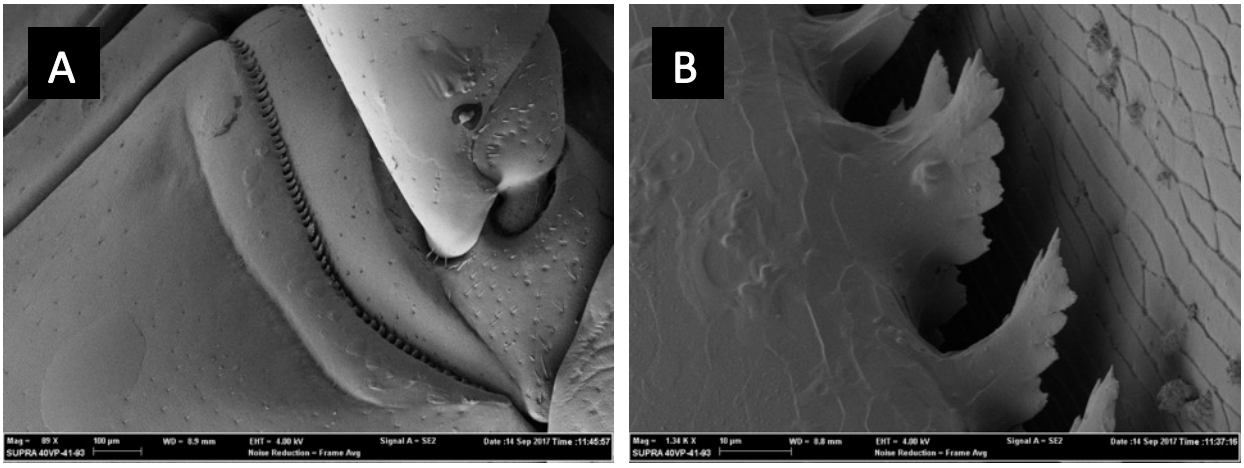

Figure 1.6: High and low magnification of posterior metasternal gearing on *Hypogena tricornis.* 1.6.A. Posterior metasternal gearing at 89X magnification with an accelerating voltage of 4 kV. 1.6.B. Posterior metasternal gearing at 1340X magnification with an accelerating voltage of 4 kV.

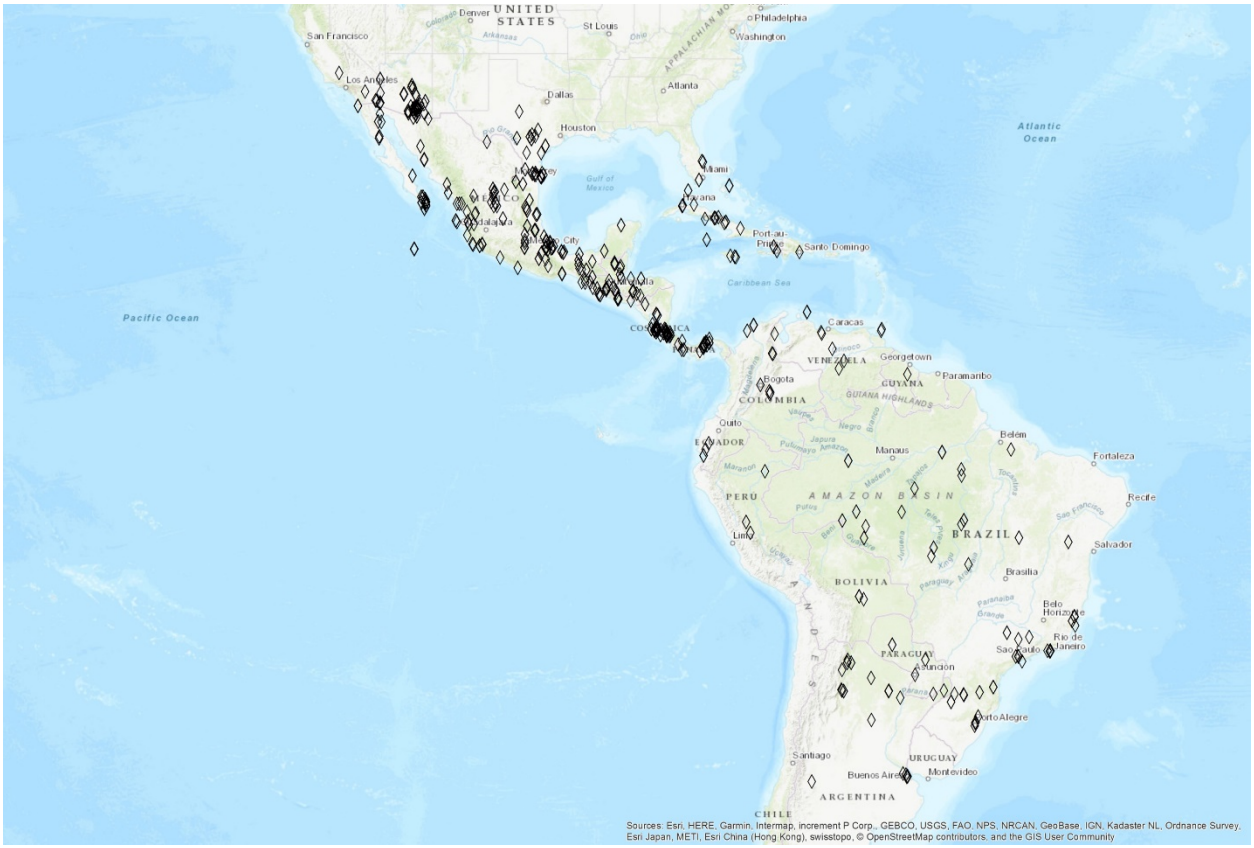

Figure 1.7: Distribution of all *Hypogena* species. Based on 1429 databased specimens. Made with ArcGIS.

Figure 1.8: Images of *Hypogena marginalis* in Dominican Amber. 1.5.A. Dorsal view. 1.5.B. Ventral view. 1.5.C. Lateral view. 1.5.D. Anterior view of head. Images obtained from Dr. George Poinar

Figure 1.9: Holotype for *Hypogena cat.* Dorsal view, Lateral view and labels for *Hypogena cat*.

Figure 1.10: Distribution of *Hypogena cat*. Based on 7 databased specimens. Made with ArcGIS.

Figure 1.11: Holotype for *Hypogena triceratops.* Dorsal view, lateral view and labels of *Hypogena triceratops*.

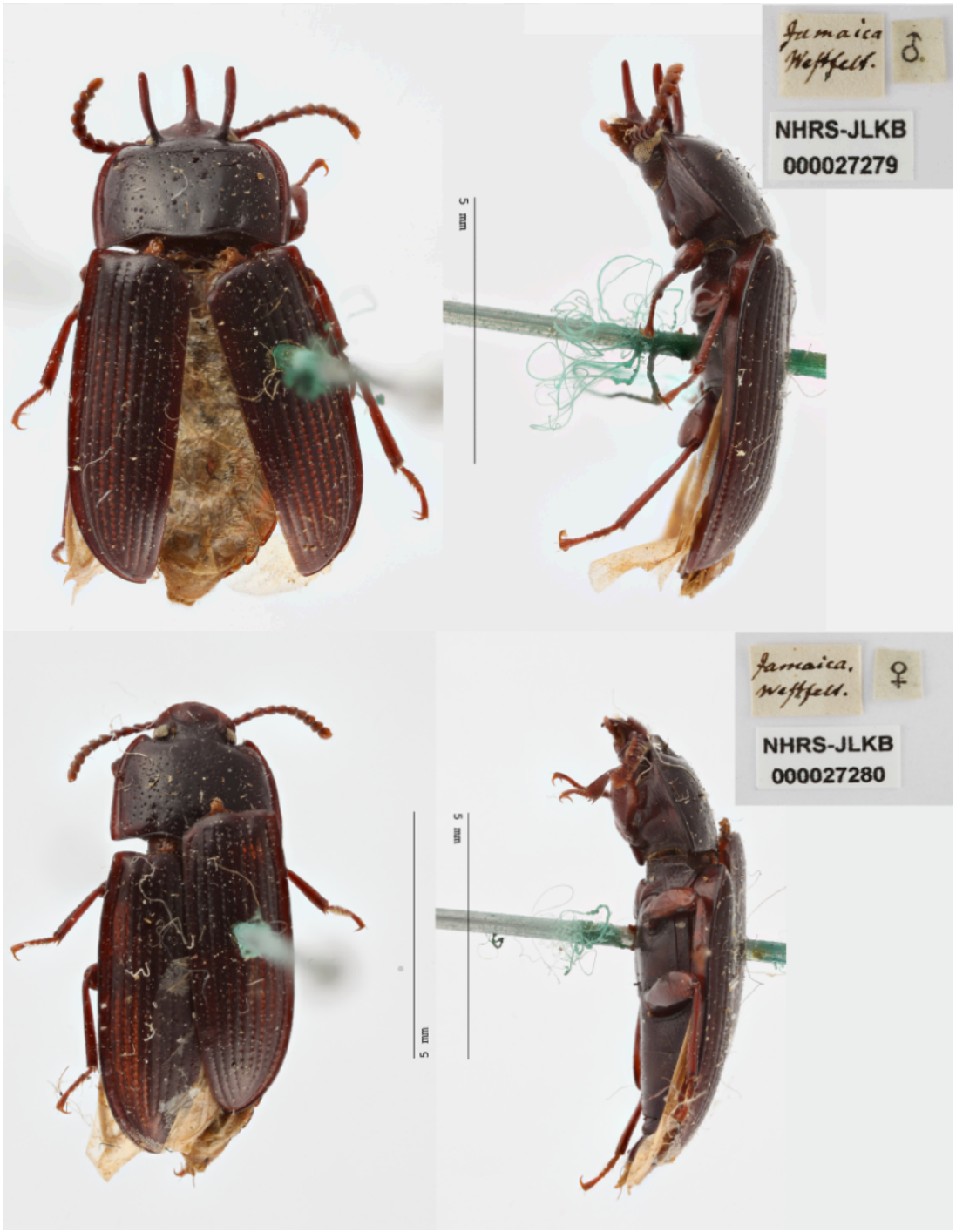

Figure 1.12: Holotype and allotype of *Hypogena tricornis*. Top: dorsal view, lateral view and labels views of male. Bottom: dorsal view, lateral view and labels views of female. Images obtained from Dr. Johannes Bergsten at The Swedish Museum of Natural History (NHRS).

Figure 1.13: Distribution of *Hypogena tricornis*. Based on 284 databased specimens. Made with ArcGIS.

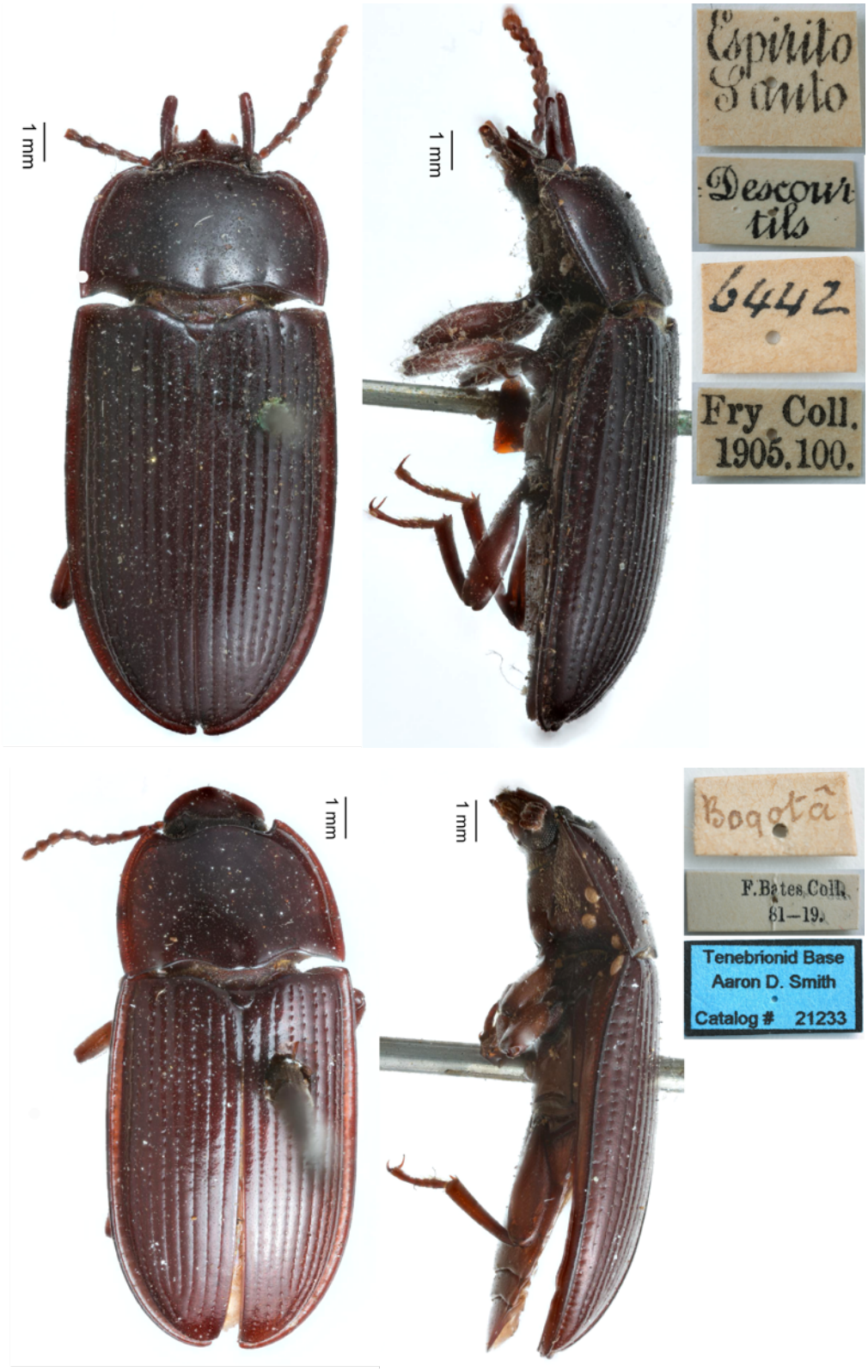

Figure 1.14: Neotypes for *Hypogena biimpressa*. Top: dorsal view, lateral view and labels of male. Bottom: Dorsal view, lateral view and labels of female. Neotypes designated from specimens in the British Museum of Natural History (BMNH).

Figure 1.15: Distribution of *Hypogena biimpressa*. Based on 269 databased specimens. Made with ArcGIS.

Figure 1.16: Holotype for *Hypogena marginata.* Dorsal view, lateral view, ventral view and labels for holotype of *Hypogena marginata*. Specimen obtained from the Harvard University type database (MCZ).

Figure 1.17: Distribution of *Hypogena marginata*. Based on 152 databased specimens. Made with ArcGIS.

