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# PHYLOGENETIC REVISION OF THE NORTH AMERICAN ASIDINI (COLEOPTERA: TENEBRIONIDAE)

By

Aaron Dennis Smith

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

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# ABSTRACT


PHYLOGENETIC REVISION OF THE NORTH AMERICAN ASIDINI (COLEOPTERA: TENEBRIONIDAE)

By

Aaron Dennis Smith

A phylogenetic revision of the North American Asidini based on molecular and morphological data is presented. Evolutionary relationships within and between the North American Asidini (Coleoptera: Tenebrionidae) genera were reconstructed using a combined dataset containing partial sequences of mitochondrial COI (660bp) and nuclear 28s (492bp), and 100 morphological characters for 50 North American asidine species, representing 20 of the 27 previously described genera and one new genus. Species from two additional tenebrionid tribes (Branchini and Coniontini) and the South American asidine genus *Cardiogenius* were chosen as outgroups. Analyses were performed using maximum parsimony and Bayesian inference methods. Clade support was inferred based on the posterior probability distribution of tree topologies, nonparametric bootstrap analysis, and partitioned Bremer support indices. The generic classification of the North American Asidini was revised based on the results.

Twenty previously described genera are placed in synonymy and ten genera are recognized. Seven current genera: *Craniotus* LeConte, *Heterasida* Casey, *Litasida* Casey, *Microschatia* Solier, *Pelecyphorus* Solier, *Philolithus* Lacordaire, *Stenomorpha* Solier, are redescribed and three **new genera**: *Micrasida*, *Ardamimicus*, and *Ferveoventer* are described, including three **new species**: *Micrasida obrienorum*, *Ardamimicus cognatoi,* and *Ferveoventer browni*.

A taxonomic revision of the North American genus *Pelecyphorus* Solier is presented. Eight subgenera are erected and described, seven based on previously described Asidini genera: *Pelecyphorus* Solier *sensu stricto*, *Astrotus* LeConte, *Stenosides* Solier, *Ucalegon* Champion, *Zaleucus* Champion, *Plesiasida* Smith (=Parasida Casey),and *Sicharbas* Champion and one **new subgenus**: *Variodorsus*.

Forty species of *Pelecyphorus* are recognized as valid, including seven **new species** described herein: *P. cavatus*, *P. cifuentesi*, *P. crypticus*, *P. deaztlani*, *P. doyeni*, *P. oaxacensis*, and *P. triplehorni*. All valid species are described or redescribed, along with diagnoses, distributions, and images of each. An illustrated key to the subgenera and species is also provided.

The Asidini, like all members of the subfamily Pimeliinae, lack defensive glands. Instead, several morphological and behavioral traits are found within the tribe which may help limit predation. These include the contrasting defensive strategies of crypsis, either through background matching or pattern disruption, and Batesian mimicry of the chemically defended tenebrionid genus *Eleodes*. A phylogenetic analysis of the North American asidines is presented and the evolution of defensive strategies exhibited within the group is examined.

This work is dedicated to Tonantzin DeAztlan
for her understanding and constant support.

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# CHAPTER ONE

## Phylogenetic revision of the North American Asidini (Coleoptera: Tenebrionidae)

## ABSTRACT

The asidine darkling beetles (Coleoptera: Tenebrionidae: Asidini) are a diverse tribe of flightless tenebrionids found in many arid and sub-arid habitats around the world. The nearly 300 currently described North American species are contained in 27 genera, all of which are restricted to the western half of the continent.

Evolutionary relationships within and between the North American Asidini (Coleoptera: Tenebrionidae) genera were reconstructed using a combined dataset containing partial sequences of mitochondrial COI (660bp) and nuclear 28S (492bp), and 100 morphological characters for 50 North American asidine species, representing 20 of the 27 currently described genera and one new genus. Species from two additional tenebrionid tribes (Branchini and Coniontini) and the South American asidine genus *Cardiogenius* were chosen as outgroups. Analyses were performed using maximum parsimony and Bayesian inference methods. Clade support was inferred based on the posterior probability distribution of tree topologies, nonparametric bootstrap analysis, and partitioned Bremer support indices. The generic classification of the North American Asidini was revised based on the results.

Ten genera are recognized. Seven current genera: *Craniotus* LeConte, *Heterasida* Casey, *Litasida* Casey, *Microschatia* Solier, *Pelecyphorus* Solier, *Philolithus* Lacordaire, *Stenomorpha* Solier, are redescribed and three **new genera**: *Micrasida*, *Ardamimicus*, and *Ferveoventer* are described, including three **new species**: *Micrasida obrienorum*, *Ardamimicus cognatoi,* and *Ferveoventer browni*.

20 genera are placed in synonymy; **new synonyms**: *Asidina* Casey (=*Stenomorpha* Solier), *Asidopsis* Casey (=*Stenomorpha* Solier), *Bothrasida* Casey (=*Stenomorpha* Solier), *Megasida* Casey (= *Stenomorpha* Solier), *Notiasida* Casey (=*Stenomorpha* Solier), *Platasida* Casey (=*Stenomorpha* Solier), *Pycnomorpha* Motschulsky (=*Stenomorpha* Solier), *Stethasida* Casey (=*Stenomorpha* Solier), *Trichiasida* Casey (=*Stenomorpha* Solier), *Glyptasida* Casey (=*Philolithus* Lacordaire), *Gonasida* Casey (= *Philolithus* Lacordaire), *Herthasida* Wilke (=*Philolithus* Lacordaire), *Tisamenes* Champion (=*Philolithus* Lacordaire), *Astrotus* LeConte (=*Pelecyphorus* Solier), *Parasida* Casey (=*Pelecyphorus* Solier), *Poliorcetes* Champion (=*Pelecyphorus* Solier), *Sicharbas* Champion (=*Pelecyphorus* Solier), *Stenosides* Solier (=*Pelecyphorus* Solier), *Ucalegon* Champion (=*Pelecyphorus* Solier), *Zaleucus* Champion (=*Pelecyphorus* Solier).

# INTRODUCTION

Darkling beetles (Coleoptera: Tenebrionidae), with over 19,000 described species, represent one of the greatest known radiations of biodiversity in the world. They are present in nearly every terrestrial ecosystem due to the amazing array of forms, feeding habits, and life histories exhibited within the family. Nowhere are they more conspicuous than in the world's deserts. Many tenebrionids have adapted to life in arid environments through changes in behavior (nocturnal activity), morphology (flightlessness to prevent water loss), or life history (subterranean larvae). One of the most successful, in terms of biodiversity and distribution, but least studied groups of tenebrionids is the tribe Asidini. The asidine darkling beetles are a large tribe of flightless midsized (4.5mm-35mm) tenebrionids found in many arid and semi-arid regions around the world. The North American component of the tribe contains nearly three hundred species in 27 genera and makes up approximately 20% of the total North American tenebrionid fauna (Aalbu *et al.* 2002). Despite their significant contribution to the biodiversity of Mexico and the western United States, no revisionary work has adequately dealt with the entire North American asidine fauna and no attempt has been made to examine their generic classification in a phylogenetic context. Consequently, the validity of most current genera and species has not been tested since their initial descriptions.

## *Taxonomic History*

The creation and application of generic names within the North American Asidini has a long and varied history. Asidini was originally erected by Fleming (1821) to

contain the Mediterranean genus *Asida* Latreille. Thomas Say (1824) described the first three North American asidine species (*Stenomorpha opaca*, *Stenomorpha polita*, and *Stenosides anastomosis*), which he collected from "under dried bison dung in the extensive region bordering the Rocky Mountains". Say placed all three species in *Asida*. Solier (1836) erected the first four North American genera (*Microschatia*, *Pelecyphorus*, *Stenomorpha*, and *Stenosides*) to contain eight Mexican species and one African species (*Afrasida capensis* (Solier)) that he considered too divergent to place in *Asida*.

In 1851 J. L. LeConte provided a replacement name for *Stenomorpha* (*Euschides* LeConte, 1851) due to the name's similarity to *Stenomorphus* Dejean, 1831. He also removed the genus *Asida* from North America by transferring *A. polita* and *A. opaca* into *Euschides* and transferring *A. anastomosis* into *Pelecyphorus* before moving it into *Microschatia* two years later (LeConte 1853). LeConte later described two new monotypic genera, *Astrotus* (LeConte 1858a) for *Microschatia contorta* LeConte and *Pactostoma* (LeConte, 1858a) for *Microschatia anastomosis* (Say), and published Lacordiare's new genus *Philolithus* (Leconte 1858b) while giving Lacordaire full credit for the genus. The next year Lacordaire (1859) provided a more complete description of *Philolithus* and the replacement name *Ologlyptus* for *Stenosides* due to that name's similarity to *Stenosis* Herbst, 1799. Lacordaire included *Asida anastomosis* in his description of *Ologlyptus*, which prompted LeConte to sink *Pactostoma* in favor of *Ologlyptus* a few years later (LeConte, 1866). The last North American asidine genus to be described in the 1800s was *Pycnomorpha* Motschulsky (1870).

Between 1851 and 1870 the species compositions of many of the genera were in flux as species were shifted between them. Horn (1870) was the first author to

consolidate the isolated species descriptions for the asidines north of Mexico into a single paper including keys for the genera and the tribe. He concluded that no characters reliably separated most of the North American genera from *Asida* and, instead of "erecting these into genera as numerous as the species", he sank all but *Astrotus*, *Ologlyptus*, and *Microschatia* back into *Asida*.

The Mexican asidine fauna was treated in the massive Biologia Centrali-Americana series by Champion (1884, 1893). Champion (1884) followed Horn by placing most of the asidines in *Asida*, but erected the monotypic genera *Poliorcetes*, *Sicharbas*, *Tisamenes*, *Ucalegon*, and *Zamolxis*. However, in a supplement Champion (1893) suppressed all of the genera that he had described except *Sicharbas*, while suggesting that if they were maintained a number of other species would also have to be placed in new genera. He also provided the replacement name *Zaleucus* Champion for *Zamolxis* (preoccupied), to be used in the event that his genera were maintained by later authors.

The next revisionary work to examine most of the North American asidine genera was Casey (1912). Casey described approximately 60% of the current valid species and subspecies in his monograph and established much of the modern taxonomy within the group. To contain the 212 taxa he treated, Casey erected 14 new genera (*Asidina*, *Asidopsis*, *Bothrasida*, *Glyptasida*, *Gonasida*, *Heterasida*, *Litasida*, *Megasida*, *Pycnonotida*, *Notiasida*, *Parasida*, *Platasida*, *Stethasida*, and *Trichiasida*) and resurrected five genera (*Euschides*, *Pactostoma*, *Pelecyphorus*, *Stenomorpha*, and *Stenosides*). Casey never saw many of the Mexican species, but he did move most of them back into resurrected genera or into his new genera based on their descriptions or

images in the Biologia Centrali-Americana. He also expressed his opinion that most of Champion's genera would need to be resurrected and that at least 15 new genera would eventually need to be described "for known aberrant Mexican types".

Ten years later, the German coleopterist Siegfried Wilke (1922) added to Casey's concept of the North American asidine genera by placing the remaining Mexican species and 14 new species into Casey's classification. Wilke also resurrected Champion's suppressed genera (*Poliorcetes*, *Tisamenes*, *Ucalegon*, and *Zaleucus*) and described one new genus (*Herthasida*) and one subgenus (*Acroschatia*). Wilke disagreed with Casey in two instances by synonymizing *Pactostoma* under *Stenosides* and *Euschides* under *Stenomorpha*.

Blaisdell (1923) reviewed the Asidini of Baja California and applied Casey's generic names as subgenera of *Asida* without explanation. However, 20 years later (Blaisdell 1943), he applied the generic names used in Casey (1912) to the same Baja Californian fauna as genera, again without explanation. The one exception was *Stethasida catalinae* Blaisdell, 1923, where he continued to use *Stethasida* as a subgenus of *Asida*. Whether or not the use of Casey and Wilke's generic names in the world catalog of Tenebrionidae (Gebien 1938-1944) played a part in Blaisdell's decision is unknown.

Several changes were also made to the North American asidine genera in the latter half of the 20th century. *Pycnonotida* and *Acroschatia* were synonymized under *Microschatia* (Brown and Doyen 1991), *Philolithus* was resurrected (Brown 1971b), *Pycnomorpha* was resurrected (Aalbu *et al.* 1995), and the North American tribe Craniotini was synonymized under Asidini (Aalbu *et al.* 2002), thus adding the genus

*Craniotus* LeConte. Brown (1971b) also provided the first key to the genera since Casey (1912), which pointed out some of the taxonomic problems underlying the current generic classification as no adequate characters were found to group all of the species in many of the genera.

*Systematics*

The tribe Asidini, in the tenebrionid subfamily Pimeliinae, currently contains approximately 1000 described species in 46 genera. The tribe is diagnosed from other pimeliines by the unique combination of the following characters (Aalbu *et al.* 2002, Doyen 1993): apterous; eyes ovate to elongate, slightly reniform or not; head not significantly constricted behind eyes; antennae eleven segmented; antennal segment 10 large, subquadrate or conical, with two simple tomentose apico-lateral sensilla, sensilla sometimes coalesced into a single apical band; Antennal segment 11 smaller than 10th, with a single simple tomentose apical sensillum, segment slightly or deeply amplected into antennal segment 11; submentum not concealed; prementum narrower than mentum, mostly membranous with the ligula scleritized, one-half or less mentum length, exposed or concealed beneath apical margin of mentum; mentum large, cordate to trapazoidal or hexagonal, width greater then length, filling half or more of buccal cavity; tentoral bridge absent; apical maxillary palp large, securiform to scalene; labrum exposed, wider than long; right mandible without dorsolateral tooth; two apical spurs on each tibia; mesocoxal cavities with trocantin visible or not; ovipositor nearly as long as abdomen, coxite lobes fused and heavily sclerotized.

Asidini is potentially a highly derived tribe within the Pimeliinae (Doyen 1993), a subfamily characterized by having the membranes between abdominal ventrites three to five concealed, the aedeagus inverted, and by their lack of defensive glands. All the major arid regions of the world have their own diverse and distinct pimeliine fauna, with the exception of Australia which has a relatively limited pimeliine fauna (Matthews 2000). In the only pimeliine phylogenetic analysis to date, Doyen (1993) recovered an asidine clade (Asidini, Branchini, Coniontini, Physogasterini, Praocini, Nyctelini, and *Elenophorus*) that represents one of the largest radiations of tenebrionids. However, the clade is entirely restricted to the New World with the exception of the Asidini and the genus *Elenophorus*. This would seem to indicate that the Asidini are basal within their clade, however the tribe was consistently recovered as highly derived. Internally, the tribe contained four clades with each corresponding to a geographic region (Mediterranean, southern Africa, southern South America, and North America).

In this study I present the first phylogenetic analyses for the North American Asidini, examine evolutionary relationships within and between the genera, and revise the generic classification based on partial sequences of two genes, COI and 28S, and adult morphology from representative species for 20 of the 27 currently described genera. Revisionary changes were guided by the resulting inferences and genera are maintained, synonymized, or erected accordingly.

## MATERIALS AND METHODS

Approximately 6,850 specimens were examined for this study, including the type material for over 90% of the previously described species. Specimens were graciously loaned by the following collectors and institutions; collection abbreviations follow Evenhuis (2007):

**AMNH** American Museum of Natural History, New York, NY, USA. (Lee Herman)

**BFLC** Brackenridge Field Laboratory Insect Collection, University of Texas, Austin, TX, USA. (John Abbott)

**BMNH** The Natural History Museum, London, United Kingdom. (Max Barclay)

**BYUC** Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT, USA. (Shawn Clark)

**CASC** California Academy of Sciences, San Francisco, CA, USA. (Dave Kavanaugh)

**CIDA** Orma J. Smith Museum of Natural History, College of Idaho, Caldwell, ID, USA. (William Clark)

**CNIN** Colección Nacional de Insectos, Mexico City, Mexico. (Harry Brailovsky)

**CSCA** California State Collection of Arthropods, Sacramento, CA, USA. (Charles Bellamy)

**EGRC** Edward G. Riley Collection, College Station, TX, USA.

**EMEC** Essig Museum of Entomology, University of California, Berkeley,

CA, USA. (Cheryl Barr)

**FMNH** Field Museum of Natural History, Chicago, IL, USA. (James Boone)

**KSUC** Kansas State University Collection (Gregory Zolnerowich)

**KWBC** Kirby W. Brown Collection, Paradise, CA, USA.

**MCZ** Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. (Philip Perkins)

**MNHN** Muséum National d'Histoire Naturelle, Paris, France. (Olivier Montreuil)

**MRSC** Marion R. Smith Collection, Austin, TX, USA.

**MSUC** Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, MI, USA. (Gary Parsons)

**NMNH** National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. (Warren Steiner and David Furth)

**OSUC** C. A. Triplehorn Insect Collection, Ohio State University, Columbus, OH, USA. (Charles Triplehorn and Norm Johnson)

**TAMU** Texas A&M University Insect Collection, College Station, TX, USA. (Edward Riley)

**TTUZ** Invertebrate Zoology Collection, Texas Tech University, Lubbock, TX, USA. (James Cokendolpher)

**UCDC** Bohart Museum of Entomology, University of California, Davis, CA, USA. (Fran Keller and Steve Heydon)

**UMMZ** Museum of Zoology, University of Michigan, Ann Arbor, MI, USA. (Barry O'Connor)

**WFBM** W. F. Barr Entomological Collection, University of Idaho, Moscow, ID, USA. (James Johnson)

**ZMHB** Museum für Naturkunde der Humboldt-Universität, Berlin, Germany. (Bernd Jaeger)

## Phylogenetic Analysis

### *Taxon Sampling*

Most asidine species are rarely encountered and many species are known from only one or a handful of collecting events. Specimens sequenced for this study were either collected by the author directly into 95% ethanol or donated by colleagues. Additional specimens of each species were also scored for morphology and used to examine potential intraspecific variability within the dataset. Fifty North American asidine species were included in the analyses (Table 1.1) representing 20 current asidine genera and two potentially undescribed genera. Outgroup taxa were selected from the South American Asidini (*Cardigenius laticollis* Solier) and the closely related tribes Coniontini (*Eusattus reticulatus* (Say)) and Branchini (*Branchus* n. sp.).

### *DNA Sequencing and Alignment*

Tissue was removed from either the head or a leg of each specimen and the DNA was extracted using DNeasy™ Tissue Kits (Qiagen). After extraction, DNA samples were stored at -20°C and specimens were either pinned or left in 95% ethanol at -80°C. All specimens were vouchered in the A.J. Cook Arthropod Research Collection at Michigan State University.

The purified DNA was used to amplify portions of the mitochondrial cytochrome c oxidase I (COI) and nuclear ribosomal 28S (D2 region) genes. PCR amplifications for COI used the published primers (Hebert *et al.* 2003) LCO1490 (5'GGTCAACAA ATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCA AAAAATCA-3') and contained 15.75µl $ddH_2O$, 2.5 µl 5X *Taq*DNA polymerase buffer (Promega, Madison, WI), 2.0 µl 25 mM Promega $MgCl_2$, 0.5 µl 40 mM dNTPs (deoxynucleotide triphosphates), 0.25 µl Promega *Taq* DNA polymerase, 1 µl of 10 ρM/µl LCO1490 primer, 1 µl of 10 ρM/µl HCO2198 primer, and 2 µl of DNA template. PCR reactions for 28S used the published primers (Dole *et al.* 2010) 3665 (5'-AGAGAGAGTTCAAGAGTACGTG-3') and 4068 (5'-TTGGTCCGTGTTTCAAGACGGG -3'). PCR reactions contained 15.75µl $ddH_2O$, 2.5 µl 10X *Taq*DNA polymerase buffer (Qiagen Inc., Santa Clara, CA), 2.0 µl 25 mM $MgCl_2$, 0.5 µl 40 mM dNTPs (deoxynucleotide triphosphates), 0.25 µl Qiagen Hotstar *Taq* DNA polymerase, 1 µl of 10 ρM/µl 3665 primer, 1 µl of 10 ρM/µl 4068 primer, and 2 µl of DNA template.

PCR amplifications for both genes were performed using a MJ thermal cycler (MJ Research, Waltham, MA) under the following conditions: activation (95°C, 5min.) for 1 cycle; denaturation (94°C, 30s), annealing (45-55°C, 45s), extension (72°C, 60s) for 35-40 cycles; final extension (72°C, 5min.). Negative controls were used to monitor for potential contamination and PCR products were examined using gel electrophoresis. PCR products were cleaned using ExoSAP-IT and the manufacturer's protocols (USB Corp., Cleveland, OH). The cleaned PCR products were sequenced in both directions, using the same primers as were used in amplification, with a BigDye® Terminator v1.1 cycle

sequencing kit (Applied Biosystems, Foster City, CA) at the Research Support Facility at Michigan State University. The resulting DNA sequences were examined and edited using Sequencer 4.5 (Genecodes, Ann Arbor, MI) and consensus sequences were created from the sense and antisense sequences.

The COI sequences showed no length variability and were aligned manually in Mega 4 (Tamura *et al.* 2007) since the alignments were unambiguous. 28S sequences were initially aligned using Clustal W (Thompson *et al.* 1994) in Mega 4 then manually adjusted in reference to a model of beetle 28S secondary structure (Gillespie *et al.* 2004) to correct misaligned conserved regions and to remove unalignable regions in the 28S dataset.

*Morphological Characters*

A total of 100 morphological characters were included in the analyses (42 binary, 58 multistate) and coded using the program Mesquite 2.5 (Maddison and Maddison, 2008). Characters include those previously used in asidine species and generic descriptions (Solier 1836; LeConte, 1853, 1858; Champion 1884, 1892; Casey 1912; Wilke 1822) and new characters identified in this study. All measurements were taken using digital calipers or an optical micrometer attached to a Leica MZ125 microscope. Overall body length was measured along the midline from the anterior margin of the pronotum to the apex of the elytra. Width was measured across the widest point of the elytra. Images of specimens or characters were taken with a Leica DFC320 camera mounted on a Leica MZ16 microscope. Montaged images were assembled with Helicon Focus 3.5 (HeliconSoft) software. Dissection of specimens to examine internal structures

followed established methods (Tschinkel & Doyen 1980, Flores 1997) for the subfamily and descriptive terminology followed Doyen (1966, 1993) and Harris (1979).

Characters were coded for both male and female specimens unless otherwise specified. Consistency index (CI) and retention index (RI) scores for the characters are based on one of four recovered most parsimonious trees. Images of characters and states are online at http://www.hisl.ent.msu.edu/research/asidini/ along with additional supplemental information.

***Antennae***

**1. Apical tomentose sensillum on antennal segment 11** (CI = 0.33; RI = 0.64) / 0: confined to tip, less than one-fourth of segment / 1: one-fourth to half of segment / 2: more than half of segment

**2. Antennal segment 11 laterally asymmetric** (CI = 0.33; RI = 0.00) / 0: no / 1: yes

**3. Antennal segment 10 encasing segment 11 past basal constriction** (CI = 0.25; RI = 0.25) / 0: no / 1: yes

**4. Tomentose sensilla on antennal segment 10** (CI = 0.33; RI = 0.67) / 0: separate / 1: separate, outer sometimes divided / 2: sometimes meeting on one side / 3: complete tomentose band

**5. Tomentose sensillum on antennal segment 9** (CI = 1.00; RI = 1.00) / 0: present / 1: absent

**6. Male antennal segment 9** (CI = 0.25; RI = 0.82) / 0: sub equal to segment 10 / 1: smaller than segment 10

**7. Antennal shape, segments 3 to 7** (CI = 0.11; RI = 0.65) / 0: rounded / 1: laterally flattened

**8. Antennal segment 3 length** (CI = 0.33; RI = 0.75) / 0: short, length less than 2.5 X width / 1: medium, length greater than 2.5 X width / 2: long, length greater than 4 X width

**9. Female antennal length** (CI = 0.6; RI = 0.33) / 0: short, not exceeding head capsule base / 1: normal, 3-5 segments past headcapsule base / 2: long, nearly twice as long as head capsule / 3: normal in female, long in male

**10. Antennal setae, predominate color** (CI = 0.19; RI = 0.59) / 0: white or clear / 1: golden or light brown / 2: brown / 3: black

***Head***

**11. Clypeal membrane** (CI = 0.17; RI = 0.69) / 0: exposed / 1: concealed

**12. Labrum, medial tormal process** (CI = 0.11; RI = 0.60) / 0: shorter than posterior tormal process / 1: equal to or longer than posterior tormal process

**13. Labrum, emargination** (CI = 0.17; RI = 0.50) / 0: none or very slight / 1: rounded emargination

**14. Labrum, unsclerotized setal sensorium** (CI = 0.40; RI = 0.89) / 0: concealed in depressions / 1: protruding past labral margin, visible on dorsal surface / 2: entire margin unsclerotized

**15. Mentum reaching mandibles** (CI = 0.50; RI = 0.75) / 0: no / 1: yes

**16. Mentum type** (CI = 0.88; RI = 0.96) / 0: Type I, Astrotus / 1: Type II, Sicharbas / 2: Type III, Philolithus / 3: Type IV, Stenomorpha / 4: Type V, Megasida / 5: Type VI, Stenosides / 6: Type VII, Cardiogenius / 7: Type VIII, Asbolus / 8: Type IX, Microschatia / 9: Type X, Pelecyphorus