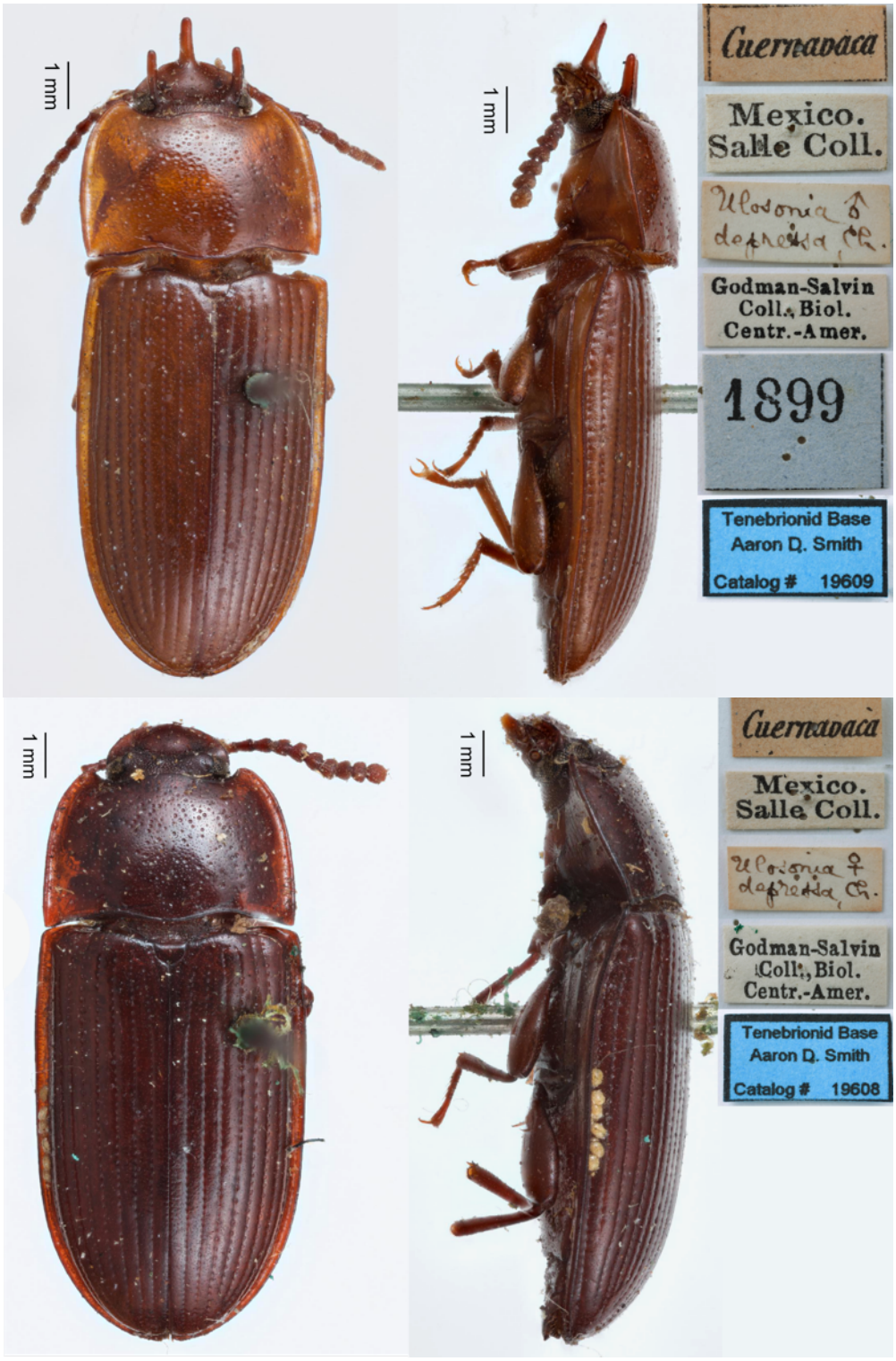

Figure 1.18: Lectotype and paralectotype for *Hypogena depressa*. Top: dorsal view, lateral view and labels of male. Bottom: dorsal view, lateral view and labels of female.

Figure 1.19: Distribution of *Hypogena depressa*. Based on 175 databased specimens. Made with ArcGIS.

Figure 1.20: Lectotype and paralectotype for *Hypogena canaliculata*. Top: dorsal view, lateral view and labels of male. Bottom: Dorsal view, lateral view and labels of female.

Figure 1.21: Distribution of *Hypogena canaliculata*. Based on 67 databased specimens. Made with ArcGIS.

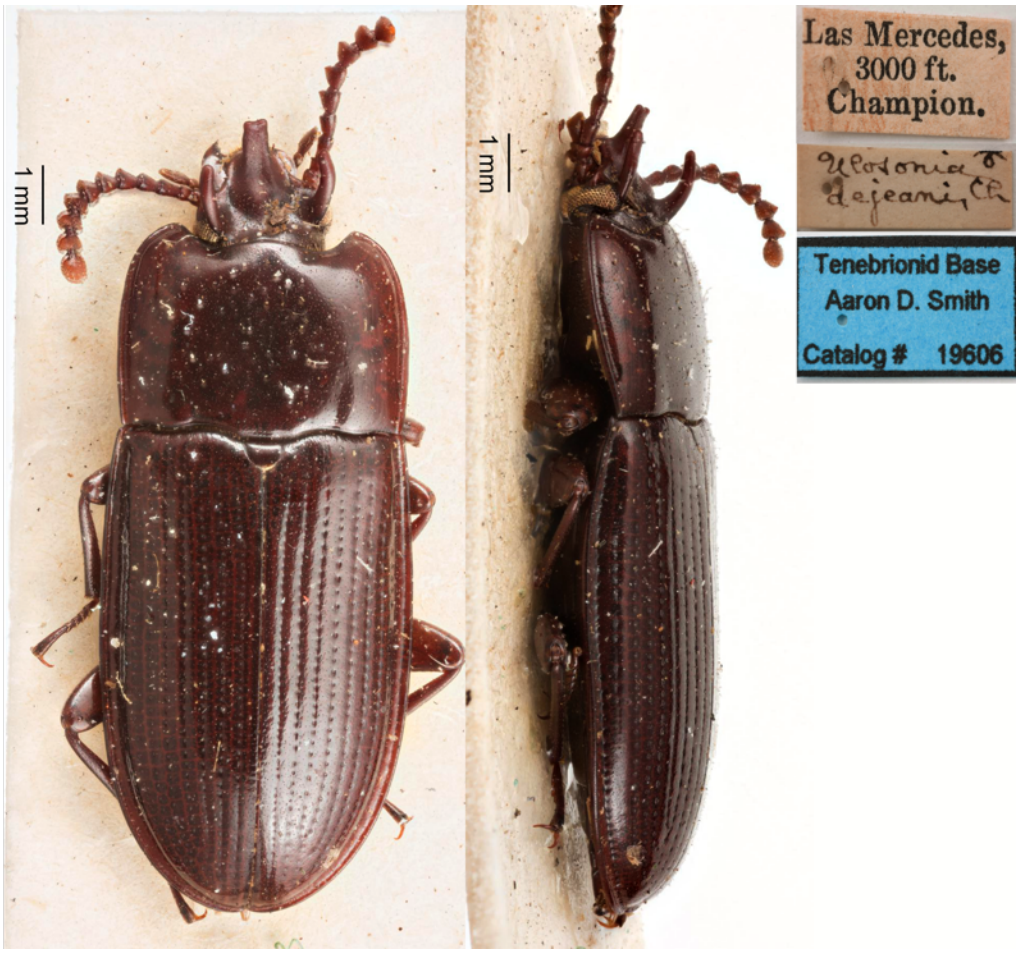

Figure 1.22: Lectotype for *Hypogena dejeani.* Dorsal view, lateral view and labels for Lectotype of *Hypogena dejeani*.

Figure 1.23: Distribution of *Hypogena dejeani*. Based on 6 databased specimens. Made with ArcGIS.

Figure 1.24: Lectotype and paralectotype for *Hypogena vacca*. Top: dorsal view, lateral view and anterior view of male. Bottom: Dorsal view, and head view of female. Images obtained from Dr. Michael Kuhlmann from The Zoological Museum of Kiel University (ZMUK).

Figure 1.25: Distribution of *Hypogena vacca*. Based on 311 databased specimens. Made with ArcGIS.

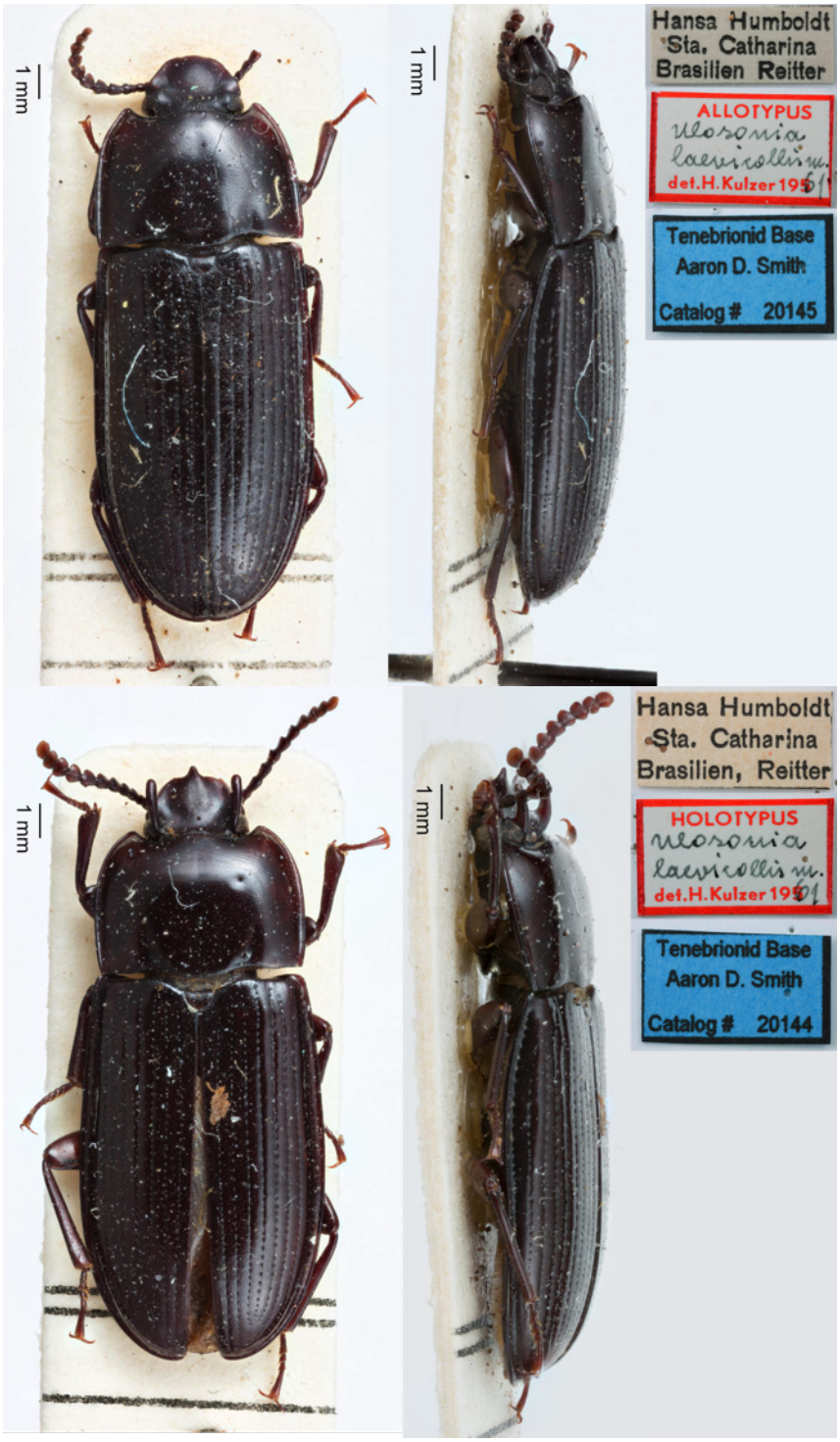

Figure 1.26: Holotype and Allotype for *Hypogena laevicollis*. Top: dorsal view, lateral view and labels of male. Bottom: Dorsal view, lateral view and labels of female.

Figure 1.27: Distribution of *Hypogena laevicollis*. Based on 25 databased specimens. Made with ArcGIS.

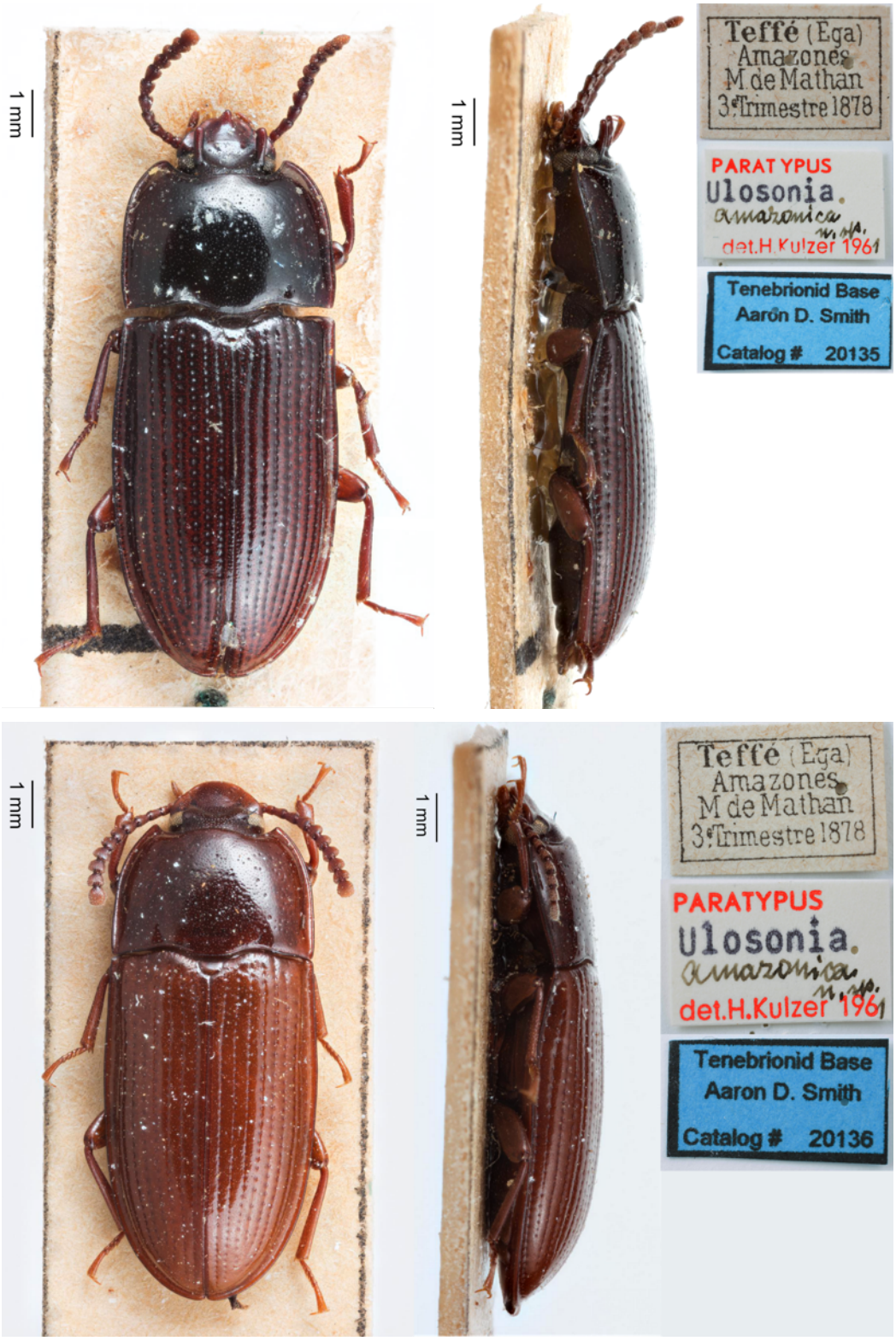

Figure 1.28: Paratypes for *Hypogena amazonica*. Top: dorsal view, lateral view and labels of male. Bottom: Dorsal view, lateral view and labels of female.