**17. Ligula position and apex shape** (CI = 0.75; RI = 0.96) / 0: concealed, almost always straight, thin / 1: partially exposed, flush with anterior margin of mentum, curved, thin / 2: exposed, rising above anterior margin of mentum, curved, thick / 3: raised, membranous, long / 4: exposed, rising above anterior margin of mentum, long

**18. Maxillary segment 2 proportion** (CI = 0.50; RI = 0.00) / 0: seg.2 subequal to seg.3 / 1: seg.2 shorter than seg.3

**19. Female maxillary palp shape** (CI = 0.43; RI = 0.64) / 0: rectangular / 1: securiform / 2: triangular or slightly scalene / 3: scalene / 4: scalene, greatly enlarged

**20. Male maxillary palp shape** (CI = 0.21; RI = 0.67) / 0: rectangular / 1: securiform / 2: triangular or slightly scalene / 3: scalene / 4: scalene, greatly enlarged

**21. Maxilla, lacinial uncus** (CI = 1.00; RI = 1.00) / 0: bifid / 1: single, pointed

**22. Submentum width** (CI = 0.50; RI = 0.83) / 0: nearly equal to buccal cavity basal width, cardos concealed / 1: ~4/5 buccal cavity width, cardos partially concealed / 2: less than 4/5 buccal cavity width, cardos exposed / 3: app. 1/2 buccal cavity width, cardos completely exposed

**23. Submentum shape** (CI = 0.50; RI = 0.82) / 0: flat, apex straight or nearly straight / 1: flat, apex shallowly concave or emarginate / 2: medially depressed to apex, apex emarginate / 3: depressed, apex straight / 4: concealed or absent

**24. Postgenal process swollen** (CI = 0.25; RI = 0.79) / 0: yes / 1: no

**25. Postgenal process reaching mentum apex** (CI = 1.00; RI = 0.00) / 0: no / 1: yes

**26. Postgenal process, viewed laterally** (CI = 0.40; RI = 0.83) / 0: not or barely produced / 1: broadly rounded, extending past middle of mentum / 2: acute, extending

past middle of mentum / 3: broadly rounded or truncate, entending to middle of mentum or less / 4: acute, extending to middle of mentum or less

**27. Genal suture** (CI = 0.4; RI = 0.57) / 0: curved underneath eye / 1: long, extending past mandible base / 2: short, not exceeding mandibular base

**28. Postgenal anterior margin** (CI = 0.33; RI = 0.83) / 0: concealing mandibular protuberance / 1: exposing mandibular protuberance / 2: exposing mandibular protuberance, strongly emarginate below mandibles

**29. Eye shape** (CI = 0.25; RI = 0.57) / 0: elongate or elongate reniform / 1: round or broad oval

**30. Frons sculpturing** (CI = 0.22; RI = 0.68) / 0: impunctate / 1: shallow punctures or fovae / 2: large deep dense fovea / 3: tuberculate, scattered punctures

**31. Frons median depression** (CI = 0.25; RI = 0.57) / 0: absent or faintly indicated / 1: present

**32. Supra-orbital carina** (CI = 1.00; RI = 1.00) / 0: absent / 1: present

**33. Gena laterally projecting, acute** (CI = 1.00; RI = 0.00) / 0: no / 1: yes

**34. Tentorial bridge (corpotentorium)** (CI = 1.00; RI = 0.00) / 0: absent / 1: present

***Prothorax***

**35. Posterior lateral margins of prothorax** (CI = 1.00; RI = 1.00) / 0: tomentose patches absent / 1: tomentose patches present

**36. Posterior pronotal apicies** (CI = 0.33; RI = 0.60) / 0: broadly rounded, projecting over sides of elytra / 1: broadly rounded to obsolete, not projecting / 2: acute, not or weakly projecting / 3: acute, distinctly prolonged, projecting over elytra / 4: acute, divergently projecting

**37. Pronotal anterior apicies** (CI = 0.14; RI = 0.57) / 0: not or slightly produced / 1: produced, acute / 2: produced, broadly rounded

**38. Pronotum posterior margin shape** (CI = 0.21; RI = 0.61) / 0: straight / 1: concave / 2: convex / 3: sinuate or convex with median dip / 4: straight with a protruding medial tooth

**39. Pronotum tumid** (CI = 0.10; RI = 0.47) / 0: no / 1: yes

**40. Pronotal discal tuberacles** (CI = 0.25; RI = 0.40) / 0: absent / 1: present

**41. Median longitudinal pronotal ridge** (CI = 0.67; RI = 0.00) / 0: absent or faint unraised line / 1: partially raised / 2: complete carinae

**42. Pronotal fossa** (CI = 0.40; RI = 0.25) / 0: absent or, rarely, very faintly indicated / 1: present, four rounded fossa / 2: present, two c-shaped fossa

**43. Pronotum median longitudinal furrow** (CI = 0.50; RI = 0.50) / 0: absent / 1: present

**44. Pronotal posterior margin with visible golden fringe of setae** (CI = 0.40; RI = 0.63) / 0: absent / 1: present, arising from lateral face / 2: present, arising from interior margin

**45. Pronotal marginal costa** (CI = 0.33; RI = 0.27) / 0: absent / 1: present, always strongly reflexed / 2: present, not or weakly reflexed / 3: present, weakly to stongly reflexed / 4: present, broadly reflexed, medially expanded and acute

**46. Prosternal process height** (CI = 0.29; RI = 0.44) / 0: declivous / 1: porrect / 2: sub-porrect, thickened at base

**47. Base of prosternal process expanded behind procoxa** (CI = 0.10; RI = 0.63) / 0: not or barely in a few specimens / 1: yes

**48. Prosternal process sagittate** (CI = 0.33; RI = 0.00) / 0: no / 1: yes

**49. Prosternum depressed anterior to procoxal cavities** (CI = 1.00; RI = 1.00) / 0: yes / 1: no

**50. Prosternum length anterior to procoxal cavities** (CI = 0.50; RI = 0.88) / 0: equal or greater than coxal cavity length / 1: less than coxal cavity length

**51. Prosternal tubercules** (CI = 0.14; RI = 0.40) / 0: absent / 1: present

**52. Prosternum punctation** (CI = 0.21; RI = 0.66) / 0: smooth, miniscule punctures / 1: foveate / 2: densely, nearly confluently foveate / 3: regularly punctate

**53. Anterior projecting hypomeron tuberacle** (CI = 1.00; RI = 0.00) / 0: absent / 1: present

**54. Suture between hypomeron and prosternum** (CI = 0.11; RI = 0.62) / 0: complete visible over entire length / 1: partly to totally obscured

**55. Pronotal length to width ratio** (CI = 1.00; RI = 1.00) / 0: much wider than long , L divided by W less than .60 / 1: L divided by W greater than .60

***Pterothorax***

**56. Scutellum raised above scutum** (CI = 0.40; RI = 0.81) / 0: no / 1: gradual, 45 degree angle / 2: sharp, 90 degree angle

**57. Mesonotal depressions** (CI = 0.47; RI = 0.76) / 0: absent / 1: tomentose, faint, transverse / 2: tomentose, usually deep, transverse, separated by medial carinae / 3: tomentose, deep, triangular / 4: tomentose, deep, triangular / 5: tomentose, deep, circle /

6: tomentose, deep, rounded, open at base / 7: tomentose, faint, rounded, open at base / 8: tomentose, deep, continuous band / 9: glaberous or with spines, transverse, open at base

**58. Elytral insertion on mesonotum** (CI = 0.40; RI = 0.87) / 0: grooves on sides of scutellum / 1: grooves underneath scutellum / 2: grooves in elytral sides / 3: grooves on top and sides of scutellum

**59. Tomentose depression on mesepisternum** (CI = 0.25; RI = 0.59) / 0: absent / 1: large, curved, posterior margin well defined or costate / 2: large, curved, posterior margin poorly defined / 3: thin, straight, posterior margin well defined / 4: thin, straight, posterior margin poorly defined

**60. Stellate elytral setae** (CI = 1.00; RI = 0.00) / 0: absent / 1: present, Astrotus type / 2: present, Pelecyphorus type

**61. Squamate setae** (CI = 0.25; RI = 0.50) / 0: absent / 1: present

**62. Hairlike elytral setae** (CI = 0.38; RI = 0.58) / 0: absent, otherwise / 1: present including disc, short stout / 2: present, not on disc, short stout / 3: present including disc, long

**63. Decumbent lanceolate scalelike setae** (CI = 0.16; RI = 0.67) / 0: absent / 1: present

**64. Tuberacles on elytral disc** (CI = 0.15; RI = 0.52) / 0: absent / 1: present / 2: present, minute

**65. Metepimeron** (CI = 1.00; RI = 1.00) / 0: concealed / 1: visible

**66. Epipleura** (CI = 0.50; RI = 0.50) / 0: thin throughout, often obscured / 1: not obscured, expanded at elytral base

**67. Elytral marginal costa** (CI = 0.19; RI = 0.43) / 0: absent, except near humera occasionally / 1: present / 2: present, divided, inner carina raised / 3: present, divided, inner carina row of tubercles / 4: present, base formed by epipleura

**68. Elytral discal costa** (CI = 0.27; RI = 0.56) / 0: absent / 1: present / 2: present, divided into two branches / 3: present, confused, rugose / 4: present divided, almost completely eroded / 5: present, faint/tuberclues, 3 branches

**69. Elytral sutural costa** (CI = 0.20; RI = 0.00) / 0: absent / 1: present

**70. Transverse elytral costae** (CI = 0.20; RI = 0.47) / 0: absent / 1: present, carinate and sometimes lines of tubercles / 2: present only as lines of tubercles / 3: rugose, confused

**71. Elytral humeral carina strongly expanded at base, usually reflexed** (CI = 0.20; RI = 0.33) / 0: yes / 1: no

**72. Elytral humeri sharply constricted before base** (CI = 1.00; RI = 1.00) / 0: yes / 1: no

**73. Elytra sharply declivous and tomentose near base** (CI = 1.00; RI = 0.00) / 0: no / 1: yes

**74. Distinct elytral setal color patterns** (CI = 1.00; RI = 0.00) / 0: none / 1: white or multicolor longitudinal lines between costa / 2: Ucalegon patterned / 3: Tisamenes patterned

**75. Mesocoxal cavity closure** (CI = 0.20; RI = 0.60) / 0: open, closed by mesepisternum or mesepimeron / 1: apparently closed, closed by sternites

**76. Metendosternite stem** (CI = 1.00; RI = 1.00) / 0: short, twice as wide as tall, sides straight / 1: approximately square / 2: half as tall as wide, V-shaped

**77. Metendosternite** (CI = 1.00; RI = 1.00) / 0: longer than mesepisternite, not fused to coxal cowlings / 1: equal or shorter than mesepisernite, fused to mesocoxal cowlings

**78. Metendosternite base forming an external sclerite** (CI = 1.00; RI = 1.00) / 0: no / 1: yes

***Legs***

**79. Protibial latero-apical spine** (CI = 0.20; RI = 0.58) / 0: absent to small, apically setose / 1: length < tibial midwidth, apically glaberous / 2: present, length app. => than tibial midwidth, apically glaberous

**80. Protibial apical spurs** (CI = 0.40; RI = 0.85) / 0: subequal in length / 1: anterior larger than posterior / 2: anterior smaller than posterior

**81. Latero-apical spines on meso- and meta- tibia** (CI = 1.00; RI = 0.00) / 0: absent / 1: present

**82. Tarsal venter setae** (CI = 0.18; RI = 0.47) / 0: spiniform setae only / 1: hairlike setae only / 2: combination of spiniform and hairlike setae

**83. Parempodia** (CI = 0.10; RI = 0.64) / 0: absent or rarely present, not extending past tarsal apex / 1: present, extending past tarsal apex

**84. Mesotrochantin** (CI = 0.67; RI = 0.67) / 0: apparently absent, concealed / 1: present, visible / 2: minute, barely visible

***Abdomen***

**85. Punctation on abdominal ventrites 1-4** (CI = 0.10; RI = 0.67) / 0: absent/minute / 1: present

**86. Setae on abdominal ventrites 1-4** (CI = 0.16; RI = 0.64) / 0: absent/minute / 1: present

**87. Spermathecal common duct shape** (CI = 0.67; RI = 0.50) / 0: long, tubular / 1: short, protrusion opposite accessory gland / 2: absent / 3: small, rounded protrusion

**88. Spermathecae arrangement** (CI = 0.50; RI = 0.91) / 0: apex of duct / 1: serial along one side to apex / 2: serial, from accessory gland to apex / 3: single spermathaca

**89. Spermathecae number** (CI = 0.43; RI = 0.79) / 0: one / 1: three to nine / 2: ten or more / 3: two

**90. Spermathecal accessory gland** (CI = 0.50; RI = 0.33) / 0: not branching / 1: branching, small side branches / 2: branching, branch size equal

**91. Enlarged chamber on spermathecal accessory gland** (CI = 0.25; RI = 0.86) / 0: present / 1: absent

**92. Spermathecal accessory gland connection to common duct** (CI = 1.00; RI = 0.00) / 0: thickened ring off common duct / 1: directly onto common duct / 2: thickened

**93. Spermathecae size** (CI = 1.00; RI = 1.00) / 0: all approximately equal / 1: much larger towards accessory gland / 2: single spermathecae

**94. Spiculum ventrale** (CI = 1.00; RI = 0.00) / 0: short, half or less length of abdomen / 1: long, two-thirds or more length of abdomen

**95. Female apical coxite ventral surface shape** (CI = 0.67; RI = 0.93) / 0: asidine type, flat / 1: asidine type, rounded / 2: non-asidine

**96. Abdominal intercoxal process interal connection to metepisternum** (CI = 0.64; RI = 0.86) / 0: raised bifid sclerite / 1: raised medial membranous patch / 2: no raised area / 3: raised sclerotized patch / 4: raised, membranous patch poorly defined / 5: raised, no patch / 6: raised, membranous patch with M-shaped sclerite above / 7: broad-slight raise, transverse or bifid patch / 8: single sclerotized knob

***General***

**97. Densely evenly encrusted with debris dorsally** (CI = 0.33; RI = 0.33) / 0: no / 1: yes

**98. Elytral setae barbed** (CI = 1.00; RI = 0.00) / 0: no / 1: yes

**99. Eleodes mimic** (CI = 0.15; RI = 0.54) / 0: not mimetic / 1: potentially mimetic / 2: mimetic

**100. Defensive posture** (CI = 0.42; RI = 0.50) / 0: legs pulled in / 1: legs scissored / 2: legs extended under body, stilted / 3: legs spread out to sides or front / 4: headstand / 5: no posture, moves

## Phylogenetic Analysis

Morphological and sequence data (100 morphological characters, 1152bp) for 55 North American asidine OTUs and 3 outgroup taxa were concatenated in Mesquite 2.5 and exported in Nexus format for analyses in PAUP* 4.0b10 and MrBayes 3.1.

Heuristic maximum parsimony analyses in PAUP* were implemented with 10,000 random stepwise additions and TBR branch swapping, and all multistate morphological characters treated as non-additive. Initial analysis was performed with equal weight assigned to all characters. A second analysis was performed with all characters weighted *a posteriori* based on their consistency index scores. Branch support was determined for both parsimony analyses using the nonparametric bootstrap (Felsenstein 1985) with 1000 replicates in PAUP* and Bremer support indices in TreeRot.v3 (Sorenson & Franzosa 2007). Bremer support was assessed for the entire dataset and for three data partitions (COI, 28S, and morphology).

For the Bayesian analysis the dataset was partitioned as follows: COI (partitioned by codon position), 28S, and morphology. MrModeltest 2.3 (Nylander 2004) was used to select the substitution models for the nucleotide data partitions using the Akaike Information Criterion (AIC). GTR+I+Γ was selected for both genes. The morphology partition used a fixed state frequency model with all states treated as equal. Flat priors were chosen for all partitions. Two searches were performed with four chains each for 5 million generations and trees were sampled every 1000 generations. Clade support was inferred based on the posterior probability distribution of tree topologies.

## RESULTS

The Asidini were recovered as monophyletic in all analyses, with the South American genus *Cardigenius* as sister to the North American asidines. Three large clades, the "*Stenomorpha*", "*Philolithus*", and "*Pelecyphorus*" were also recovered in all three phylogenetic analyses; however the relationships between them were conflicted between the analyses and poorly supported. Together, these clades contained all but two of the North American asidine genera included in the analyses.

Unweighted cladistic analysis yielded 4 most parsimonious trees (L=3615, CI=0.22, RI=0.47), of which the strict consensus tree (Fig 1.1) and one of the most parsimonious trees (Fig 1.2, Fig 1.3) are shown. Weighted parsimony analysis found one tree (L=760.53, CI=0.38, RI=0.55, not shown) with the same branching pattern as one of the most parsimonious unweighted trees. Partitioned and average Bremer support values found in the unweighted parsimony analysis are listed in Table 1.2 with node numbers corresponding to one of the most parsimonious trees (Fig 1.3).

Average standard deviation of split frequencies between the two Bayesian searches reached 0.01 before the "burn-in", which was set at 2 million generations and a majority rule consensus (Fig 1.4) was made for 6,000 sampled trees (-LogL= 16269). Bootstrap (BS), averaged Bremer, and posterior probability (p.p.) values for select clades from both analyses are listed in Table 1.3.

The "*Stenomorpha*" clade was recovered in both Bayesian and parsimony analyses with relatively strong support (Table 1.3). The relationship of the "*Stenomorpha*" clade within the tribe was indeterminate with "*Stenomorpha*" + "*Pelecyphorus*" weakly supported in the cladistic analysis (Bremer = 1) and "*Stenomorpha*" + "*Philolithus*" weakly supported (p.p. = 67) in the Bayesian analysis. Most of the terminal nodes within the clade were well supported in both analyses, however many of the deeper nodes were poorly supported (BS<50, Bremer = 0-2, p.p. <80) and varied between the two inference methods.

The "*Philolithus*" clade was also strongly supported (BS = 100, Bremer = 23, p.p. = 100) in both analyses, though its placement within the tribe varied. In the Bayesian the clade was sister to the "*Stenomorpha*" clade. In the parsimony analyses it was sister to (*H. bifurca* + *H. connivens*) in a clade sister to "*Stenomorpha*" + "*Pelecyphorus*". Relationships within the clade were the same in both analyses with *Gonasida elata* as sister to the rest of the group and *Philolithus* paraphyletic with respect to *Glyptasida aegra* + *G. sordida*.

The "*Pelecyphorus*" clade was found in both analyses with moderate support (BS<50, Bremer = 5, p.p. = 80). It was sister to the "*Stenomorpha*" clade in the parsimony analysis and part of a basal polytomy "*Pelecyphorus*" + ((*H. bifurca* + *H.*

*connivens*) *Craniotus pubescens*) + ("*Stenomorpha*" + "*Philolithus*") in the Bayesian analysis. *Ardamimicus cognatoi* **n. gen. n. sp.** was sister to the rest of the clade in both analyses. Internally the clade differed between the analyses primarily in the placement of members of the genus *Parasida* and *Astrotus fasciculatus* + *Astrotus guanajuatensis*.

In the parsimony topology *Parasida* was polyphyletic, with *Parasida lirata* sister to most of the "*Pelecyphorus*" clade, *P.* n. sp. + *P. sexcostata* supported as sister species, and *P. longicollis* recovered as sister to *Microschatia rockefelleri* in a more derived position within the clade. The Bayesian consensus tree returned Parasida as a monophyletic group sister to the rest of the clade, excluding *A. cognatoi*.

*Astrotus* was not recovered as a monophyletic group in either analysis. *Astrotus* was polyphyletic in the most parsimonious trees with *Astrotus fasciculatus* + *Astrotus guanajuatensis* outside of the clade (((U. pulchellus + P. mexicanus) + ((*P. longicollis* + *M. rockefelleri*) + (*Z. dilatatus* (*A. regulais* + *S. anastomosis*))))). In the Bayesian analysis *Astrotus* was paraphyletic with respect to *Stenosides*.

The genus *Heterasida* was not recovered as monophyletic in any of the analyses. *H. subvittata* was consistently recovered as a sister taxon to *Stethasida obsoleta* in the "*Stenomorpha*" clade. *H. bifurca* + *H. connivens* were recovered as a sister group to the "*Philolithus*" clade in parsimony analyses and sister to *Craniotus* in the Bayesian analysis. *Craniotus* was sister to (*Heterasida bifurca* + *H. connivens*) in the Bayesian analysis and basal to the rest of the North American Asidini in the parsimony analysis.

## DISCUSSION

### *Generic concept*

Changes to the generic classification were made primarily on the basis of monophyly. All of the asidine genera maintained or described as new are defined by synapomorphic characters and/or a unique combination of homoplastic characters, and delimit monophyletic groups based on the currently available data. Synonymies were made in cases where a previously described genus was clearly not monophyletic and/or when a larger clade to which the genus belongs was well supported in the phylogenetic analyses, including the presence of morphological synapomorphies or a unique combination of homoplastic characters.

### *Species concept*

The phylogenetic species concept of Wheeler and Platnick (2000) is employed to define a species as "the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states". This species concept is appropriate due to its emphasis on character transformations between species and the lack of data, beyond adult morphology, available for many of the asidine species. Species were maintained or erected based on the presence of morphological synapomorphic characters and/or a unique combination of homoplastic characters shared by all of the specimens assigned to a species. Recognized species should be considered as scientific hypotheses based on the available data and, as such, their validity can be tested as more information is gathered. Previously described species were synonymized in instances where the morphological features used to define them were found to be variable traits within a larger sampling of specimens bound by invariant characters.

### *Biogeography*

Few geographic patterns can be discerned from the phylogenetic relationships proposed in the analyses. The ranges of the "*Stenomorpha*" and "*Philolithus*" clades roughly correspond, with both groups being poorly represented in central and southern Mexico and appearing to reach their greatest species diversity in northern Mexico and the southwestern United States. Both clades are also represented throughout the western US on both sides of the Rocky Mountains and as far north as British Colombia and Alberta, Canada. The majority of genera and species in the "*Pelecyphorus*" clade on the other hand occur only from central Mexico south to Oaxaca and only two species (*Astrotus alveolatus* Casey and *Stenosides anastomosis* (Say)) have ranges that extend as far north as Kansas and Colorado. *Microschatia* is the only genus in the clade represented in California or Baja California, with the exception of two *Parasida* species (*P. sexcostata* and *P.* n.sp.), both of which are restricted to the Cape region of Baja California Sur.

### "*Stenomorpha*" clade

The "*Stenomorpha*" clade consists of the genera *Stenomorpha*, *Asidina*, *Platasida*, *Megasida*, *Asidopsis*, *Trichiasida, Pycnomorpha*, *Stethasida*, one species currently in the genus *Heterasida* (*H. subvittata*), and the undescribed taxon "*Pseudoglyptasida*". This is the most specious clade of North American asidines and, while variable in dorsal habitus, the group contains several synapomorphies based on internal morphology (76:1, 57: 6 or 7; 88:1) and a unique combination of symplesiomorphic characters (8:1, 14:1, 16:3 or 4, 17:2, 31:0, 84:1, 95:1). Many of the current *Stenomorpha* clade genera, all of which were described by Casey (1912) with the exception of *Stenomorpha* and *Pycnomorpha*, were described based upon a gestalt of relatively variable dorsal characters (elytral costae,

pronotal shape, and the presence/absence of setae). None of the *Stenomorpha* clade genera that were represented by more than a single taxon were recovered as monophyletic in either analysis. Due to the lack of internal support within the clade, the paraphyletic or polyphyletic makeup of most of the genera, the high amount of homoplasy in characters previously used to separate the genera, and the diagnosability of the "*Stenomorpha*" clade as a whole, the constituent genera making up the clade are placed in synonymy with *Stenomorpha* Solier herein. A more detailed analysis of the clade, including increased taxon sampling, will most likely result in the maintenance of many of the previous genera as subgenera within *Stenomorpha*, with modifications in the placements of a number of species.

**"*Philolithus*" clade**

The "*Philolithus*" clade is composed of the genera *Philolithus*, *Gonasida*, and *Glyptasida* in the current dataset, but likely includes the monotypic and extremely rare genera *Herthasida* and *Tisamenes* (not in phylogeny) based on a suite of shared morphological characters (1:0; 4:1, 16:2, 17:0, 19:4, 23:0, 46:0, 50:0). This clade has previously been hypothesized (Brown 1971b, Brown & Doyen 1991) but this is the first time that it has been confirmed using quantitative phylogenetic methods. *Gonasida* was sister to *Philolithus* + *Glyptasida* in both analyses; however *Philolithus* was paraphyletic with respect to *Glyptasida*, though branch support was low. The genus *Glyptasida* was recently revised (Lockwood and Pollock 2009) and reduced from 22 species-group names to 3, mostly through the synonymy of species described by Casey (1912). The remaining *Glyptasida* species share two synapomorphies (35:1 and 72:0) and should be considered a subgenus within *Philolithus*. Given that the morphological synapomorphies (16:2, 50:0,

57:0, 93:1, 96:7) or symplesiomorphies (17:0, 20:4, 23:0, 26:0, 56:4, 79:0, etc.) that define the clade are present in all three of the genera in the analysis, and that the external characters were confirmed as present in *Herthasida* and *Tisamenes*, the genera *Gonasida*, *Glyptasida*, *Herthasida*, and *Tisamenes* are synonymized with *Philolithus* herein, but maintained as subgenera pending further studies.