Figure 1.29: Distribution of *Hypogena amazonica*. Based on 17 databased specimens. Made with ArcGIS.

Figure 1.30: Holotype of *Hypogena brasiliensis.* Dorsal view, lateral view and labels for holotype of *Hypogena brasiliensis*.

Figure 1.31: Distribution of *Hypogena brasiliensis*. Based on 2 databased specimens. Made with ArcGIS.

Figure 1.32: Holotype and Allotype for *Hypogena cryptica*. Top: dorsal view, lateral view and labels of male. Bottom: Dorsal view, lateral view and labels of female.

Figure 1.33: Distribution of *Hypogena cryptica*. Based on 69 databased specimens. Made with ArcGIS.

Figure 1.34: Holotype and Allotype for *Hypogena hirsuta*. Top: dorsal view, lateral view and labels of male. Bottom: Dorsal view, lateral view and labels of female.

Figure 1.35: Distribution of *Hypogena hirsuta*. Based on 51 databased specimens. Made with ArcGIS.

Figure 1.36: Holotype for *Hypogena reburra.* Dorsal view, lateral view and labels for holotype of *Hypogena reburra*.

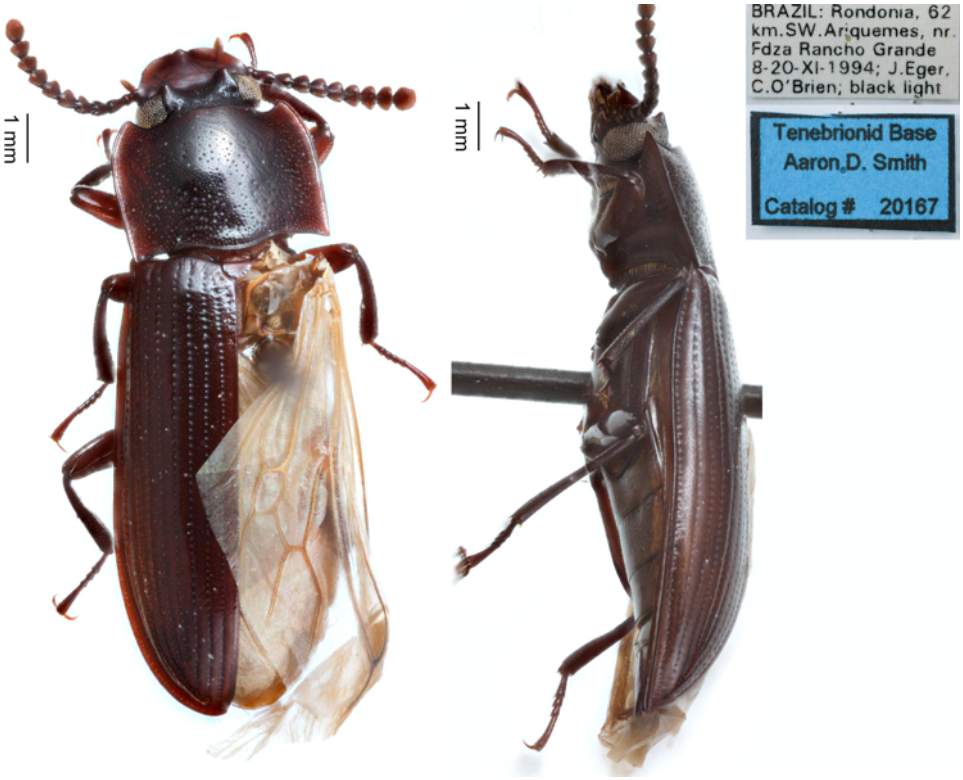

Figure 1.37: Holotype for *Hypogena akuma* Dorsal view, lateral view and labels for holotype of *Hypogena akuma*.

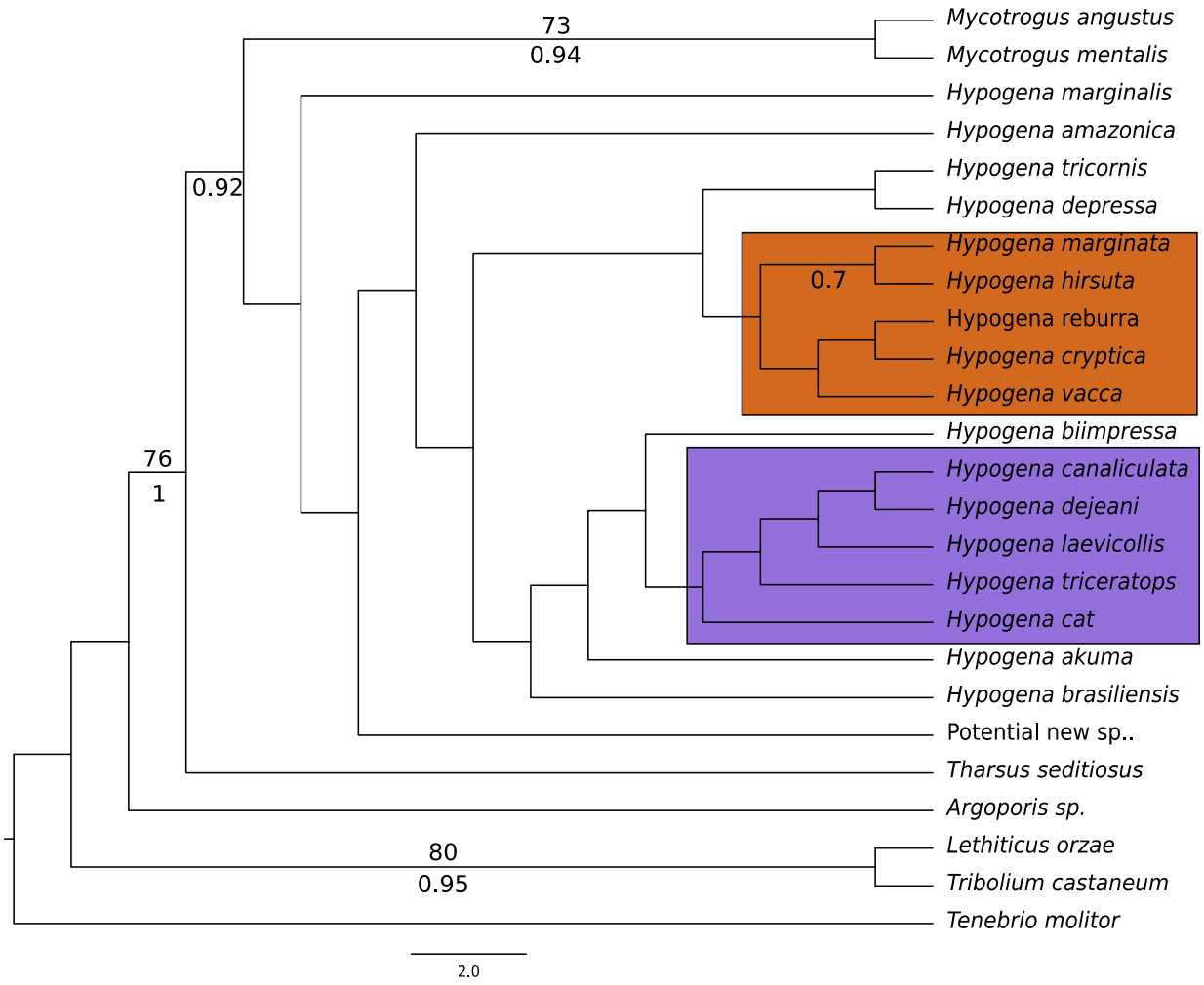

Figure 1.38: Strict Consensus tree based on morphology of Hypogena and closely related taxa. Tree made as a consensus of three most parsimonious trees. Tree length: 361. Bootstrap values with 1000 replicates is shown by the top number. Posterior probabilities shown by the bottom number. Scores of lower than .5 or 50, respectfully, are not shown. Colored boxes show species that share morphological characters.

Chapter 2: Review of antennal sensory structures in Tenebrionidae (Coleoptera)

Introduction

The family Tenebrionidae is a diverse, worldwide family of Coleoptera with over 20,000 species described (Bousquet *et al.*, 2018) that live in many ecological niches. This family also has a wide diversity in size, color, and morphology. Across Tenebrionidae there are sensory structures on the antennae called sensoria. The antennae are of particular importance as a chemosensory organ in many groups of insects, including Lepidoptera and other Coleoptera families (*e.g.*, Curculionidae) (Kang, 2012). Within Tenebrionidae three types of sensoria appear. The first type is simple sensoria, which are composed of one sensilla. The second type is stellate sensoria, which are when multiple sensilla are grouped into a circle. The third type are placcoid sensoria, which are sensoria that are not composed of any sensilla, forming flattened circular areas on the antennae (Medvedev, 1977, Doyen *et al.,* 1982). (Figure 2.1).

Stellate sensoria may be of greater use taxonomically than is currently acknowledged. Many papers refer to compound sensoria in Tenebrionidae as a binary character on the antenna or on specific antennomeres (Matthews, 2011; Aballay *et al.*, 2016). However, some refer to the relative number and position of the sensoria on the antennomeres as well (Medvedev, 1977, Hopp *et al.*, 2008, Medvedev, 1977). As there is often selection pressure on the antennae and antennal structures, they can be modified (Medvedev, 1977, Kang, 2012). Examination of sensoria within Tenebrionidae

show that the presence of stellate sensoria is a highly conserved trait and that placcoid sensoria have evolved at least twice within the family.

The objective for this project is to explore the diversity of sensoria on the Tenebrioninae branch of Tenebrionidae as defined by Kanda *et al.* (2017). This has not been done since Medvedev reviewed the taxonomic importance of stellate sensoria (Medvedev, 1977). Electron microscopy has vastly improved and resolution of the images produced is much better. This project will identify patterns in the sensory structures in Tenebrionidae.

Materials and Methods

Antennal Preparation

Specimens were chosen from the major tribes of Tenebrionidae and were donated from the Kanda, Smith, and Lumen collections. Vouchers of each specimen are deposited in the arthropod collections at NAU (CPMAB) (Table 2.1). One antenna was removed from each beetle, taking care not to damage the terminal antennomeres. If an antenna was damaged or otherwise unusable, the second antenna was used. Antennae were taken from pinned specimens stored in low humidity environments. Specimens were mounted on SEM aluminum stubs using double sided carbon tape. The antennae were sputtercoated with gold/palladium for six seconds. If there was charging when viewed with the SEM, the specimens were recoated for an additional ten seconds.

SEM Examination

A Zeiss Supra 40VP was used to produce SEM images. The specimens were viewed using 5 KeV accelerating voltage. If there was charging that occurred that

affected the image, then the accelerating voltage was decreased. If the accelerating voltage was decreased to 1 kV then to increase the signal the working distance was decreased. Two sets of images were taken from each sample. The first was taken at a 35x magnification to 160x magnification to show the layout of the structure and show the location of the structure of interest. The second set was taken at 550x magnification to 2200x magnification to show the structures in detail.

Results

SEM studies

In *Tribolium confusum* (Triboliini), there are no stellate sensoria. Instead, on the apical portion of the terminal three antennomeres there are bifurcated sensoria (Figure 2.2.B). This structure is connected at the base and located in a depression.

The sensoria on the antennae of two genera of Alphitobiini show that they both have stellate sensoria. In *Alphitobius* the sensoria are present on the terminal 6 antennomeres (Figure 2.3.A). They are composed of 5-7 sensoria that are raised up from the surrounding cuticle (Figure 2.3.B). The sensoria themselves are arranged in a circle on the laterally distal portion of the antennomeres. In the genus *Metaclisa* the 3-4 sensoria are grouped together more heavily than how they are arranged in *Alphitobius* (Figure 2.3.D). The stellate sensoria are present on the terminal 5 antennomeres (Figure 2.3.C). Similar to *Alphitobius,* the stellate sensoria are located in the laterally distal area of the antennomeres.

The sensoria in Amarygmini are stellate. The stellate sensoria are located in a deep depression and are arranged in a circle, but they converge, rather than diverge

(Figure 2.4.B). In the depression of the sensoria there are also cuticular holes. The stellate sensoria are located throughout the antennomere (Figure 2.4.A).

The tribe Amphidorini show that some genera have stellate sensoria while other genera do not. In the genus *Nycterinus,* there are stellate sensoria that are located on the distal edge of the antennomere (Figure 2.5.A). The sensoria are located in a shallow depression and are arranged in a circle with sensoria in the middle of the circle (Figure 2.5.B). In the genus *Eleodes*, the antennomeres are covered in a dense layer of setae and also have long sensilla interspersed in the layer of setae (Figure 2.5.D).

In the tribe Centronopini, the genus *Taurocerus* have placcoid sensoria that are surrounded by a raised area of cuticle (Figure 2.6.A-B). On the area around the placcoid sensoria there are secondary sensory structures that are loosely covered in cuticle. These secondary sensoria are located throughout the antennomeres and are within one sensorial diameter from each other (Figure 2.6.C).

In the tribe Cerenopini the genera have placcoid sensoria that are located in a depression. In the genus *Argoporis,* the distal edge of the antennomeres extend backwards to halfway down the antennomere and the distal side of the antennomeres are densely covered with placcoid sensoria (Figure 2.7.A). The edges of the depression where the sensoria are located are steep and the base of the sensoria are not visible Figure 2.7.B). In the genus *Cerenopus* the edges of the depression are much shallower than in *Argoporis* (Figure 2.7.C). The placcoid sensoria are more concentrated at the distal edge of the antennomere (Figure 2.7.D).

The genera in the tribe Diaperini have stellate sensoria. In the genus *Neomida,* the sensoria are weakly raised and are divergent (Figure 2.8.B). The stellate sensoria

are on the distal edge of the antennomeres (Figure 2.8.A). In the genus *Sitophagus,* the sensoria are arranged in a circle and are strongly raised and converge (Figure 2.8.D). The stellate sensoria are located on the distal side of the antennomeres (Figure 2.8.C). In the genus *Diaperus* the sensoria are arranged in a circle and the cuticle beneath the sensoria is raised up above the surrounding cuticle and the interior of the circle (Figure 2.8.F). The sensoria are on the lateral edge of the antennomere towards the distal edge (Figure 2.8.E).

The genera in the tribe Eulabini have stellate sensoria. The sensoria in the genus *Epantius* are located in deep depressions and the sensoria arranged in a circle. The sensoria are weakly convergent with sensoria in the center of the circle (Figure 2.9.B). The sensoria are located on the distal edge of the antennomere (Figure 2.9.A).

The genera in the tribe Hypophlaeini there are stellate sensoria. In the genus *Corticeus*, the stellate sensoria are located on the distal portion of the antennomere and are only present on the lateral sides of the distal portion of the antennomere (Figure 2.10.A). The sensoria are slightly raised and are arranged in a circle where the sensoria are strongly convergent.

In the tribe Opatrini the genera have simple sensoria. In the genus *Ulus*, on the apical three antennomeres, there are raised sensoria intermixed with setae. On all the segments there are also long mechanosensory setae (Figure 2.11. B).

In the tribe Phalerini there are stellate sensoria. In the genus *Phaleria* the sensoria are placed into a deep depression with steep sides. The bottom of the depression is not visible. The sensoria themselves are strongly convergent and are

strongly angled (Figure 2.12.B). The stellate sensoria are located on the distal portion of the antennomere (Figure 2.12.A).

In the tribe Stenochiini there are stellate sensoria. In the genus *Strongylium* the stellate sensoria are in a deep depression and are surrounded by setae (Figure 2.13.B). The sensoria are composed of 8-11 sensilla and are arranged in a circle with simple sensoria in the middle. The sensoria are slightly raised out of the depression and are located throughout the antennomere and are separated by less than the width to one width of one stellate sensoria from each other (Figure 2.13.A). There are also long setae at the distal end of every antennomere.

The genera in the tribe Scaurini have stellate sensoria. In the genus *Scaurus* the stellate sensoria are very small and are located throughout the antennomere interspersed with short setae (Figure 2.14.A). The stellate sensoria are composed of 1-5 sensilla and are arranged in a circle (Figure 2.14.B). The stellate sensoria are located in a deep pit that has steep edges. In Figure 2.14.C the base of the depression is viewable and the sensoria are connected at the base.

The genera in the tribe Scotobiini have stellate sensoria. In the genus *Emmallodera* the stellate sensoria are located on the distal side of the antennomeres (Figure 2.15.A). The stellate sensoria are arranged in circles of 7-11 sensilla with sensilla located in the center of the circle (Figure 2.15.B). The circle of sensoria is located in a shallow depressions and are separated by a thin, ridge-like wall of cuticle. The sensoria themselves are highly reduced, resembling nubs.

Some genera in the tribe Tenebrionini have stellate sensoria. In the genus *Zophobas*, the stellate sensoria are located on the terminal three antennomeres and are

more concentrated at the distal portion of the antennomere (Figure 2.16.A). The stellate sensoria are in deep depressions with shallow edges. At the base of the pit the sensoria are raised (Figure 2.16.B). The simple sensoria are arranged in a circle with sensoria also appearing inside the circle. At the base of each depression there are cuticular holes. In the genus *Neatus* the stellate sensoria are located on the terminal three antennomeres and are on the distal portion of the antennomere (Figure 2.16.C). The stellate sensoria are arranged in a tightly compacted circle of approximately 6 simple sensoria and are located in a deep depression (Figure 2.16.D). The circle of sensoria is raised slightly from the base of the depression. In the genus *Rhinandrus,* the stellate sensoria are located throughout the antennomere in the apical four antennomeres (Figure 2.16.E). The stellate sensoria are located in deep depressions with steep edges. The simple sensoria are arranged in a circle of 6-7 simple sensoria (Figure 2.16.F). In *Tenebrio molitor,* the apical portion of the antennomere has simple sensory structures. The sensory structures are composed of a single sensorium that is produced in a depression (Figure 2.16.H). These sensoria do not point outwards, rather they point apically.

The genera in the tribe Ulomini have stellate sensoria. The Stellate sensoria in Uloma are only present in the apical antennomere on the distal side (Figure 2.17.A). The stellate sensoria are composed of 2-4 closely grouped simple sensoria (Figure 2.17.B). The sensoria are surrounded by a ring of upraised cuticle.

In the tribe Cnodalonini, there are stellate sensoria. The stellate sensoria are located throughout the antennomeres but are separated by the diameter of approximately two stellate sensoria (Figure 2.18.A). The stellate sensoria are

interspersed with many setae. The stellate sensoria are located in a very shallow depression and are arranged in a circle of 7-8 simple sensoria. The circle is upraised slightly. At the base of the depression there are cuticular holes.

In the tribe Nilionini there are stellate sensoria and simple sensoria. The stellate sensoria are located in a line on the distal edge of the apical five antennomeres (Figure 2.19.A). The stellate sensoria are arranged in a circle of 7-9 simple sensoria with sensoria arising from the middle of the circle (Figure 2.19.B). There are also simple sensoria that are not located within the stellate sensoria. There are also many cuticular holes that are not located in the stellate sensoria.

Discussion

Stellate Sensoria Phylogeny

By mapping stellate sensoria onto a recent phylogeny of Tenebrionidae (Kanda, 2017), the evolution of these sensory structures can be estimated (Figure 2.20). The tribes that are basal to Opatrini do not have compound sensoria (Figure 2.11). Stellate sensoria likely evolved once and is conserved throughout Tenebrionidae. Placcoid sensoria arise at least two times in the tribes Centronopini and Cerenopini (Figures 2.6 and 2.7).

Within Tenebrionidae multiple patterns arise. (1) Sensoria are common on the apical 4-5 antennomeres, which may vary depending on the tribe (Medvedev, 1977). (2) Sensoria usually appear on the apical portion of the antennomeres. (3) When the sensillae are aggregated into stellate sensoria, they form a ring-like structure, which may or may not have additional sensoria appearing in the middle of the ring. (4) If compound sensoria (stellate or placcoid) are present they are usually raised or located

in a depression, which may vary in depth and steepness of the edges. (5) There are cuticular openings that occur located around sensillae and mechanoreceptors.

The sensoria in Tenebrionidae are usually present on the apical 4-6 antennomeres. The tribes Opatrini and Ulomini only have sensoria on the apical two segments (Figure 2.11 & Figure 2.17). The number of sensoria usually increases toward the distal segments of the antennae. As the number of sensoria increases, the distance separating the sensoria decreases, sometimes to within a diameter of each other (*e.g.*, Scotobini). This is likely a mechanism to increase the amount of chemical information that an insect can receive farther from its body.

Throughout Tenebrionidae the sensoria are located on the apical portion of the antennomeres. Closer to the terminal antennomere, more of the antennomere itself is covered with sensory structures (Figure 2.3, Figure 2.14, Figure 2.16). Having the sensoria arranged at the apical portion of the antennomere is likely a more efficient means of picking up chemicals from the environment than if the sensory structures are at the basal portion of the antennomere. This trend varies throughout the tribes. There are also tribes that have the sensory structures dispersed evenly throughout the antennomeres (Figure 2.4, Figure 2.6, Figure 2.7 and Figure 2.13). Examination of the lifecycle of those tribes would give insight into why they may have sensory structures throughout their antennomeres rather than have them concentrated on the apical portion of each antennomere.

One of the most common noticeable patterns is the ring-like structure of the stellate sensoria. This is present in most lineages that are more derived than Opatrini. The positioning of the simple sensoria that compose these structures vary widely across

the tribes of Tenebrionidae. The sensoria can be convergent, as in Ulomini, Phalerini, and Hypophlaeini (Figures 2.17, 2.12 and 2.10), or they can be divergent as in Scaurini, Nilionini and Stenochiini (Figures 2.14, 2.19 and 2.13). The function of this may be to promote or limit the amount of chemosensory information the insect encounters. It should be noted that in Nilionini (Figure 2.19), there are both stellate sensoria, and simple sensoria that are located outside of the stellate sensoria. This is likely to facilitate in chemical communication with conspecific individuals.

Many of the tribes that have either placcoid or stellate sensoria that are raised above the rest of the cuticle, as in Diaperini or Alphatobini (Figures 2.8 and 2.3), or in a depression, as in Eulabini, Scotobini, and Tenebrionini (Figure 2.9, 2.15 and 2.16). Having the sensoria located in a depression is well conserved across the family Tenebrionidae as 10 of the 19 tribes examined have this structure. As such, raised sensoria has likely evolved more than once. These adaptations may be another means to increase the surface area of these structures so they can more efficiently detect chemicals in the environment.

In many tribes, there are cuticular openings that likely act as additional chemoreceptors. These openings usually occur at the base of setae as in some Diaperini and some Tenebrionini. (Figure 2.8 and 2.16). The cuticular holes are also present in the stellate sensoria in the tribes: Amarygmini, Centronopini, Cerenopini, Diaperini, Hypophlaeini, Phalerini, Tenebionini, Cnodalonini, and Nilionini. This is a highly conserved trait in Tenebrionidae as it is present in some form in all tribes examined. In Nilionini, these cuticular openings are much more common than in other tribes as they occur throughout the antennal cuticle (Figure 2.19). This may be another

source of chemoreception with conspecific individuals. It is also interesting that in *Taurocerus sp.* there are large openings into the cuticle (Figure 2.6.C). These openings are then covered with a loose framework of cuticle and are arranged in a circle around the placcoid sensoria. This is likely a different type of chemoreceptor that is designed to allow certain sized particles into the opening.

The stellate sensoria may also be used to clarify some phylogenetic relationships. The genus *Nycterinus* is currently classified in the tribe Amphidorini, however, most of this tribe does not have stellate sensoria while *Nycterinus* does (Figure 2.5). This reflects where it is recovered in other studies (Kanda*,* 2017; Smith *et al.,* in prep).

This study shows that stellate sensoria are a highly conserved character within Tenebrionidae. This study also outlines a relatively inexpensive method to examine beetle cuticle using an SEM. Increased sampling is needed to further elucidate the evolution of sensoria in Tenebrionidae.

References

Aballay, F.H., Flores, G.E., Silvestro, V.A., Zanetti, N.I., Centeno, N.D. 2016. An illustrated key to, and diagnoses of the species of Tenebrionidae (Coleoptera) associated with decaying carcasses in Argentina. Annales Zoologici 66(4): 703-726.

Aloquio, S., Lopes-Andrade, C. 2017. A new species of *Lelegeis* (Coleoptera: Tenebrionidae: Diaperini) from the Atlantic Forest of Brazil. Zoologia 34:1-5.

Bousquet, Y., Thomas, D. B., Bouchard, P., Smith, A. D., Aalbu, R. L., Johnston, M. A., & Steiner Jr., W. E. (2018). Catalogue of Tenebrionidae (Coleoptera) of North America. *ZooKeys*, 1: 1–455. https://doi.org/10.3897/zookeys.728.20602

Doyen, J.T. & Tschinkel, W.R. (1982). Phenetic and cladistics relationships among Tenebrionid beetles (Coleoptera). *Systematic Entomology.* 7:127-183.

Doyen, J.T. 1985. Reconstruction of the tribes Ulomini and Triboliini for North and Central America (Tenebrionidae: Coleoptera). Proceedings of the Entomological Society of Washington 87(3): 512-524.

Doyen, J.T. 1988. Tenebrionidae and Zopheridae of the Chamela Biological Station and Vicinity, Jalisco, Mexico (Coleoptera). Folia Entomoligica Mexicana 77:211-276.

Harrison, J. 2012. Cleaning and preparing adult beetles (Coleoptera) for light and scanning electron microscopy. Entomological Society of Southern Africa: 20(2): 395-401.

Hopp, K.J., Ivie, M.A. 2008. First report of *Tyrtaeus rufus* Champion and *Tyrtaeus dobsoni* Hinton (Tenebrionidae: Diaperinae: Anopidiina) from Florida. The Coleopterists Bulletin 62(3): 427-436.

Kanda, K. (2017). Phylogenetic studies in Tenebrionidae. Research dissertation from Oregon State University.

Kang, G., Zhu, Z., Cheng, J., Way, M.O. 2012. Antennal sensilla of parthenogenetic and bisexual *Lissorhoptrus oryzophilus* (Coleoptera: Curculionidae). Florida Entomologist 95(1): 8-15.

Kuo, J. 2007. Electron Microscopy: Methods and Protocols Second Edition. Humana Press. Totowa, NJ. 461-462.

Matthews, E.G. 2011. Australian Alleculinae: New genera, new combinations, and a lectotype designation (Coleoptera: Tenebrionidae). Psyche 2012: 1-5.

Medvedev, G.S. 1977. The taxonomic significance of the antennal sensillae of the Darkling Beetles (Coleoptera: Tenebionidae). Trudi vsesoyuz-novo entomologicheskovo obshehestva. 58: 61-86.

Figures

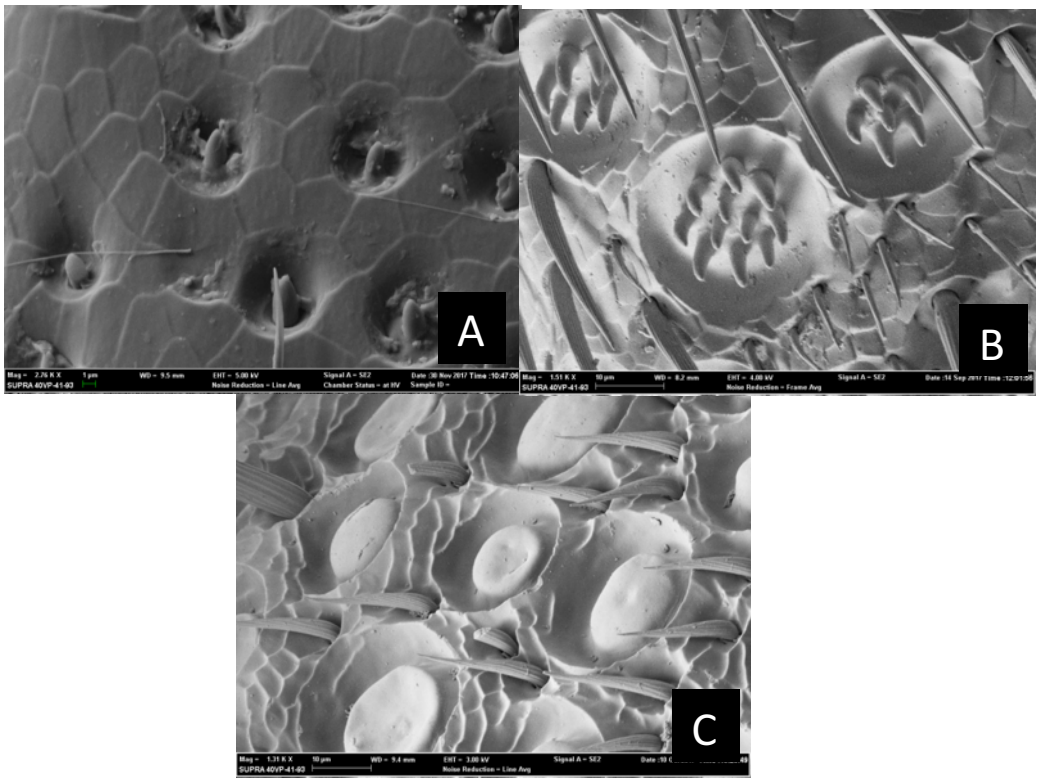

Figure 2.1: Examples of sensoria types. 2.1.A. Simple sensoria on *Tenebrio molitor*. 2.1.B. Stellate sensoria on *Hypogena tricornis*. 2.1.C. Placcoid sensoria on *Cerenopus concolor*.