**"*Pelecyphorus*" clade**

The "*Pelecyphorus*" clade is the most morphologically heterogeneous and least supported of the three major clades recovered. In the current dataset it is composed of the genera *Ardamimicus* **n.gen.**, *Astrotus*, *Parasida*, *Pelecyphorus*, *Microschatia*, *Stenosides*, *Ucalegon*, and *Zaleucus*. It is worth noting that the clade includes the only previously described genera (*Astrotus*, *Microschatia*, *Stenosides*) that were not synonymized with *Asida* by Horn (1870).

*Ardamimicus cognatoi* **n.gen. n.sp.** was placed at the bases of the "*Pelecyphorus*" clade in all resulting topologies. It is a difficult species to place within the current generic classification due to its unique combination of morphological characters (6:1, 16:3, 17:1, 20:3, 39:1, 57:5, 61:1, 64:1, 76:0) and three autapomorphic characters (lanceolate setae arising from the apex of micropunctate tubercles on pronotum, squamate scales on the legs, and prosternal process wider than procoxal cavities) not included in the analyses. Hence, *Ardamimicus* is formally erected below as a new monotypic genus.

*Microschatia* was placed as either sister to *Parasida longicollis* (parsimony analysis) or as part of a large polytomy (Bayesian analysis) within the "*Pelecyphorus*" clade. In a separate analysis (not shown) of the COI and 28S datasets, *Microschatia* was sister to the rest of the North American Asidini. Hence, the placement of *Microschatia*

within the "*Pelecyphorus*" clade is questionable and appears to be due to the number of homoplasious morphological character states that they share. *Microschatia*, which was revised in Brown and Doyen (1991), is a well defined genus within the Asidini based on a unique combination of characters (16:8, 46:1, 66:1, 87:1). *Microschatia* and its presumed sister genus, the monotypic *Litasida* (not in analysis), share a unique configuration of the spermathecal common duct (87:1) within the Asidini and are the only known asidine genera outside of the Mediterranean region that have the epiplura (66:1) visible, basally expanded, and forming a marginal carina in some species. Further analyses that include Mediterranean specimens are needed to ascertain the relationships between the Palearctic and North American Asidini. *Microschatia* is maintained as a valid genus within this study.

*Astrotus* was para- or polyphyletic with respect to *Stenosides* in both analyses. However, morphology indicates that *Astrotus* should be divided into two separate groups, both of which are distinct from *Stenosides*. *Astrotus sensu strictu*, represented in the analyses by *Astrotus regularis* Horn, contains several autapomorphic characters (16:0, 53:1, 57:9, 60:1) in the current dataset that are synapomorphic for the species in *Astrotus sensu strictu*. *Astrotus fasciculatus* and *Astrotus guanajuatensis* share a unique combination of symplesiomorphies (10:2, 13:1, 16:9, 31:1, 42:1, 59:4, 68:2) and are included in the subgenus *Variodorsus* **n.s.gen.** described herein.

The monotypic genera *Pelecyphorus*, *Ucalegon*, and *Zaleucus* vary in their positions between the analyses, though *Ucalegon* + *Pelecyphorus* was consistently recovered. All three genera are identified by autapomorphic characters and are morphologically distinct from each other as well as other asidine species groups.

The genus *Parasida* was monophyletic in the Bayesian analysis (p.p. = 90), but polyphyletic in the most parsimonious trees. The placement of *P. longicollis* with *Microschatia* in the parsimony analysis was surprising and is not supported by morphological data. The model-based approach did recover *Parasida* as a monophyletic group, which contains a unique combination of sympleisiomorphic character states (16:9, 17:1, 22:2, 23:2, 31:1, 46:0, 57:1 or 2, 62:2, 63:1, 89:1). Increased taxon sampling within the group and the inclusion of more gene regions are warranted to clarify the validity of *Parasida*. The genus is maintained as a subgenus of *Pelecyphorus* in the current study, pending future analyses. A separate issue relating to *Parasida* is nomenclatural. The genus name is a junior homynym of an earlier crustacean genus, thus the replacement name *Plesiasida* is provided below.

While the dorsal habitus of different subgroups can be highly variable within the "*Pelecyphorus*" clade, all groups, excluding *Ardamimicus* and *Microschatia*, share two synapomorphies on the mesonotum (56:0, 57:1, 2, or 9) and a unique combination of symplesiomorphies (6:1, 7:0, 17:0 or 1; 26:1 or 2, 58:1, 76:0, 80:0, 85:1; 88:0, 89:1, 95:0). Due to the lack of internal support within the clade, the paraphyletic or polyphyletic makeup of most of the genera, the high amount of homoplasy in characters previously used to separate the genera, and the diagnosability of the "*Pelecyphorus*" clade as a whole, the constituent genera, excluding *Ardamimicus* and *Microschatia* (as discussed above), making up the clade are synonymized or reduced to subgeneric status within *Pelecyphorus* Solier herein.

### *Heterasida*

The genus *Heterasida* was not recovered as monophyletic in any of the analyses. *H. subvittata* was consistently recovered within the "*Stenomorpha*" clade, while *H. bifurca* + *H. connivens* were recovered outside of the three named clades and as a sister group to either the "*Philolithus*" clade or *Craniotus*. All three *Heterasida* species are endemic to the Baja Sur Cape region, which is one of the reasons given by Casey (1912) for hesitantly placing them into the same genus. However, *H. subvittata* is clearly part of the "*Stenomorpha*" clade based on both morphology (discussed above) and DNA, while *H. bifurca* and *H. connivens* share three morphological synapomorphies (9:2, 32:1, 89:3) found nowhere else in the tribe.

### *Craniotus*

The genus *Craniotus* currently contains two species (*C. pubescens* and *C. blaisdelli*), one of which (*C. pubescens*) was included in the analyses. *Craniotus* was sister to (*Heterasida bifurca* + *H. connivens*) in the Bayesian analysis and basal to the rest of the North American Asidini in the parsimony analysis. Historically *Craniotus* was placed in its own tribe, Craniotini. Doyen (1993) recognized its similarity to the Asidini and the tribe was subsequently synonymized under Asidini (Aalbu *et al.* 2002).

**Key to the North American Asidini genera [modified from Brown 1971b]**

1 Epiplura widening towards base; epiplural fold distinct over entire length, forming a marginal costa or not; prosternal process strongly raised and produced behind procoxa .....2

- Epiplura thin over entire length, epiplural fold weakly or not indicated beyond 3rd abdominal ventrite; prosternal process variable .....3

2(1) Mentum small, cordate, exposing maxillary cardos; antenna long and slender; posterior pronotal apicies projecting over elytra .....***Litasida*** **Casey**

- Mentum large, sub-trapazoidal, concealing maxillary cardos; antennae compact; posterior pronotal apicies not projecting over elytra .....***Microschatia*** **Solier**

3(1') Inflated, hemispherical reddish-orange setae present on abdominal ventrite 1; minute tomentose sensilla generally present on lateral apicies of antennal segment 9.....***Ferveoventer*****, n. gen.**

- Abdominal ventrite 1 setose or not, but never with hemispherical setae; antennal segment 9 without tomentose sensilla.....4

4(3') Epistoma acutely laterally produced, mesotrocantin minute and concealed; apical segment of maxillary palpi rectiform and not enlarged in female, greatly enlarged and scalene in male; antennal segment 11 conical, tapering to apex ..... ..... ***Craniotus*** **LeConte**

- Epistoma rounded, not acutely produced, mesotrocantin variable; apical segment of maxillary palpi enlarged in both sexes, securiform, isotriangular, or scalene; apex of antennal segment 11 broadly rounded .....5

5(4') Eyes small and nearly round; protibial outer lateral margin carinate and serrated; posterior protibial spur greatly reduced, less than 1/8 length of anterior spur; pronotum lacking marginal costa;length less than 6.5 mm; Nuevo Leon..... .....***Micrasida*****, n. gen.**

- Eyes elongate, slightly reniform or rarely broadly oval; protibial outer lateral margin rounded, with or without small tubercles; posterior protibial spur at least 1/2 length of anterior spur; pronotum with marginal costa; length greater than 6.5 mm .....6

6(5') Legs densely clothed with whitish squamate scales; prosternal process wider than width of procoxal cavity; pronotal disc tuberculate with decumbent lanceolate or squamate scales arising from apex of tubercles ..... ***Ardamimicus*, n. gen.**

- Legs glabrous or with hair-like setae; prosternal process width less than width of procoxal cavity; pronotal disc rarely with tubercules, if tuberculate then never with lanceolate or squamate scales arising from apex of tubercles.....7

7(6') Ligula exposed, tumid, length 3X width or less; scutellum raised above scutum, mesonotum with two rounded tomentose depressions.....8

- Ligula partially exposed or concealed, not tumid, length 4X width or more; scutellum rarely raised above scutum, if raised then lacking tomentose depressions on mesonotum .....9

8(7) Supraorbital costae present from apices of eyes to gena; antennae long, tomentose sensilla on antennal segment 10 coalesced into a continuous band, segment 11 deeply amplected into segment 10; pronotum medially longitudinally impressed; Baja California Sur ..... ***Heterasida* Casey**

- Supraorbital costae absent or present only above eyes; tomentose sensilla on antennal segment 10 separate or sometimes meeting on one side only, segment 11 slightly or not amplected into segment 10; pronotum not medially longitudinally impressed ..... ***Stenomorpha* Solier**

9(7') Mentum broadly hexagonal; head nearly hypognathous; ligula small, straight, and concealed underneath mentum; apical protibial spurs subequal;..... mesonotum lacking paramedial depressions ..... ***Philolithus*** **Lacordaire**

- Mentum broadly cordate or subtrapazoidal; head nearly prognathous; ligula small, straight or curved, concealed underneath mentum or partially exposed; anterior protibial spur longer than posterior spur; mesonotum with two transverse deep or faint tomentose depressions often leaving a medial carina running to scutellum..... ..... ***Pelecyphorus*** **Solier**

## Generic Descriptions

### *Ardamimicus* Smith, New Genus

Type species: *Ardamimicus cognatoi* Smith, **n. sp.**

**Description (see fig. 1.5).** Length: 8.3-12.8mm, width: 4.3-7.7mm; integument black; body obovate; head retractable into pronotum to epistoma; elytra wider than pronotum and 2.9-4.1times longer. **Head:** Mentum cordiform, mid-width more than 2X basal width, not reaching postgena or mandibles, anterior margin slightly medially emarginate. Ligula sclerotized small, less than one-fourth mentum width, slightly curved and partially visible above mentum emargination. Apical segment of maxillary palps enlarged, triangular to scalene. Submentum narrow and raised, laterally exposing maxillary cardos. Postgenal processes slightly produced, acute or rounded. Labrum broadly shallowly emarginate; medial tormal process shorter than posterior tormal process; clypeal membrane exposed.

Clypeal margin straight. Eyes elongate, broadly oval to slightly reniform, approximately two-thirds of eye above epistoma. Antenna weakly clavate; nearly moniliform; segments 9-11 flattened, forming a club; antennal segment 10 subquadrate; two tomentose sensilla present at lateral apices; antennal segment 11 with a broad apical tomentose sensillum, approximately one-half size of and slightly amplected into segment 10. **Prothorax:** Pronotum tumid and tuberculate, each tubercle bearing a single apical or lateral scale, lacking median costa and fossae; lateral costae present, anterior margins acute or broadly rounded, basal margins obtuse; posterior pronotal margin convex. Prosternal process broader than procoxal cavity, declivous behind procoxae. **Pterothorax:** Apterous. Scutellum triangular, gradually raised above scutum; mesonotum with two rounded tomentose depressions. Elytra rugose, with irregular anastomizing ridges and protuberences. Epipleura indistinct. Metendosternite stem approximately as twice wide as tall. **Legs:** Black to ferruginous, tarsal formula 5-5-4; coxae globular; mesotrocantin clearly visible; femura rugose-punctate, tibia shallowly nearly confluently foveolate, both densely clothed with scales; protibia with outer apical margin flared, occasionally forming a small distinct spine, inner apical margin with two unequal spurs, anterior spur larger than posterior. **Abdomen:** Punctate and setose; intercoxal process broader than mesosternal apex, anterior margin nearly straight. Female apical coxites ventrally rounded; 10 or more spermathecal branches present, emerging from apex of common duct.

**Diagnosis.** *Ardamimicus* is distinguished from all other asidine genera by a unique combination of the following characters: mentum cordiform, not reaching postgena or mandibles; ligula thin and partially concealed or flush with mentum; pronotum tumid

with decumbent lanceolate or squamate scales arising from the apex of pronotal tubercles; dorsal and lateral sides of femura and tibia densely clothed with squamate scales; and prosternal process wider than procoxal cavity.