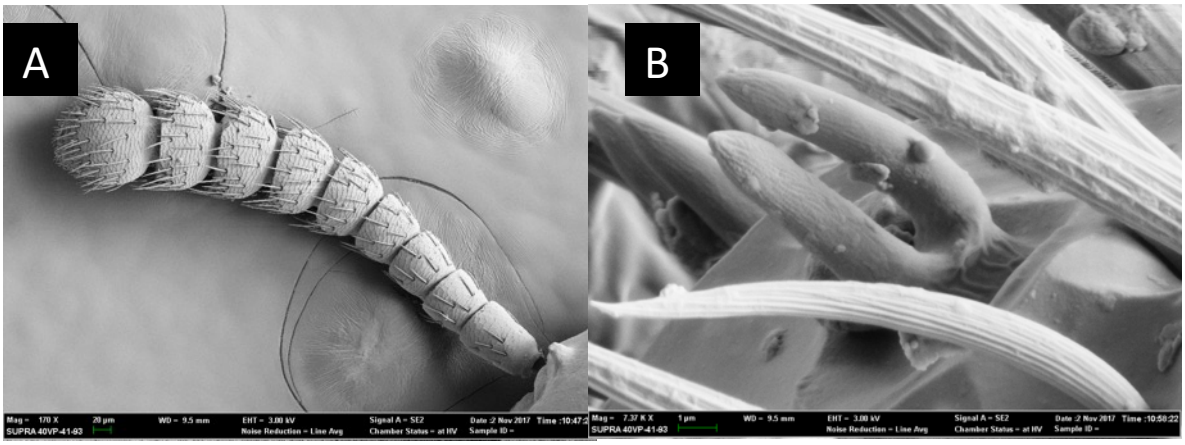

Figure 2.2: Sensoria in the Triboliini. 2.2.A. Antennal sensoria of *Tribolium confusum* at 233X magnification at an accelerating voltage of 3 kV. 2.2.B. Antennal sensoria of *Tribolium confusum* at 5390X magnification at an accelerating voltage of 3 kV.

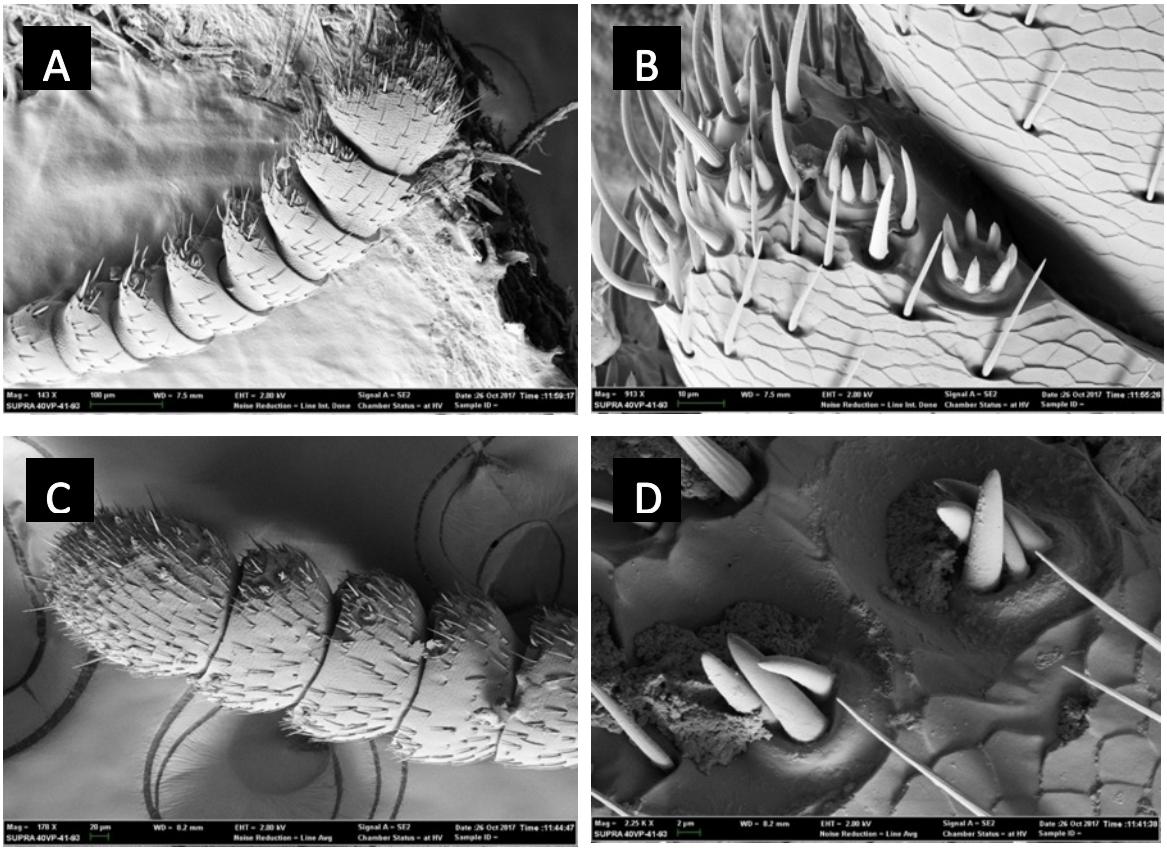

Figure 2.3: Stellate sensoria of Alphatobiini. 2.3.A. Stellate sensoria of *Alphatobius* sp. at 143X magnification with an accelerating voltage of 2 kV. 2.3.B. Stellate sensoria of *Alphatobias* sp. at 913X magnification with an accelerating voltage of 2 kV. 2.3.C. Stellate sensoria of *Metaclisa* sp. at 178X magnification with an accelerating voltage of 2 kV. 2.3.D. Stellate sensoria of *Metaclisa* sp. at 2250X magnification with an accelerating voltage of 2 kV.

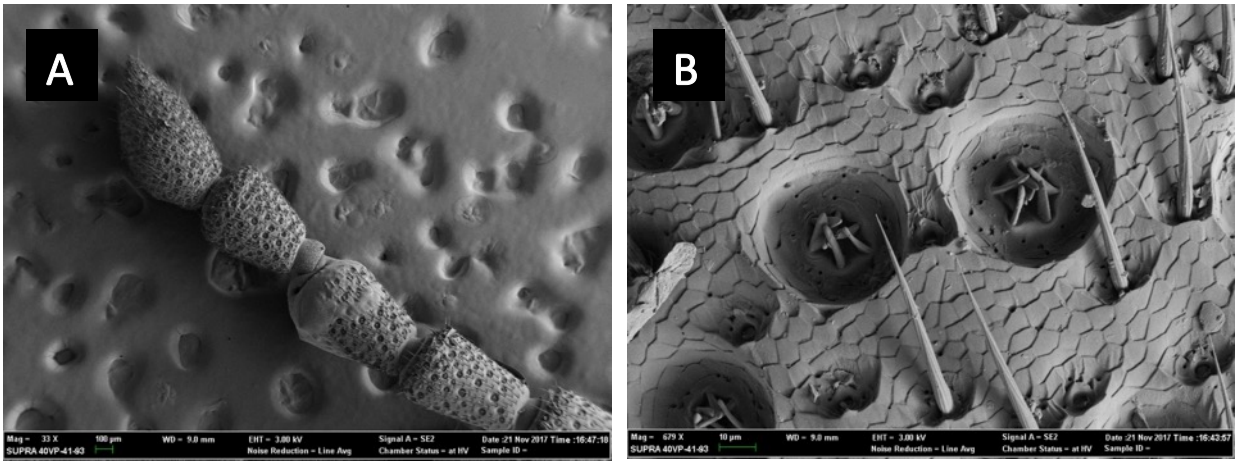

Figure 2.4: Stellate sensoria in the tribe Amarygmini. 2.4.A. Stellate sensoria of *Cymatothes uiformis* at 33X magnification with an accelerating voltage of 3 kV. 2.4.B. Stellate sensoria of *Cymatothes uniformis* at 679X magnification with an accelerating voltage of 3 kV.

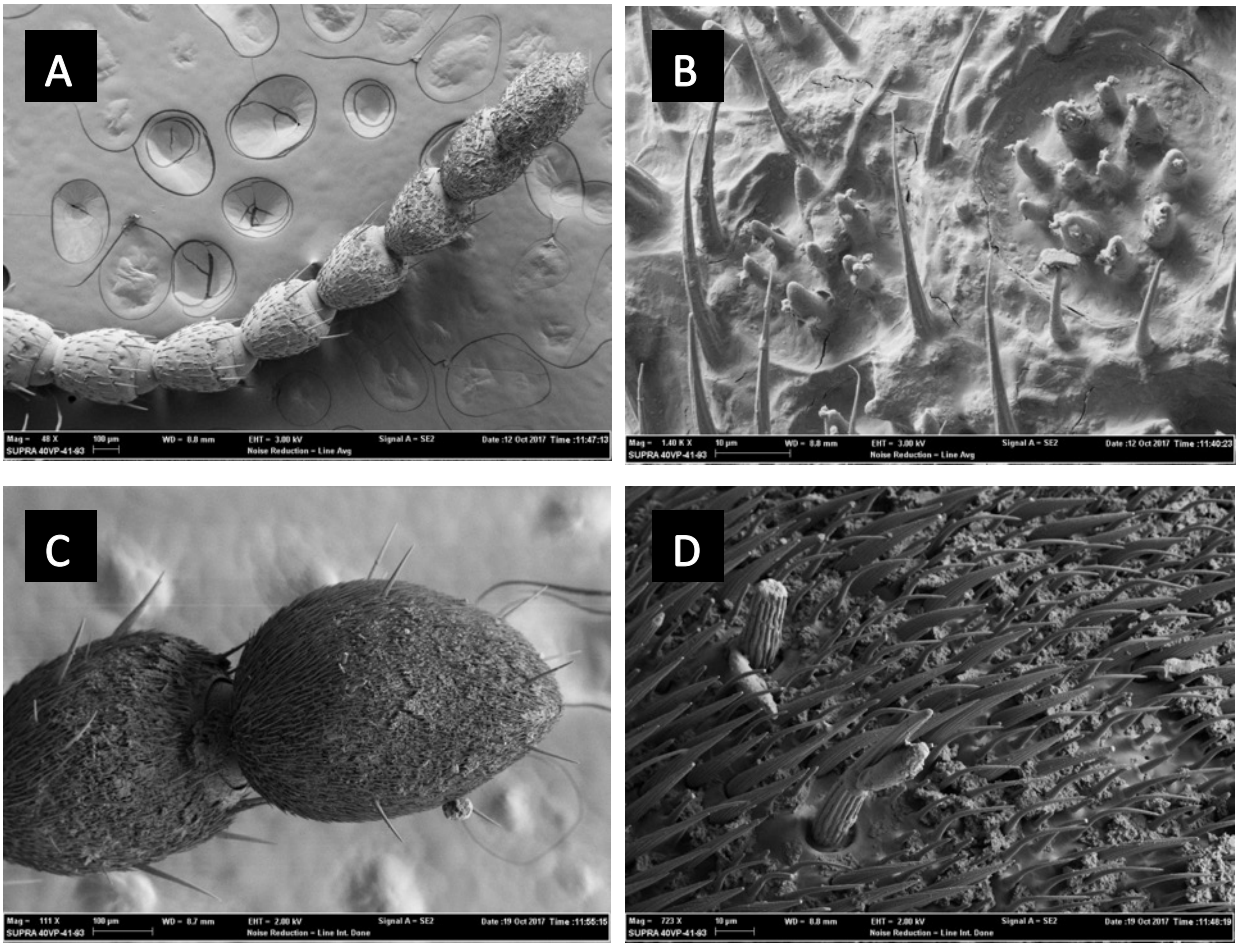

Figure 2.5: Sensoria in the tribe Amphidorini. 2.5.A. Stellate sensoria of *Nycterinus sp.* at 48X magnification with an accelerating voltage of 3 kV. 2.5.B. Stellate sensoria of *Nycterinus sp.* at 1400X magnification with an accelerating voltage of 3 kV. 2.5.C. Sensoria of *Eleodes sp.* at 111X magnification with an accelerating voltage of 2 kV. 2.5.D. Sensoria of *Eleodes sp.* at 723X magnification with an accelerating voltage of 2 kV.

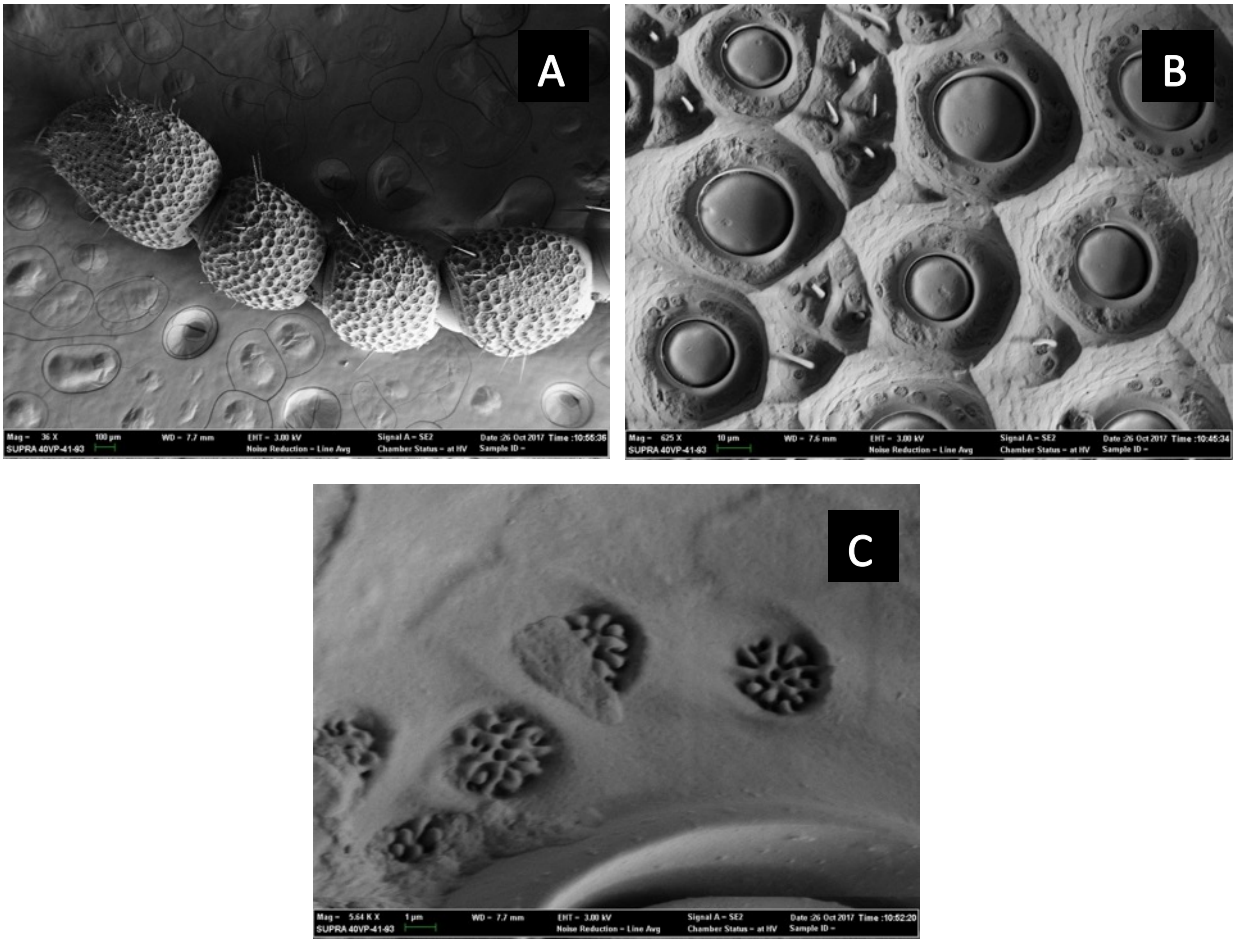

Figure 2.6: Placcoid sensoria in the tribe Centronopini. 2.6.A. Placoid sensoria of *Taurocerus sp.* at 36X magnification with an accelerating voltage of 3 kV. 2.6.B. Sensoria of *Taurocerus sp.* at 625X magnification with an accelerating voltage of 3 kV. 2.6.C. Sensoria of *Taurocerus sp.* at 5640X magnification with an accelerating voltage of 3 kV.

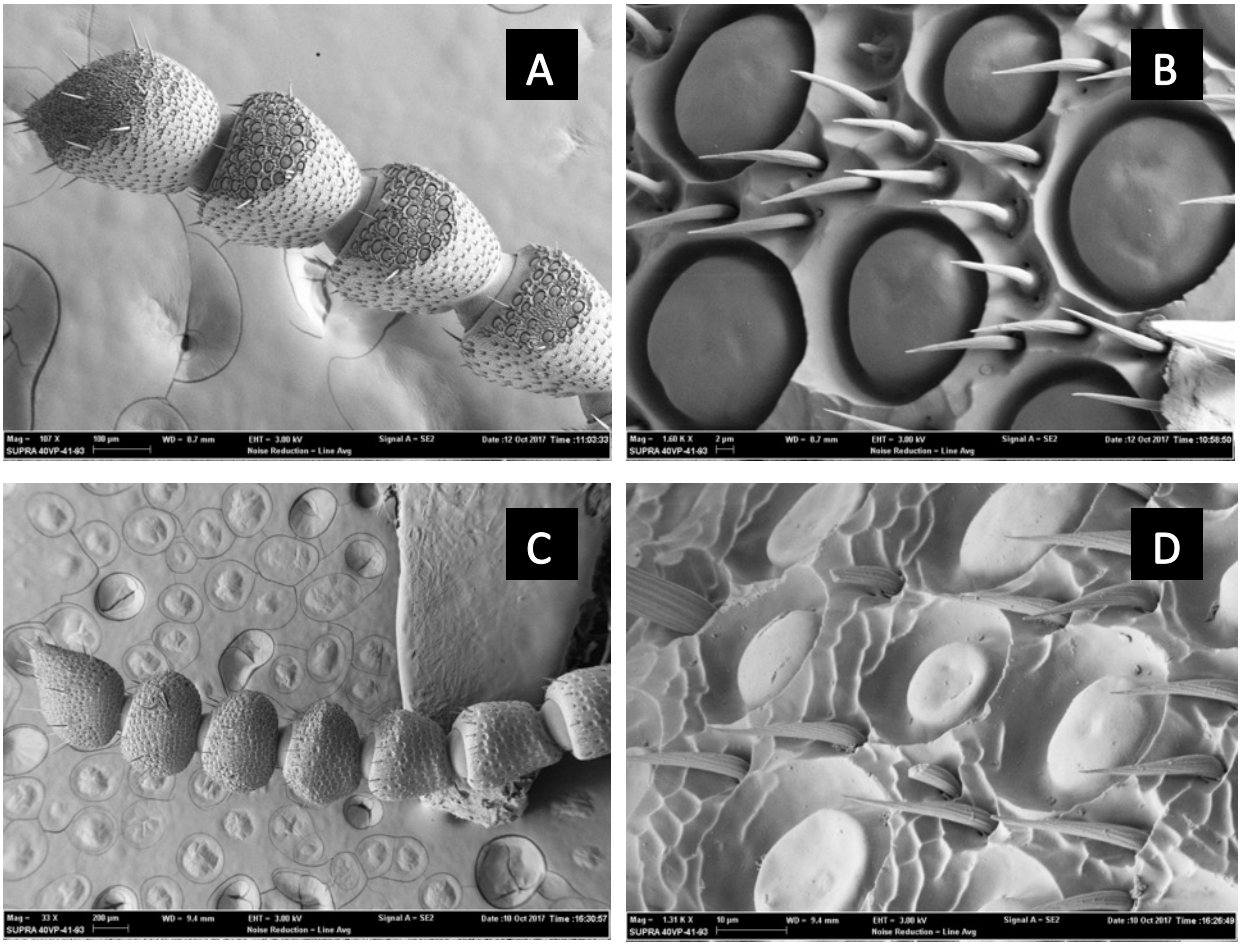

Figure 2.7: Placcoid sensoria in the tribe Cerenopini. 2.7.A. Placcoid sensoria of *Argoporis sp.* at 107X magnification with an accelerating voltage of 3 kV. 2.7.B. Stellate sensoria of *Argoporis sp.* at 1600X magnification with an accelerating voltage of 3 kV. 2.7.C. Sensoria of *Cerenopus concolor* at 33X magnification with an accelerating voltage of 3 kV. 2.7.D. Sensoria of *Cerenopus concolor* at 1310X magnification with an accelerating voltage of 3 kV.

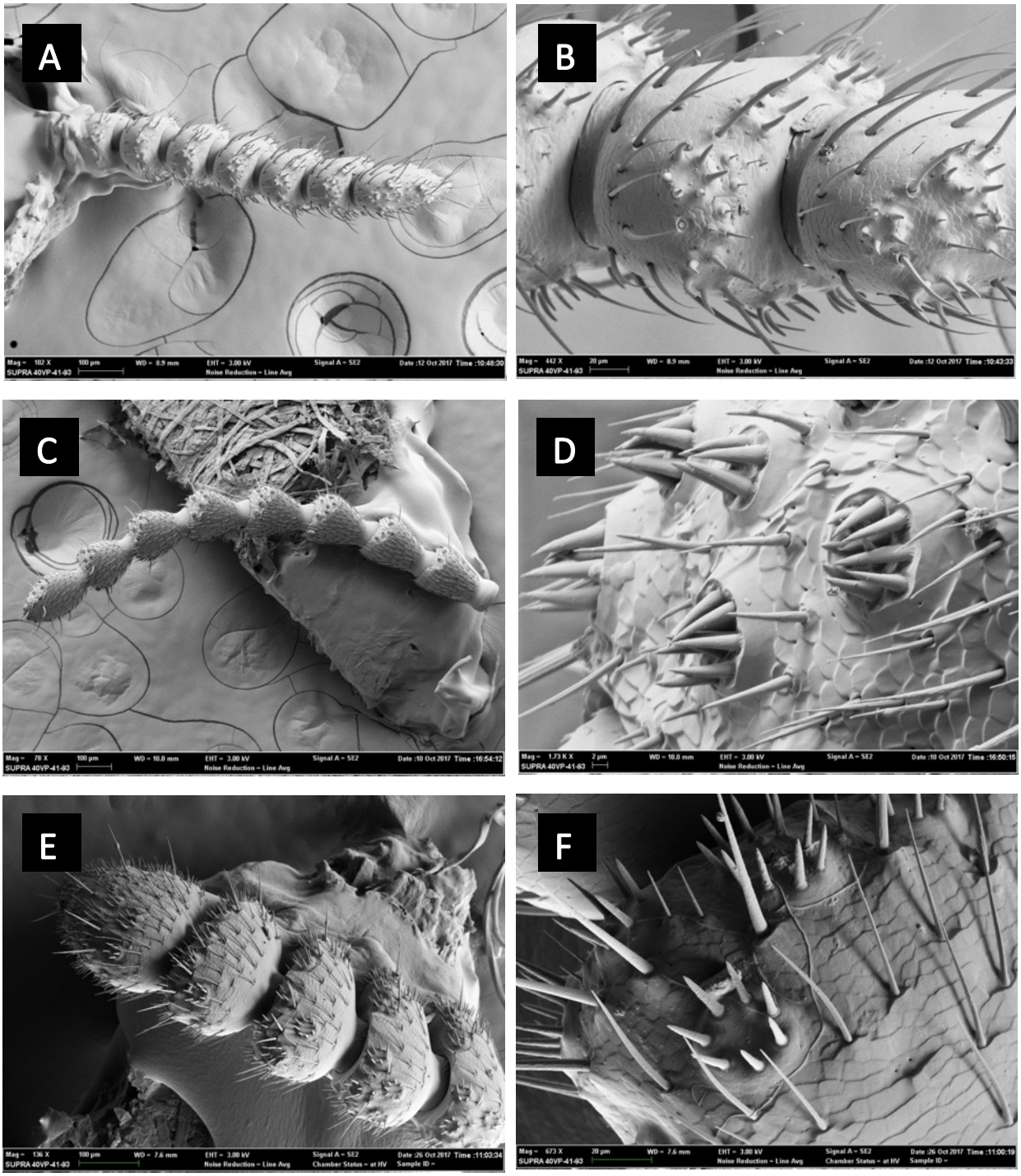

Figure 2.8: Stellate sensoria in the tribe Diaperini. 2.8.A. Stellate sensoria of *Neomida sp.* at 102X magnification with an accelerating voltage of 3 kV. 2.8.B. Stellate sensoria of *Neomida sp.* at 442X magnification with an accelerating voltage of 3 kV. 2.8.C. Sensoria of *Sitophagus holeptoides* at 78X magnification with an accelerating voltage of 3 kV. 2.8.D. Sensoria of *Sitophagus holeptoides* at 1730X magnification with an accelerating voltage of 3 kV. 2.8.E. Stellate sensoria of *Diaperus sp.* at 136X magnification with and accelerating voltage of 3 kV. 2.8.F. Stellate sensoria of *Diaperus sp.* at 673X magnification with an accelerating voltage of 3 kV.

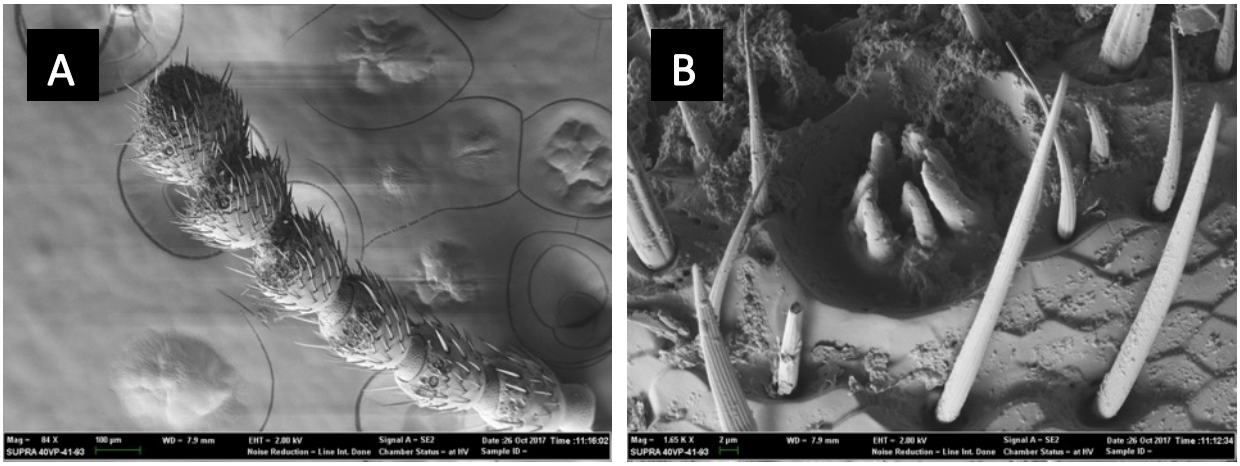

Figure 2.9: Stellate sensoria in the tribe Eulabini. 2.9.A. Stellate sensoria of *Epantius sp.* at 84X magnification with an accelerating voltage of 2 kV. 2.9.B. Stellate sensoria of *Epantius sp.* at 1650X magnification with an accelerating voltage of 2 kV.

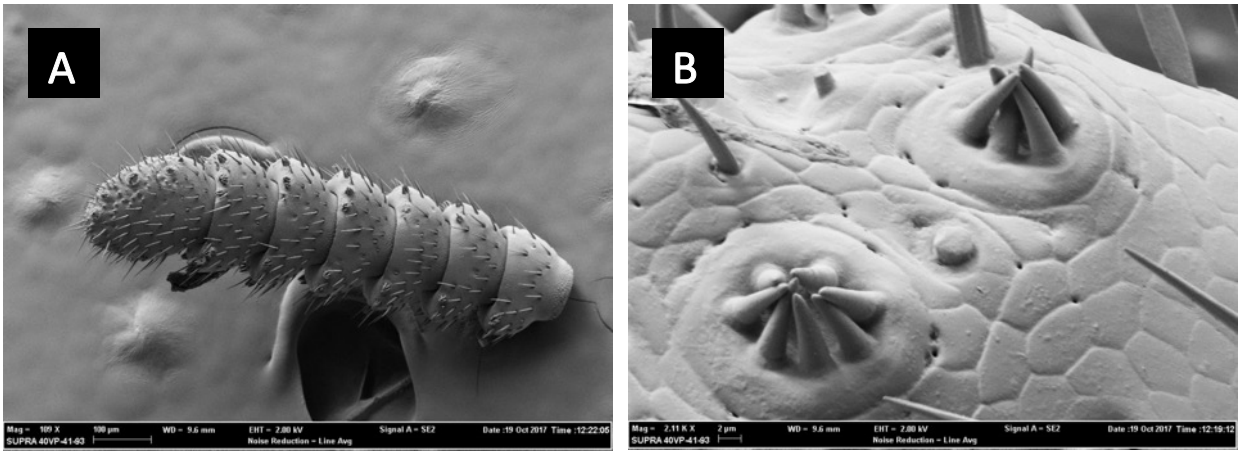

Figure 2.10: Stellate sensoria in the tribe Hypophlaeini. 2.10.A. Stellate sensoria of *Corticeus sp.* at 109X magnification with an accelerating voltage of 2 kV. 2.10.B. Stellate sensoria of *Corticeus sp*. at 2110X magnification with an accelerating voltage of 2 kV.