**Distribution.** The only know species of *Ardamimicus*, *A. cognatoi*, has been collected from the Mexican states of Chihuahua and Durango and the western portion of Texas in the United States.

**Etymology.** The name *Ardamimicus* is derived from the Greek words "*arda*", meaning dirt or filth, and "*mimicus*", meaning mimic or imitator, in reference to the species strong dorsal resemblance to a clod of dirt or jackrabbit droppings. It is in the masculine form.

## Species Description

### *Ardamimicus cognatoi* Smith, New Species

**Type Material.** HOLOTYPE (female) labeled: a) "USA: TX: Reeves County / Balmorhea, Lake Balmorhea / Co. Rd. 319 N30°58'22.7" / W102°33'01.1", 05.IX.2005 / Under rocks, Coll. ADSmith"; b) on red paper, "HOLOTYPE /*Ardamimicus* / *cognatoi* ♀ / Aaron D. Smith" (MSUC). PARATYPES (54 specimens) [all bearing the label "PARATYPE /*Ardamimicus* / *cognatoi* / Aaron D. Smith" on yellow paper]: 15 (3-MSUC; 4-ADSC; 3-BMNH; 4-CNIN) with same label data as holotype. 11 paratypes (MRSC) labeled a) "Texas: Reeves Co. / Balmorhea Lake, Co.Rd.319 / Found under hillside rocks / 05-September-2005 / Coll. Marion R Smith II". 1 paratype (ADSC) labeled a) "USA: TX: Presidio Co. / Big Bend Ranch SP / 29°32'58.8"N 104°10'7.2"W / 05.IX.2005, ADSmith". 1 paratype (FMNH) labeled a) "3mi. NE of Porvenir, / Presidio

Co., TEX / IX:26:1946"; b) "F M Pale. Exp. / ~~B Patterson &~~ / J H Quinn Col.". 1 paratype (UNSM) labeled a) "Presidio, Texas / J.W.Dollahite / Sept.1960 #1 / Gutierrezia"; b) "60.25015"; c) "USNM". 1 paratype (OSUC) labeled a) "Marfa / VII 12 Tex"; b) "JW Green / Collector"; c) "H. W. Wenzel / Collection". 1 paratype labeled a) "Ft. Davis / Jeff Davis Co., TEXAS / VII-2/3-1966, ~~Tradescantia~~ / ~~occidentalis~~, J.D. Pinto & / G.E. Eertmoed. Notes ~~8-66 J~~". 2 paratypes (UNSM) labeled a) "Midland / Tex XI-12-14"; b) "Bishopp / No 3978"; c) "USNM" 1 paratype (FMNH) labeled exactly as other FMNH paratype except collection date "X:27:1946". 1 paratype (UMMZ) labeled a) "70 Texas / Ft. Davis 7-29 1914 / C. Thompson"; b) "UMMZ". 1 paratype (TAMU) labeled a) "Alpine, Tex. / VIII-10-1961 / H.R.Burke"; b) "Texas A&M College / Collection"; c) "Morphology drawing / Genus A ♂ / date XI-2 K. Brown". 2 paratypes (TTUZ) labeled a) "10 mi. E / Fort Stockton, Tx. / Pecos Co. / 15-IX-1978"; b) "J. K. Wangberg / Coll. 046-01". 1 paratype (KSUC) labeled a) "TEXAS, Howard Co / 28 XII 58 / R.L. Hayes". 4 paratypes (KWBC) labeled a) "TEX: Howard Co. 4mi. / S. Big Spring, Hwy87 / X-14-1971 C. / O'Brien & Marshall"; b) ex. collection / Charles W. O'Brien / 1972 by exchange"; c) green paper circle denoting the KWBC. 2 paratypes (KWBC) labeled a) "TEX: Howard Co., / 4 mi. S. Big Spring / on Hwy. 33 III-25-1973"; b) "C.W. & L.B. O'Brien / under stones"; c) green paper circle denoting the KWBC. 2 paratypes (KWBC) labeled a) "TEX. Howard Co. 10 / mi. S. Big Spring / Hwy 33 X-14-1971 C. / O'Brien & Marshall"; b) ex. collection / Charles W. O'Brien / 1972 by exchange"; c) green paper circle denoting the KWBC. 5 paratypes (KWBC) labeled a) "TEX: Howard Co., / 10 mi. S. Big Spring / on Hwy. 33 III-25-1973"; b) "C.W. O'Brien, dead / under stones & dung"; c) green paper circle denoting the KWBC. 1

paratype (CASC) labeled a) "MEX. Dgo. / 20 mi. S. of / Rodeo / 21-VIII-60"; b) P. H. Arnaud, Jr. / E. S. Ross / D. C. Rentz"; c) "Calif. Acad. Sci. / Collection"; d) "Morphology drawing / Genus A ♂ / date XI-2 K. Brown"; e) "102". 1 paratype (UCDC) labeled a) "6 mi S / Villa Matamoros / Chih. Mex. / VIII-8-1967"; b) R.C. Gardner / C.R. Kovacic / K. Lorenzen".

**Additional material examined.** 72 specimens (ADSC) with same locality data as holotype were excluded from the type material due to missing legs, antennae, etc.

**Description (female, see fig. 1.5).** Length: 9.8-12.8 mm, width: 5.3-7.7 mm (holotype length: 11.9mm, width: 7.0mm). Body ovate, black, generally coated in debris. **Head:** Frons tuberculate, tubercules small or nearly eroded with each bearing a single scale; median depression faintly or not impressed; frontoclypeal suture broadly impressed; epistoma punctate, lateral margin notched; dorsal sulcus present above apices of eyes; maxillary palps setose, apical segment expanded, triangular to slightly scalene; mentum densely foveate with erect spiniform setae at anterior apicies and whitish-yellow scales at base extending onto submentum; antennae black to ferruginous, clothed in erect brown spiniform setae; antennal segment 3 1.2-1.3X longer than segment 4, antennal segment 9 asymetrical, outer margin wider than inner. **Prothorax:** Pronotal margin costate, broadly actuate, widest near middle; marginal costa partially eroded in most specimens, visible as line of setiferous tubercules; pronotal disc densely tuberculate, circularly impressed around tubercles in basal half, with a single decumbent yellowish-white scale arising from the apex or side of each tubercle; hypomeron deeply punctate with setiferous tubercles; prosternum punctate and setose; prosternal process with scattered tubercles,

depressed between coxae, truncate at base. **Pterothorax:** Scutellum small, partially covered by elytra; elytra clothed with decumbent lanceolate scales arising from tubercles or not; discal costae generally present on basal fourth of elytra, otherwise reduced to irregular anastomizing ridges and protuberences bearing setiferous tubercles; marginal elytral costa present as slightly raised dense line of tubercles. Elytral humera obsolete. **Legs:** Tarsi venter with stout spiniform setae; protarsal segments 2-4 compact, width greater than length.

**Distribution.** Same as generic distribution.

**Sexual dimorphism.** Males generally smaller, length: 8.3-10.7mm, width: 4.3-6.2mm; apical segment of maxillary palps strongly scalene.

**Etymology.** The species is named in honor of Anthony I. Cognato for supporting the study of Coleoptera in general and this research specifically.

**Biology.** Specimens have been collected from underneath rocks and plant debris.

### *Craniotus* LeConte 1851

Type species: *Craniotus pubescens* LeConte 1851: 142, by monotypy.

**Redescription (see fig. 1.6).** Length: 8.3-11.2mm, width: 4.0-5.9mm; integument black; body obovate; head retractable to hind margin of eye; elytra wider than pronotum and 3-3.5X longer. **Head:** Densely punctate and setose, punctures occasionally subtended by minute marginal tubercles; frontoclypeal suture obscured, slightly impressed. Mentum cordiform, not reaching postgena or mandibles, anterior margin broadly emarginate.

Ligula sclerotized, visible above mentum emargination; width approximately one-third that of mentum, length 3X width; medially depressed at apex. Apical segment of maxillary palps rectiform in females, enlarged and scalene in males. Submentum apex raised, approximately three-fifths as wide as buccal cavity, exposing maxillary cardos laterally. Postgenal processes not or slightly produced. Anterior labral margin straight, setal brush not medially interrupted; medial tormal process shorter than posterior tormal process; clypeal membrane concealed. Clypeal margin straight or broadly emarginate. Epistoma laterally expanded, slightly reflexed, and acute; apicies impunctate and glaberous, with a shallow, elongate, setose depression posteriorly. Eyes broadly oval, slightly tapering towards vertex. Antenna weakly clavate, nearly filiform, reaching base of pronotum; antennal segment 3 longer than segments 4 and 5 combined, length more than 5X width; antennal segment 10 rounded, length ~ 1.5X width, tomentose sensilla forming an indistinct band around the apex; antennal segment 11conical and deeply amplected into segment 10, tapering to apex, tomentose sensillum present on apical half. **Prothorax:** Pronotum convex and tumid, setation and punctation variable; lateral costa absent or represented as an acute, divergent, tooth on anterior margin; posterior pronotal margin convex. Prosternal process slightly, laterally, expanded over procoxa, declivous behind. **Pterothorax:** Apterous. Scutellum triangular, obliquely raised from scutum; mesonotum with two deep rounded tomentose depressions. Elytra convex, setation and punctation variable; elytral humera obsolete; epipleura indistinct. Metendosternite stem approximately as twice wide as tall. **Legs:** Color black to ferruginous; tarsal formula 5-5-4; coxae globular; mesocoxal cavities closed by sternites, mesotrocantin minute and concealed; protibia with outer apical margin unarmed or occasionally forming a small

distinct spine, inner apical margin with two subequal spurs. **Abdomen:** Setose; intercoxal process straight or broadly rounded apically. Female apical coxites ventrally rounded; 10 or more spermathecal branches present, emerging from apex of common duct; accessory gland long, with an enlarged chamber medially.

**Diagnosis.** *Craniotus* is distinguished from all other asidine genera by a unique combination of the following characters: epistoma acutely laterally produced, mesotrocantin minute and concealed; antennal segment 11 conical, tapering to apex, tomentose sensilla on antennal segment 10 coalesced into a complete apical band.

**Distribution.** Mexico: Baja California Norte. USA: Arizona, California, Nevada,

### *Craniotus* Species Checklist

*Craniotus blaisdelli* Tanner 1963:169. Type: BYUC

*Craniotus pubescens* LeConte 1851:142. Type: MCZ

### *Ferveoventer* Smith, New Genus

Type species: *Ferveoventer browni* Smith, **n. sp.**

**Description (see fig. 1.7).** Length: 7.9-12.0 mm, width: 4.1-6.7 mm; integument black to ferruginous; body obovate; head retractable into pronotum to epistoma; elytra wider than pronotum and 1.7-2.7 times longer. **Head:** Mentum sub-trapazoidal, not reaching postgena or mandibles, anterior margin slightly medially emarginate. Ligula sclerotized small, less than one-fourth mentum width, slightly curved and partially visible above

mentum emargination. Apical segment of maxillary palps enlarged, securiform to triangular. Submentum barely projecting, approximately four-fifths width of buccal cavity, partially exposing maxillary cardos laterally. Postgenal processes slightly produced, acute or rounded. Labrum broadly shallowly emarginate; clypeal membrane exposed. Clypeal margin straight or slightly emarginate. Eyes broadly oval not emarginate. Antenna weakly clavate; nearly moniliform; segments 9-11 flattened, forming a club; antennal segment 9 with two minute tomentose sensilla present at lateral apices; antennal segment 10 subquadrate with two tomentose sensilla present at lateral apices; antennal segment 11 nearly as large as segment 10, with a broad apical tomentose sensillum. **Prothorax:** Pronotum lacking median costa and fossae; lateral costae present, anterior margins acute or broadly rounded, basal margins obtuse; posterior pronotal margin convex. Prosternal process declivous behind procoxae. **Pterothorax:** Apterous. Scutellum triangular, not raised above scutum; mesonotum lacking tomentose depressions. Elytra broadly convex or planate, without discal costae; marginal costa present or absent. Epipleura indistinct. **Legs:** Black to ferruginous, tarsal formula 5-5-4; coxae globular; mesotrocantin large, clearly visible; protibia with outer apical margin flared or not, rarely forming a small spine, inner apical margin with two short sub-equal spurs, length one-third or less basitarsal length. **Abdomen:** Punctate and setose, abdominal ventrite 1 medially clothed with hemispherical inflated reddish-orange setae; apex of intercoxal process broadly rounded.

**Diagnosis.** *Ferveoventer* is distinguished from all other asidine genera by a unique combination of the following characters: inflated, hemispherical reddish-orange setae present on abdominal ventrite 1; minute tomentose sensilla generally present on lateral

apicies of antennal segment 9; ligula small and partially concealed; discal elytral costae absent; protibia lacking distinct apical spine.

**Distribution.** Mexico: Morelos (Cuernavaca). United States: Texas (Culberson, Presidio, and Val Verde counties), New Mexico (Eddy county).