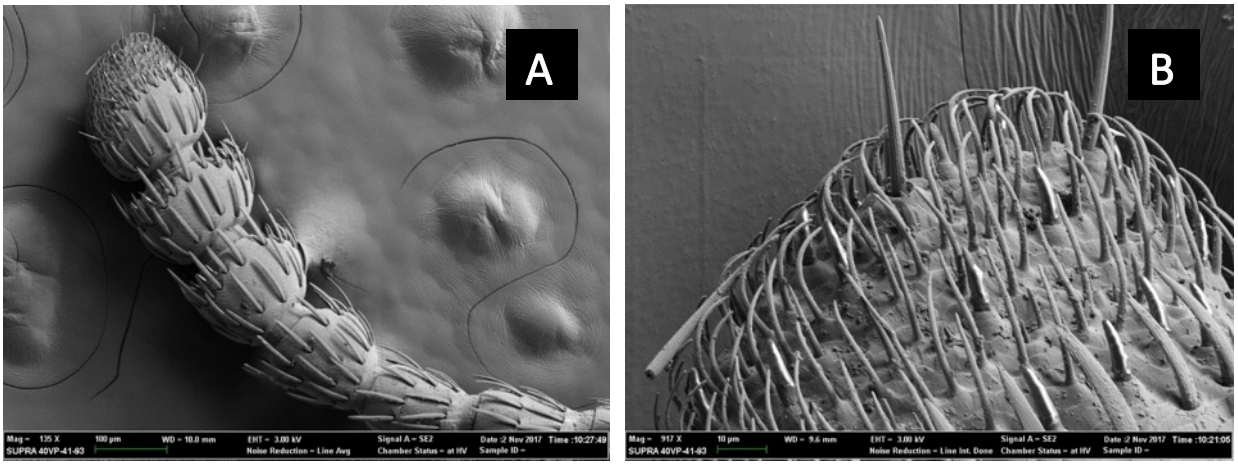

Figure 2.11: Sensoria in the tribe Opatrini. 2.11.A. Stellate sensoria of *Ulus sp.* at 135X magnification with an accelerating voltage of 3 kV. 2.11.B. Stellate sensoria of *Ulus sp.* at 917X magnification with an accelerating voltage of 3 kV.

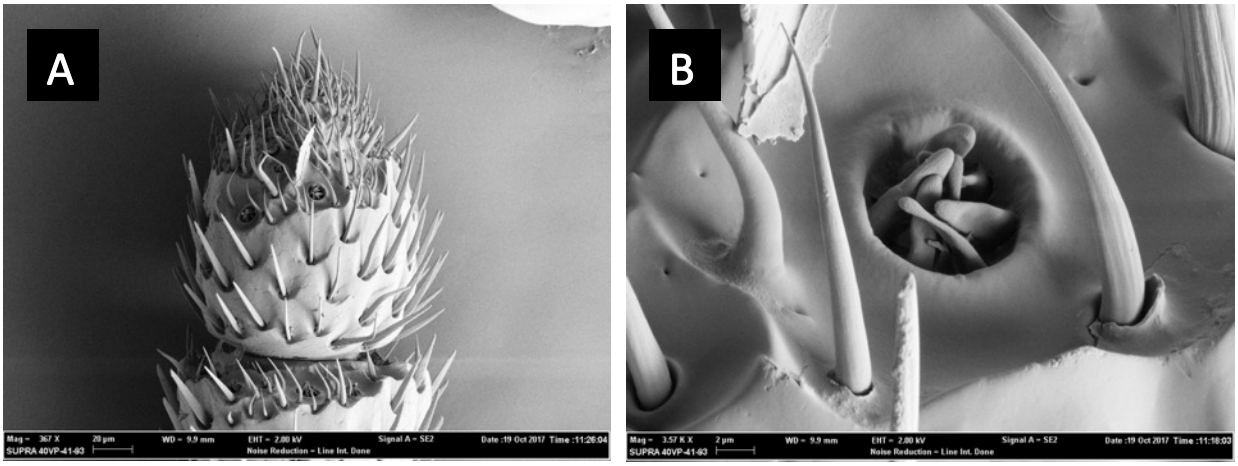

Figure 2.12: Stellate sensoria in the tribe Phalerini. 2.12.A. Stellate sensoria of *Phaleria sp.* at 367X magnification with an accelerating voltage of 2 kV. 2.12.B. Stellate sensoria of *Phaleria sp.* at 3570X magnification with an accelerating voltage of 2 kV.

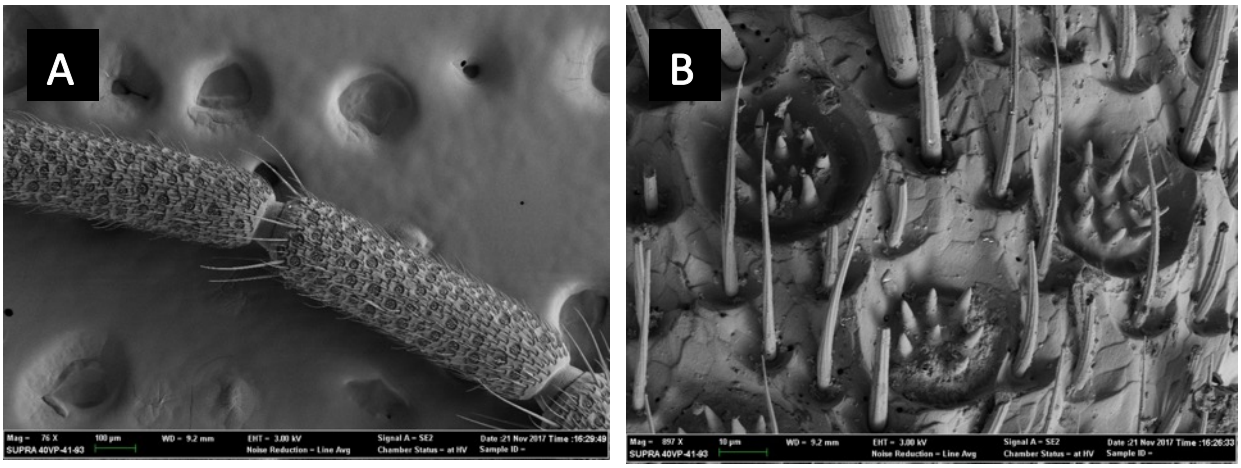

Figure 2.13: Stellate sensoria in the tribe Stenochiini. 2.13.A. Stellate sensoria of *Strongylium sp.* at 76X magnification with an accelerating voltage of 3 kV. 2.13.B. Stellate sensoria of *Strongylium sp*. at 897X magnification with an accelerating voltage of 3 kV.

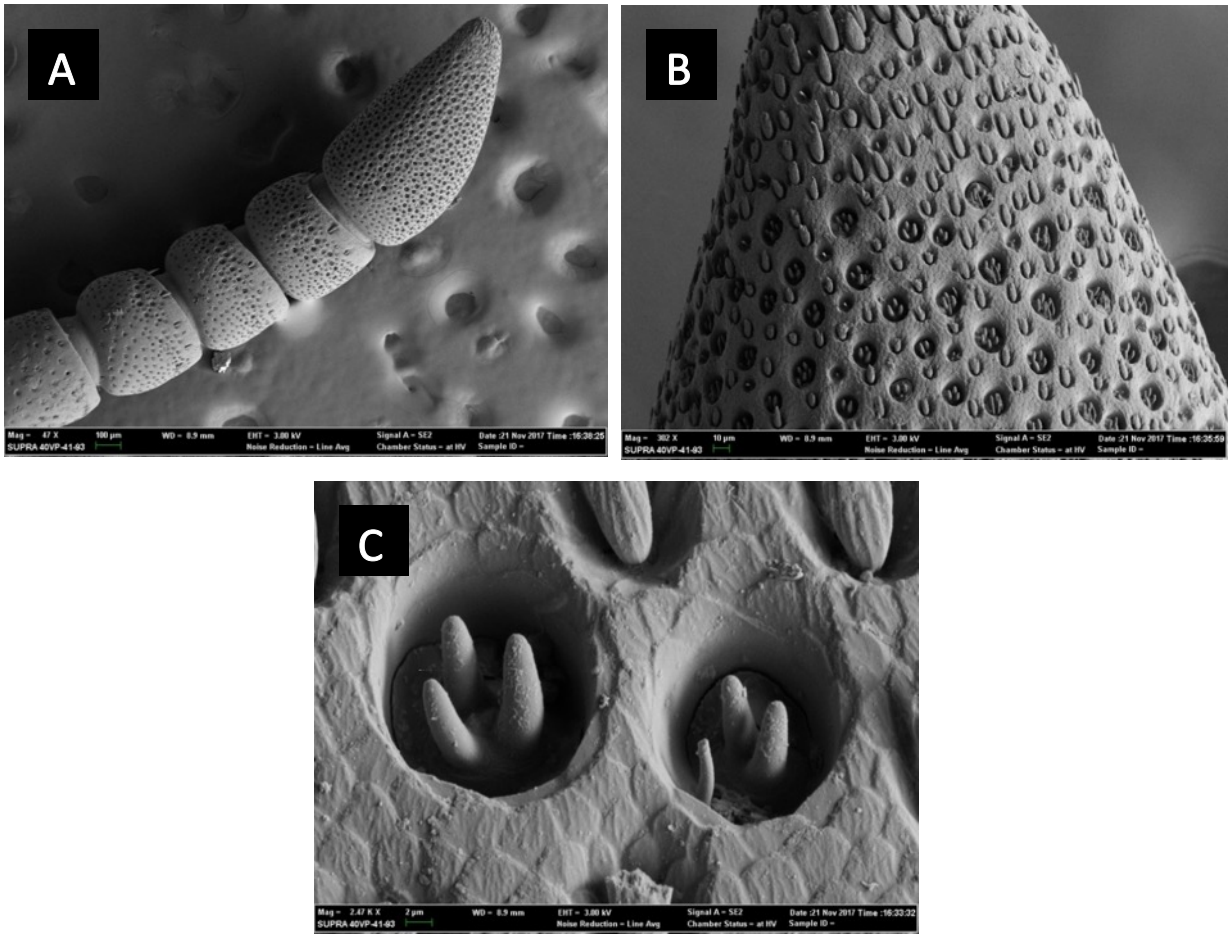

Figure 2.14: Stellate sensoria in the tribe Scaurini. 2.14.A. Stellate sensoria of *Scaurus sp.* at 47X magnification with an accelerating voltage of 3 kV. 2.14.B. Stellate sensoria of *Scaurus sp*. at 302X magnification with an accelerating voltage of 3 kV. 2.14.C. Sensoria of *Scaurus sp*. at 2470X magnification with an accelerating voltage of 3 kV.

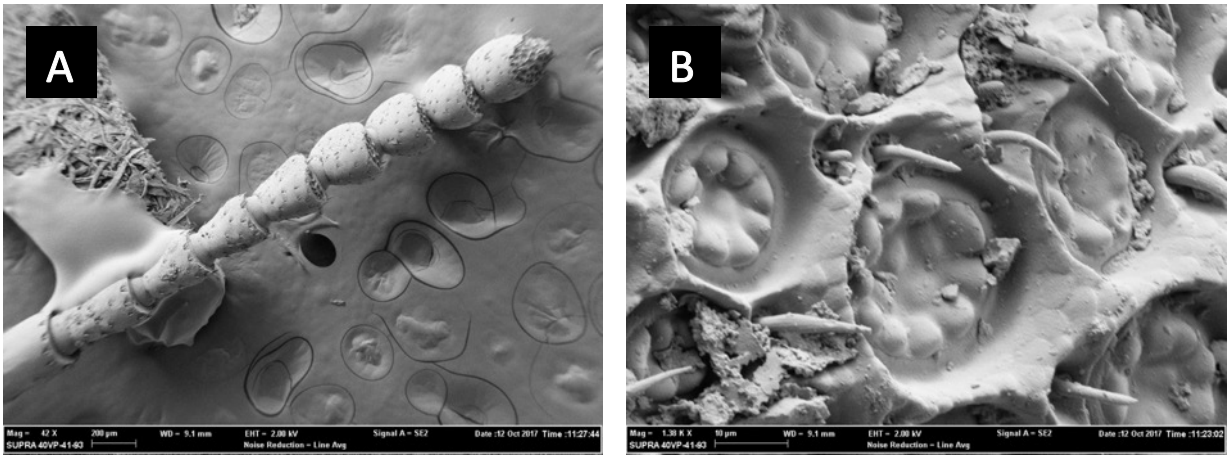

Figure 2.15: Stellate sensoria in the tribe Scotobini. 2.15.A. Stellate sensoria of *Emmallodera obesa punctipennis* at 42X magnification with an accelerating voltage of 2 kV. 2.15.B. Stellate sensoria of *Emmallodera obesa punctipennis* at 1380X magnification with an accelerating voltage of 2 kV.

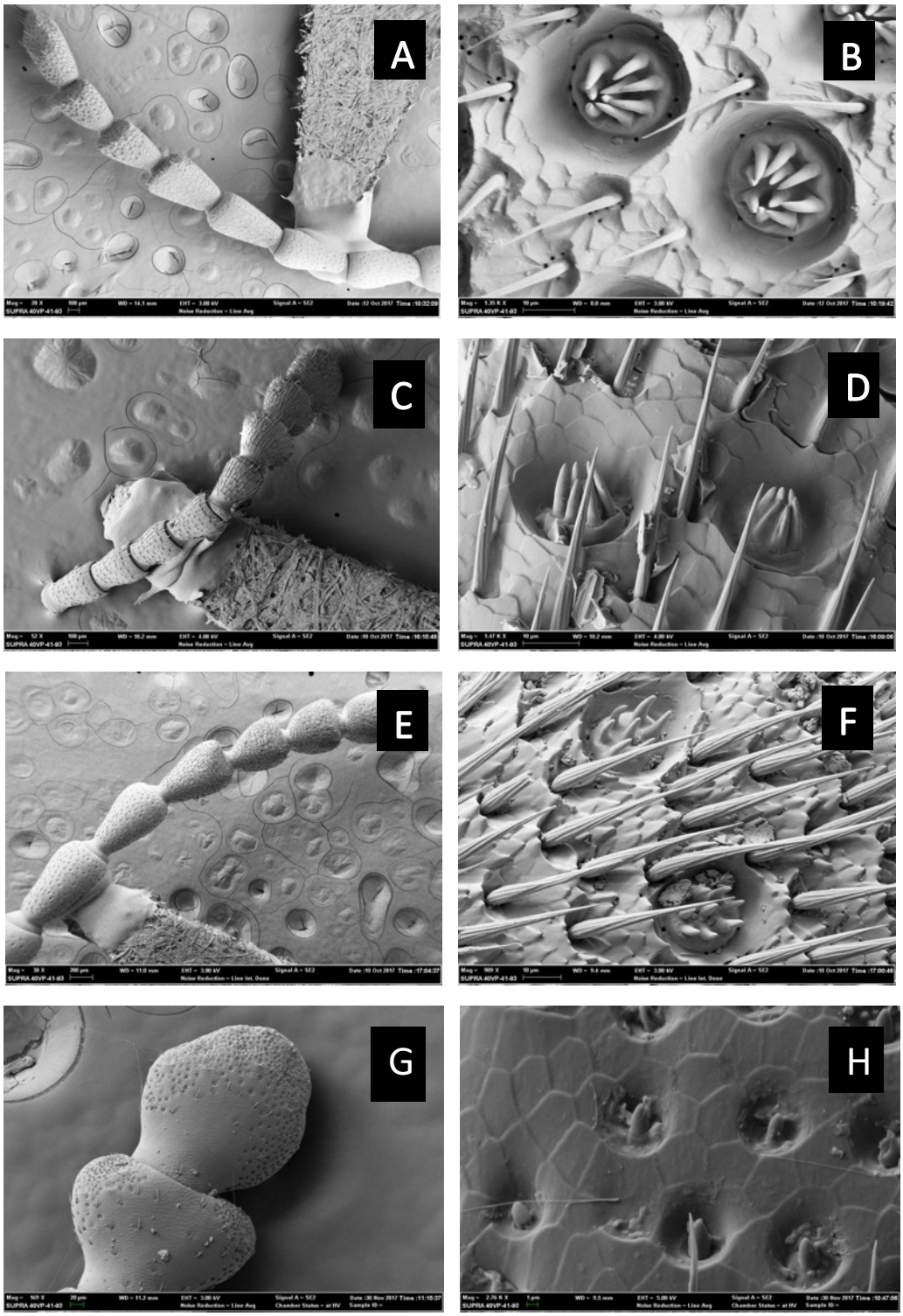

Figure 2.16: Sensoria in the tribe Tenebrionini. 2.16.A. Stellate sensoria of *Zophobas sunitens.* at 28X magnification with an accelerating voltage of 3 kV. 2.16.B. Stellate sensoria of *Zophobas subnitens* at 1350X magnification with an accelerating voltage of 3 kV. 2.16.C. Sensoria of *Neatus tenebrionoides* at 52X magnification with an accelerating voltage of 4 kV. 2.16.D. Sensoria of *Neatus tenebrionoides* at 1470X magnification with an accelerating voltage of 4 kV. 2.16.E. Stellate sensoria of *Rhinandrus helopioides* at 30X magnification with and accelerating voltage of 3 kV. 2.16.F. Stellate sensoria of *Rhinandrus helopioides* at 989X magnification with an accelerating voltage of 3 kV. 2.16.G. Stellate sensoria of *Tenebrio molitor* at 169X magnification with an accelerating voltage of 3 kV. 2.16.H. Antennal sensoria of *Tenebrio molitor* at 2760X magnification at an accelerating voltage of 5 kV.

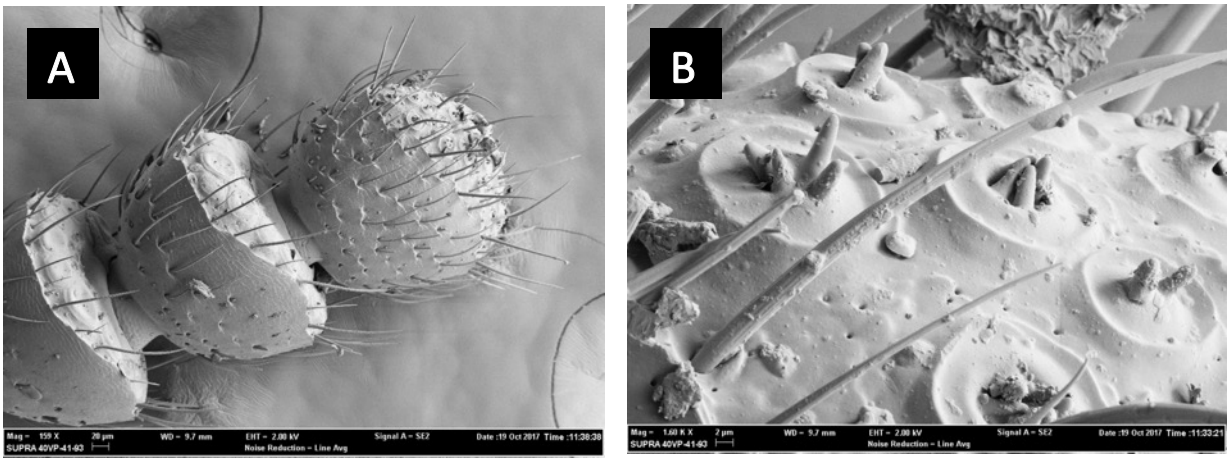

Figure 2.17: Stellate sensoria in the tribe Ulomini. 2.17.A. Stellate sensoria of *Uloma sp.* at 159X magnification with an accelerating voltage of 2 kV. 2.17.B. Stellate sensoria of *Uloma sp.* at 1600X magnification with an accelerating voltage of 2 kV.

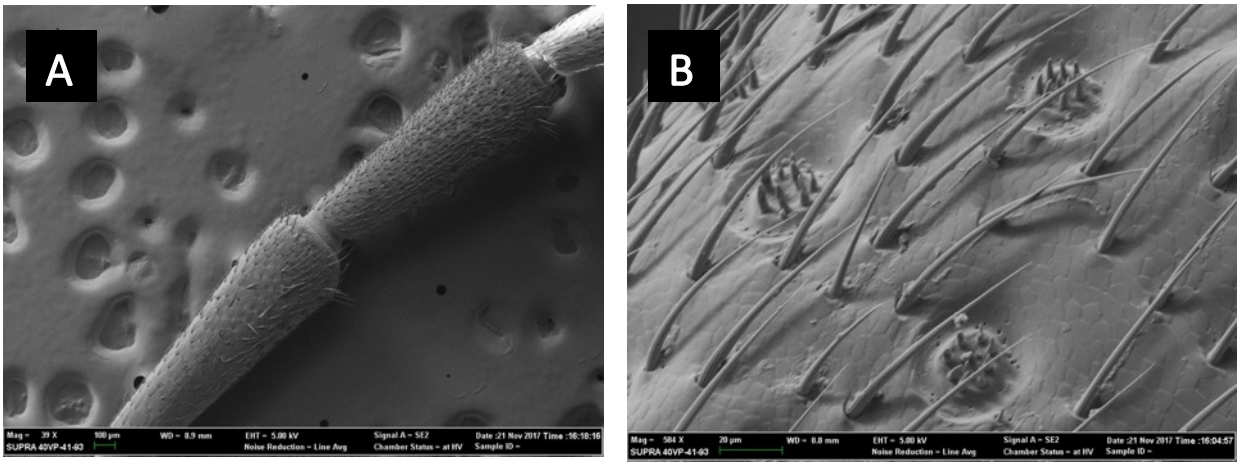

Figure 2.18: Stellate sensoria in the tribe Cnodalonini. 2.18.A. Stellate sensoria of *Hegemona sp.* at 39X magnification with an accelerating voltage of 5 kV. 2.18.B. Stellate sensoria of *Hegemona sp*. at 584X magnification with an accelerating voltage of 5 kV.

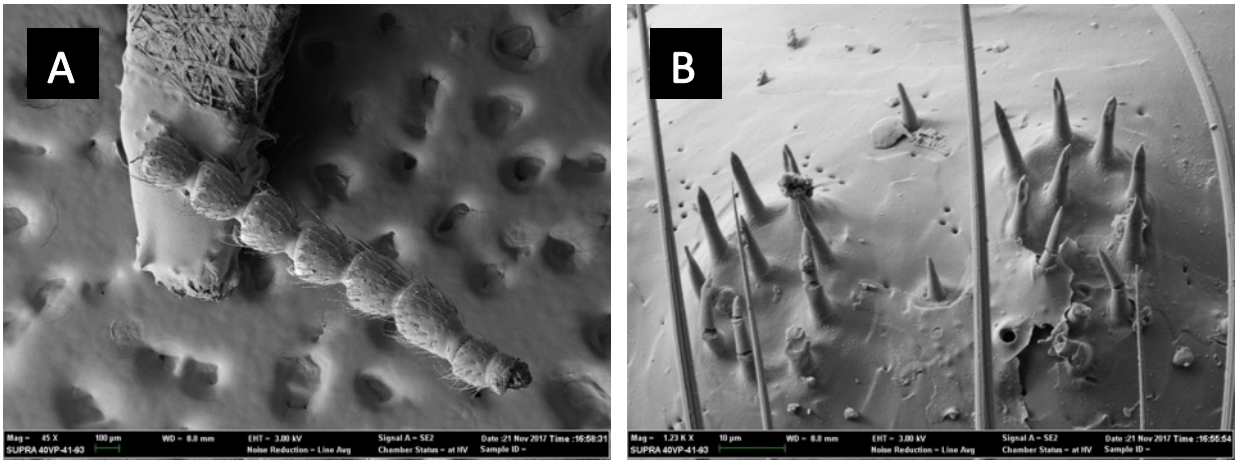

Figure 2.19: Stellate sensoria the tribe Nilionini. 2.19.A. Stellate sensoria of *Nilio sp.* at 45X magnification with an accelerating voltage of 3 kV. 2.19.B. Stellate sensoria of *Nilio sp.* at 1230X magnification with an accelerating voltage of 3 kV.

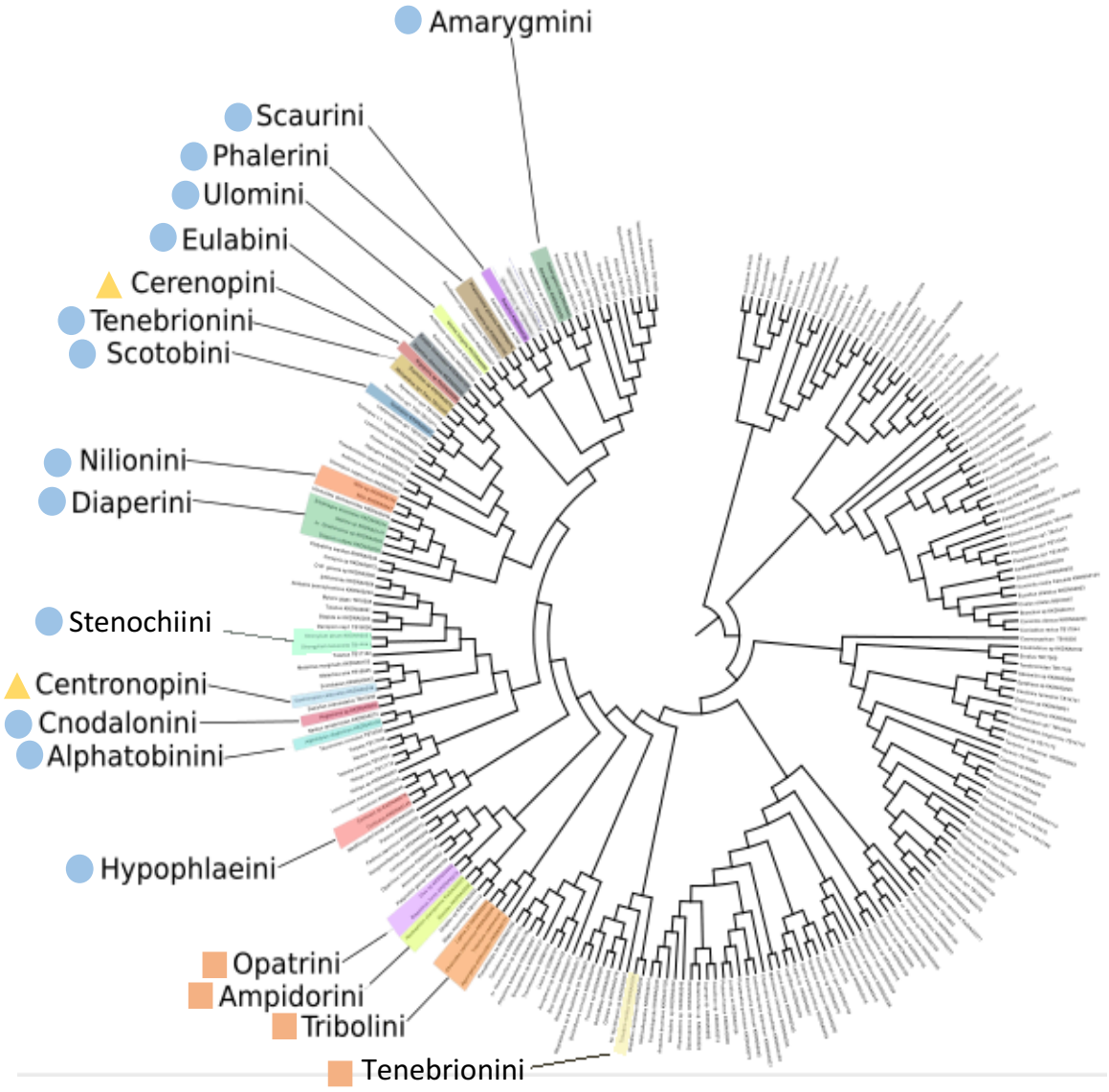

Figure 2.20: Mapped sensoria types on the phylogeny of Tenebrionidae. This figure was modified from Kanda (2017). The taxa examined have been highlighted and labeled. The orange squares refer to species that have simple sensoria. The blue circles refer to the species that have stellate sensoria. The yellow triangles refer to species that have placcoid sensoria. Tenebrionini appears twice as some of the species appear near Cerenopini and Eulabini (Rhinandrus and Zophobas). The Tenebrionini is where Tene*brio molitor* appears.

Tables

Table 2.1: List of Vouchered specimens from SEM examination. Tenebrionid Base identifier is the unique identifier given to the pinned specimen after being databased in mx.speciesfile.org.

Species	Tribe	Collection	Tenebrionid Base Identifier
Alphatobias diaperinus	Alphatobiini	Kojun Kanda	17549
Metaclisa marginata	Alphatobiini	Kojun Kanda	17600
Nycterinus sp.	Amphadorini	Kojun Kanda	15833
Eleodes subnitens	Amphadorini	Kojun Kanda	17546
Taurocerus sp.	Centronopini	Kojun Kanda	17545
Argoporis rufipes	Cerenopini	Kojun Kanda	15830
Neomida sp.	Diaperini	Kojun Kanda	15829
Diaperis bimaculata	Diaperini	Kojun Kanda	17602
Epantius obscurus	Eulabini	Kojun Kanda	17599
Corticeus substriatus	Hypophlaeini	Kojun Kanda	17603
Ulus	Opatrini	Ryan Lumen	16416
Phaleria rotundata	Phaleriini	Kojun Kanda	17604
Strongilium sp.	Stenochiini	Kojun Kanda	18519
Scaurus sp.	Scaurini	Aaron Smith	15111
Uloma longula	Ulomini	Kojun Kanda	17601
Hegemona filabuster	Cnodalonini	Aaron Smith	18511
Nilio sp.	Nilionini	Aaron Smith	18512
Emmallodera obesa punctipennis	Scotobini	Kojun Kanda	15809
Zophobas subnitens	Tenebrionini	Kojun Kanda	15810
Neatus tenebrionoida	Tenebrionini	Kojun Kanda	15831
Rhinandrus helopioides	Tenebrionini	Kojun Kanda	16017
Tenebrio molitor	Triboliini	Aaron Smith	20850
Tribolium castaneum	Triboliini	Aaron Smith	20851
Tribolium confusum	Triboliini	Aaron Smith	20852
Hypogena tricornis	Triboliini	Aaron Smith	20849
Sitophagus holeptoides	Diaperini	Kojun Kanda	15832
Cerenopus concolor	Cerenopini	Kojun Kanda	15484
Cymatothese uniformis	Amarygmini	Aaron Smith	16117