**Etymology.** The name *Ferveoventer* is derived from the Greek words "*ferveo*", meaning boil, and "*venter*", meaning abdomen, in reference to the inflated, hemispherical reddish-orange setae present on abdominal ventrite 1. It is in the masculine form.

### Key to Species of *Ferveoventer*

1 Pronotum tuberculate; elytral marginal costa present; Morelos, Mexico ..... ..... ***F. planatus*** **(Champion), new combination**

\- Pronotum without tubercules; elytral marginal costa absent; New Mexico and Texas, USA ..... ***F. browni*** **Smith, n. sp.**

### Species Descriptions

### *Ferveoventer browni* Smith, New Species

**Type Material (see fig. 1.7).** HOLOTYPE (sex undetermined) labeled: a) "TEXAS. Langtry, / Val Verde Co., / III-19-1960"; b) "W.J. Gertsch & / R. Schrammel / Collectors"; c) on red paper, "HOLOTYPE / *Ferveoventer* / *kirbyi* / Aaron D. Smith" (AMNH). PARATYPES (3 specimens) [all bearing the label "PARATYPE / *Ferveoventer* / *kirbyi* / Aaron D. Smith" on yellow paper]: 1 paratype (AMNH) labeled a) "White's City, / Eddy Co., N.M. / 3600 ft. / Sept. 24, 1950"; b) "M.Cazier / W.Gertsch

/ Collectors". 1 paratype (NMNH) labeled a) "Culberson Co / IX.16 Tex."; b) "GeoMGreene / collection". 1 paratype (KWBC) labeled a) "TEX. 4mi. / SW. Shafter / Presidio Co. / IV-19-1970 / [printed along right side] 2600' "; b) "Collector: L& / C.W. O'Brien"; c) ex. collection / Charles W. O'Brien / 1972 by exchange"; d) green paper circle denoting the KWBC. 1 paratype (ZMHB) labeled a) "Mexico / J.Flohr G."

**Description.** Length: 9.4-12.0 mm, width: 5.6-7.3 mm (holotype length: 9.4 mm, width: 5.6 mm). Body ovate, black, generally coated in debris. **Head:** Densely punctate, punctures subtended by stout, erect, pale setae; median depression absent; frontoclypeal suture weakly impressed; dorsal sulcus present above apices of eyes; genal suture thin, extending to base of mandibles; postgenal processes produced and acute; maxillary palps setose, apical segment expanded, securiform in females to triangular in males, distal angle prolonged and acute; mentum punctate with erect pale spiniform setae, slightly medially emarginate at apex; antennae ferruginous, clothed in erect pale spiniform setae; antennal segment 3 1.7-1.8X longer than segment 4, antennal segments 9-11 nearly equal in size. **Prothorax:** Pronotum sinuate, widest just behind middle; marginal costa crenulate, straight or slightly reflexed, anterior apicies acute and projecting, posterior apicies broadly rounded, not projecting; pronotal disc densely punctate, punctures subtended by stout, erect, pale setae; posterior margin convex. Hypomeron and prosternum densely punctate, with longer decumbent setae. **Pterothorax:** Scutellum small, partially covered by elytra; elytral disc nearly planate with scattered punctures, erect spiniform setae, and faintly coalesced patches of erect squamate setae; marginal carina absent, margins and apical third of elytra with yellowish or clear setae arising from

minute tubercles. **Legs:** Color ferruginous; tarsi venter with stout spiniform setae; protarsal segments 2-4 compact, width greater than length.

**Diagnosis.** Separated from *F. planatus* by the larger size, lack of pronotal tubercles, absence of a marginal elytral costa, and distribution.

**Distribution.** Texas: Culberson, Presidio, and Val Verde counties; New Mexico: Eddy County.

**Etymology.** The species is named in honor of Kirby W. Brown for his work on the Asidini and the guidance he has provided to the next generation of tenebrionid workers.

**Biology.** Unknown.

### *Ferveoventer planatus* (Champion), New Combination

*Ologlyptus planatus* Champion 1884:69

*Stenosides planatus* (Champion). Wilke 1922:268

**Type Material.** LECTOTYPE (sex undetermined, BMNH), designated here, labeled: a) [orange bordered white circle] "Type"; b) "CUERN / AVACA"; c) "Ologlyptus / planatus, Champ"; d) "Sp. figured."; e) "B.C.ACol.IV.1. / Ologlyptus / planatus.". One PARALECTOTYPE (BMNH) labeled as lectotype, except lacking "sp. figured" label and bearing the label "PARALECTOTYPE / *Ologlyptus* / *planatus* Champion / Aaron D. Smith" on yellow paper].

**Desription (see fig. 1.8).** Length: 7.9-9.0 mm, width: 4.1-5.5 mm (holotype length: 9.0 mm, width: 5.5 mm). Body ovate, black. **Head:** Densely punctate, punctures subtended

by decumbent, brown setae; median depression faintly impressed; frontoclypeal suture impressed; dorsal sulcus present above apices of eyes; genal suture thin, extending to base of mandibles; maxillary palps setose, apical segment expanded, securiform in females to triangular in males; postgenal processes produced and rounded; mentum punctate with erect brownish spiniform setae, medially notched at apex; antennae ferruginous, clothed in erect brownish spiniform setae; antennal segment 3 slightly longer than segment 4, antennal segments 9-11 nearly equal in size. **Prothorax:** Pronotum sinuate, widest at middle; marginal costa crenulate, nearly absent in apical third, straight, anterior apicies barely projecting and broadly rounded, posterior apicies broadly rounded, not projecting; pronotal disc densely punctate, punctures subtended by tubercles bearing stout, erect, brownish setae; posterior margin slightly convex. Hypomeron and prosternum densely foveate with brownish hair-like setae. **Pterothorax:** Scutellum small, partially covered by elytra; elytral disc slightly convex with scattered punctures and small setae bearing tubercles; setae erect, spiniform or squamate; marginal carina present and tuberculate. **Legs:** Color ferruginous; outer apical protibial margin not flared or forming a spine; tarsi venter with stout black spiniform setae; protarsal segments 2-4 compact, width greater than length.

**Diagnosis.** See *F. browni* diagnosis.

**Distribution.** Known only from the vicinity of Cuernavaca in the Mexican state of Morelos.

**Biology.** Unknown.

## *Heterasida* Casey

*Heterasida* Casey 1912: 165. Type species: *Heterasida bifurca* (LeConte), 1861, by original designation.

**Redescription (see fig. 1.9).** 7.6-16.6mm long, 3.3-8.0 wide. Integument black to ferruginous. **Head:** Mentum cordiform, not reaching post-genal processes or mandibles; anterior margin medially emarginate. Ligula large, approximately one-fourth mentum width, broadly curved and raised above apical margin of mentum. Apical segment of maxillary palps iso-triangular to slightly scalene. Submentum narrow and raised, laterally exposing maxillary cardos. Postgenal processes produced and acute. Labrum with apical margin broadly emarginate; medial tormal process equal to posterior tormal process; clypeal membrane exposed. Clypeal margin straight. Frons densely foveate, each fovea bearing a single seta; median depression deep or faintly impressed; frontoclypeal suture obscurred; dorsal sulcus present above apices of eyes; Supraorbital costae present from apices of eyes to gena. Eyes elongate, broadly oval to slightly reniform. Antenna weakly clavate, nearly filiform, extending past pronotal base in males; antennal segment 10 subquadrate, with tomentose sensilla forming a complete band around the apex; antennal segment 11 with a broad apical tomentose sensory patch, deeply amplected into segment 10. **Prothorax:** Pronotum tumid, medially longitudinally impressed, and foveate, anterior margin of each fovea bearing a single decumbent seta; lateral costae present, anterior margins acute and projecting, basal margins acute or projecting; posterior margin medially convex. Prosternal process broad, declivous behind procoxae. **Pterothorax:**

Apterous. Scutellum triangular, obliquely raised at 45° from scutum; mesonotum with two rounded setae lined depressions. Elytra broadly convex, sparsely foveate, clothed in short decumbent lanceolate setae. Marginal costa present, divided in basal half of elytron; inner branch carinate, curved towards midline, abruptly ending in apical fourth of elytron. Discal costae absent. Epipleura thin and slightly raised. Mesosternum basally nearly flat, then sharply raised at base of mesocoxal cavities. Metendosternite stem approximately as twice wide as tall. **Legs:** Black to ferruginous; coxae globular; mesotrocantin clearly visible; femura rugose-punctate, setose; tibia shallowly nearly confluently foveolate, setose; protibia with indistinct row of erect golden-brown spiniform setae along inner margin from base to apex, outer apical margin slightly flaired, but lacking a distinct spine, two inner apical spurs present, subequal. **Abdomen:** Densely punctate setose; intercoxal process broader than mesosternal apex, anterior margin nearly straight. Female apical coxites ventrally rounded; two long thin spermathecal branches present, emerging from apex of common duct.

**Diagnosis.** *Heterasida* species are easily distinguished from members of all other asidine genera by a unique combination of the following characters: Antennae long, nearly reaching pronotal base in females and extending past pronotal base in males; antennal segment 10 with a complete apical tomentose sensilla band, antennal segment 11 deeply amplected into apex of segment 10; mentum cordiform, not contacting postgena; ligula approximately one-forth width of mentum, raised above anterior margin of mentum; pronotum with a median longitudinal depression; elytral marginal costae present and divided; discal elytral costae absent.

**Distribution.** *Heterasida* species are restricted to the Cape Region of Baja California Sur from sea level to approximately 500 meters elevation. A single specimen of *H. connivens* has also been collected from Isla Cerralvo, an island approximately 17 km off the coast from La Paz.

**Sexual dimorphism.** Males smaller, rarely as large as conspecific females, some only half the size of females; antenna longer, extending past pronotal base. Other differences follow general sexual characteristics as previously described for the tribe.

**Discussion.** *Heterasida subvittata* (Horn, 1894:416) was hesitantly placed within the genus by Casey (1912), though he stated that it most likely represented a new genus. The species was sister to *Stethasida obsoleta* (LeConte) in both phylogenetic analyses and morphologically falls well within the expanded genus *Stenomopha sensu lato* redescribed herein.

### Key to Species of *Heterasida*

1 Elytra with decumbent lanceolate setae and erect spiniform setae; pronotal posterior lateral margins always prolonged, acute and reflexed; dorsum generally evenly coated with debris..... ***H. connivens* (LeConte)**

\- Elytra with decumbent lanceolate setae only; pronotal posterior lateral margins angulate, rarely prolonged; dorsum not or incidentally coated with debris..... ..... ***H. bifurca* (LeConte)**

### *Heterasida bifurca* (LeConte)

*Pelecyphorus bifurcus* LeConte, 1861: 337. Holotype female, designated here by monotypy, labeled "P. bifurcus/ LeC./ S. Lucas", "Type/ 4533" (MCZ)

*Heterasida bifurca* (LeConte); Casey 1912: 166

**Diagnosis (see fig. 1.9).** *H. bifurca* specimens are easily differentiated from specimens of *H. connivens* by their lack of erect spiniform setae on the elytra, less prolonged and reflexed pronotal posterior margins, and cleaner dorsal surface.

### *Heterasida connivens* (LeConte), Raised from Synonymy

*Pelecyphorus connivens* LeConte 1866:110

*Heterasida connivens* (LeConte). Casey 1912:166

=*Heterasida exilis* Casey 1912:168, **New Synonym**

=*Heterasida tantilla* Casey 1912:167, **New Synonym**

**Diagnosis (see fig. 1.10).** See differences listed under *H. bifurca.*

**Discussion.** *H. connivens* and *H. tantilla* were synonymized under *H. bifurca* by Blaisdell (1943) without explanation. *H. tantilla* and *Heterasida exilis* were both described by Casey (1912) from single specimens, both of which are small male specimens of *H. connivens.*

## *Litasida* Casey

*Litasida* Casey, 1912: 184. Type species: *Litasida townsendi* Casey, 1912: 185, by original designation. Holotype, by monotypy, male labeled: "Mex" (NMNH).

**Redescription (see fig. 1.11).** Length: 10.0-14.0 mm, width: 5.3-7.5 mm; integument black; body obovate; elytra barely wider than pronotum and 2.5-2.6 times longer. **Head:** Mentum small and cordate, not reaching postgena or mandibles, anterior margin broadly shallowly emarginate. Ligula sclerotized tumid and thick, width approximately 2.5X length, width approximately one-fourth that of mentum, sharply depressed medially and exposed above anterior margin of mentum. Apical segment of maxillary palps enlarged and triangular, larger in males. Submentum projecting and approximately two-thirds width of buccal cavity, exposing maxillary cardos laterally, apex nearly straight. Postgenal processes barely produced and rounded. Labral margin medially emarginate, setal brush present on rounded apicies; labral medial tormal process shorter than posterior tormal process; clypeal membrane concealed. Clypeal margin straight or slightly emarginate. Eyes elongate and reniform, posterior margin straight. Antenna long, extending approximately to base of pronotum, longer in males, weakly clavate and laterally flattened; antennal segment 10 subquadrate with two tomentose sensilla at lateral apices, nearly meeting on outer side in some speciemns; antennal segment 11 approximately one-half size of segment 10, apical tomentose sensilla covering nearly one-fourth of segment. **Prothorax:** Pronotum laterally arcuate, widest in basal half, narrowing towards apex; pronotal margin costate and reflexed, anterior apicies slightly

produced and rounded, basal apicies acute and projecting over elytral humera, posterior margin straight or slightly convex. Prosternal process raised and projecting behind procoxal cavities, apex broadly rounded and received in emargination between mesocoxae. **Pterothorax:** Apterous. Scutellum triangular, broader than wide, sharply raised above scutum; mesonotum with continuous depressed tomentose band between scutellum and scutum. Elytra convex, lacking discal costae; epipleura distinct over entire length, epiplural fold forming a marginal costa and reflexed at elytral humera. Metendosternite stem approximately as twice wide as tall. **Legs:** Ferruginous to nearly black, tarsal formula 5-5-4; pro- and mesocoxae globular, metacoxae transverse; mesocoxal cavities open, mesotrocantin large, exposed; femora and tibia laterally flattened; protibia with outer apical margin slightly flaired, but not forming a distinct spine; inner apical margin of protibia with two spurs, posterior spur shorter than anterior spur, anterior spur approximately one-half length of basitarsi; tarsi venter with two lateral rows of stout spiniform setae, medially glabrous. **Abdomen:** Intercoxal process triangular, narrowing to rounded apex. Female apical coxites ventrally flattened; three to nine spermathecal branches present, emerging from apex of common duct, common duct with short rounded protrusion opposite accessory gland; accessory gland long, enlarged medial chamber present.

**Diagnosis.** *Litasida* is distinguished from all other asidine genera by a unique combination of the following characters: Epiplura widening towards base, epiplural fold forming a marginal costa; prosternal process strongly raised and produced behind procoxa; mentum small, cordate, exposing maxillary cardos; antenna long and slender; posterior pronotal apicies projecting over elytra.

**Distribution.** Mexico: Chihuahua; United States: southeastern Arizona.

**Discussion.** *Litasida* is currently a monotypic genus, represent by the high elevation (6000 ft. +) species *L. townsendi.*

**Etymology.** *Litasida* is in the feminine form.

## *Micrasida* Smith, New Genus

Type species: *Micrasida obrienorum* Smith, **n. sp.**

**Description (see fig. 1.12).** Length: 5.1-6.5 mm, width: 3.0-3.8 mm; integument ferruginous to nearly black; body obovate; elytra barely wider than pronotum and 2.0-2.7 times longer. **Head:** Mentum sub-trapazoidal, contacting postgena but not reaching mandibles. Ligula sclerotized small, less than one-fifth mentum width, slightly curved and exposed above anterior margin of mentum. Apical segment of maxillary palps enlarged and securiform. Submentum barely projecting, approximately four-fifths width of buccal cavity, partially exposing maxillary cardos laterally. Postgenal processes produced and rounded. Labral margin straight, medial tormal process shorter than posterior tormal process; clypeal membrane concealed. Clypeal margin straight or slightly emarginate. Eyes small, diameter approximately 0.2 mm, and round. Antenna weakly clavate; nearly moniliform; segments 10-11 flattened, forming a club; antennal segment 10 with two tomentose sensilla present at lateral apices; antennal segment 11 approximately two-thirds as large as segment 10, apical tomentose sensilla small, covering less than one-fourth of segment. **Prothorax:** Pronotum convex, lacking median

costa and fossae; anterior margins slightly produced and rounded, basal margins oblique; marginal costa absent; posterior pronotal margin convex. Prosternal process thin, one-half width of procoxal cavity, declivous and slightly expanded behind procoxae.

**Pterothorax:** Apterous. Scutellum triangular, not raised above scutum; mesonotum lacking tomentose depressions. Elytra broadly convex, without discal or marginal costae; epipleura indistinct. Metendosternite stem approximately as twice wide as tall. **Legs:** Ferruginous to nearly black, tarsal formula 5-5-4; coxae globular; mesocoxal cavities open; mesotrocantin minute, concealed; protibia with outer apical margin forming a large glabrous spine, longer than protibial width; protibial outer lateral margin carinate and serrated; inner apical margin of protibia with two spurs, posterior spur greatly reduced, less than 1/8 length of anterior spur, anterior spur longer than basitarsi, curved and acute; outer apical margins of meso- and metatibia each armed with a small, shorter than tibial width, setose spine. **Abdomen:** abdominal ventrite 4 reduced, medially approximately two-fifths length of ventrite 3, and strongly curved; apex of intercoxal process broadly rounded. Female apical coxites ventrally flattened; three spermathecal branches present, emerging from apex of common duct; accessory gland long, enlarged medial chamber absent.

**Diagnosis.** *Micrasida* is distinguished from all other asidine genera by a unique combination of the following characters: Pronotum lacking marginal costa; eyes small and nearly round; protibial outer lateral margin carinate and serrated; posterior protibial spur greatly reduced, less than 1/8 length of anterior spur; length less than 6.5 mm

**Distribution.** Mexico: Nuevo Leon.

**Etymology.** The name *Micrasida* is derived from the Greek word "*micro*", meaning small, and the name of the type genus for the tribe. The name refers to the extremely small size of the specimens and is in the feminine form.

## Species Description

### *Micrasida obrienorum* Smith, n. sp.

**Type Material.** HOLOTYPE (female) labeled: a) "Mex. N.L. 3 mi. / E. Jcn. 57 & 60 / VI-23-1971 / L. & C.W. O'Brien"; b) on red paper, "HOLOTYPE / *Micrasida* / *obrienorum* ♀ / Aaron D. Smith" (TTUZ). PARATYPES (228 specimens) [all bearing the label "PARATYPE / *Micrasida* / *obrienorum* / Aaron D. Smith" on yellow paper]: 221 paratype (10-OSUC; 5-RLAC; AMNH) bearing the same locality data as the holotype. 4 paratypes (CASC) labeled a) "MEX: Nuevo Leon / 6mi. E.Est.Roberto / V-27-1981 J.Doyen";. 3 paratypes (CASC) labeled a) "MEX:Nuevo Leon / Rte. 58 6.4 mi.E. / Est. San Roberto / 26-27 May 1981 / J.K. Liebherr / El. 6500 ft.".

**Description (see fig. 1.12).** Length: 5.1-6.5 mm, width: 3.0-3.8 mm (holotype length: 6.4 mm, width: 3.5 mm); often coated in debris. **Head:** Hypognathous; clothed in decumbent, elongate, squamiform setae, most arising from the side or apex of small tubercles; frons without median depression; frontoclypeal suture weakly impressed at sides; epistoma laterally nearly straight; dorsal sulcus absent or thin above apices of eyes; setal brush on labral margin complete or exposing a small space medially; genal suture not indicated; postgenal processes produced and rounded; apical segment of maxillary

palp expanded, securiform in both sexes, slightly larger in males; mentum punctate with long yellowish setae, not or slightly medially emarginate at apex; submentum deeply emarginate at apex; antennae ferruginous, sparsely clothed in erect yellowish, nearly transparent spiniform setae; antennal segment 3 equal to 1.2X longer than segment 4, antennal club two segmented, segment 9 equal in size to segment 8. **Prothorax:** Lateral margins arctuate, widest at middle; disc tuberculate, tubercles minute, increasing in size towards margins; decumbent, elongate, squamate or lanceolate setae arising from tubercles, becoming erect and lanceolate at lateral margins. Hypomeron and prosternum with setose tubercles similar to pronotal disc, except prosternal setae longer and hair-like. **Pterothorax:** Scutellum small, partially covered by elytra; elytral humera oblique, not reflexed; elytra evenly coated in decumbent, elongate, squamiform setae arising from minute tubercles; elytra gradually declivous in apical third, tapering to caudally. **Legs:** Color ferruginous; femora and tibia foveate and setose, lacking socketed spiniform setae; tarsi venter with sparse pale spiniform setae; protarsal segments combined approximately two-thirds length of protibia. **Abdomen:** impunctate, clothed in pale-yellowish hair-like setae, most arising from minute tubercles.

**Diagnosis.** See generic diagnosis.

**Distribution.** Mexico: Nuevo Leon.

**Etymology.** The species is named in honor of Charles and Lois O'Brien for collecting the vast majority of the type series and for their contributions to the study of Coleoptera.

**Biology.** Unknown.

## *Microschatia* Solier

*Microschatia* Solier, 1836: 474. Type species: *Microschatia punctata* Solier 1836: 475, by monotypy.

=*Pycnonotida* Casey, 1912: 89. Synonymized in Doyen and Brown 1991: 546.

=*Acroschatia* Wilke, 1922: 269. Synonymized in Doyen and Brown 1991: 546.

**Redescription (see fig. 1.13);** [modified from Brown and Doyen 1991]. Length: 10.7-19.7 mm, width: 5.5-12.0 mm; integument black; body obovate; elytra barely wider than pronotum. **Head:** Mentum large, completely filling buccal cavity, sub-trapezoidal; anterior margin broadly emarginate, with or without a narrow median notch; lateral margins curved inward at apicies. Ligula small, approximately one-fouth mentum width, curved and partially visible above anterior margin of mentum. Apical segment of maxillary palps enlarged, isotriangular or slightly scalene, larger in males. Submentum broad, laterally contacting or nearly postgena, concealing maxillary cardos, apex broadly emarginate. Postgenal processes produced and rounded. Labral margin narrowly notched, broadly emarginate, or straight; medially without setal brush; labral medial tormal process shorter than posterior tormal process; clypeal membrane concealed. Clypeal margin straight or emarginate. Epistoma with anterior border arcuately emarginate. Eyes elongate, oval or weakly reniform, concealed when head is retracted. Antenna compact, weakly clavate and laterally flattened; antennal segment 10 subquadrate with two tomentose sensilla at lateral apices; antennal segment 11 approximately one-fourth size of and amplected into segment 10 ; apical tomentose sensilla on antennal segment 11 small,

asymmetrical or not. **Prothorax:** Pronotum laterally arcuate, widest in basal half and narrowing towards apex or widest near middle; pronotal margin costate and not reflexed, anterior apicies slightly produced and rounded, posterior apicies obtuse or acute, projecting over elytral humera or not, posterior margin convex to bisinuate or biangulate, occasionally with paramedian basal gibbosities. Prosternal process raised and projecting behind procoxal cavities, apex subtruncate to sagittate and received in shallow or moderate emargination between mesocoxae. **Pterothorax:** Apterous. Scutellum triangular, 1.5-2.0 times as wide as long, sharply raised above scutum; mesonotum with continuous depressed tomentose band between scutellum and scutum. Elytral sculpturing variable; epipleura widening towards base and distinct over entire length, epiplural fold forming a marginal costa or not. Metendosternite stem approximately as twice wide as tall. **Legs:** Ferruginous to nearly black, tarsal formula 5-5-4; pro- and mesocoxae globular, metacoxae more transverse; mesocoxal cavities open, mesotrocantin large, exposed; femora and tibia laterally flattened; protibia with outer apical margin forming a distinct spatulate process or spine; inner apical margin of protibia with two spurs, posterior spur subequal or shorter than anterior spur; tarsi venter with two lateral rows of stout spiniform setae, medially glabrous. **Abdomen:** Intercoxal process impressed around margin, rounded or truncate at apex. Female apical coxites ventrally flattened; three to nine spermathecal branches present, emerging from apex of common duct, common duct with short rounded protrusion opposite accessory gland; accessory gland long, enlarged medial chamber present.

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**Diagnosis.** *Microschatia* is distinguished from all other asidine genera by a unique combination of the following characters: Epiplura widening towards base, epiplural fold distinct over entire length; prosternal process strongly raised and produced behind procoxa; mentum large, sub-trapezoidal and completely filling buccal cavity. Most easily confused with the genus *Litasida*, but separated by the configuration of the mouthparts.

**Distribution.** Central and northern Mexico, including Baja California Norte, and the adjacent US states (Arizona, California, New Mexico, and Texas).

**Discussion.** *Microschatia* was revised Brown and Doyen (1991).

### *Microschatia* Species Checklist

*Microschatia cedrosensis* Brown and Doyen, 1991:568

*Microschatia costulata* Brown and Doyen, 1991:570

*Microschatia championi* Horn, 1893:140

*Microschatia inaequalis* LeConte, 1851:129

*Microschatia morata* Horn, 1878:56

*Microschatia planata* Doyen and Brown, 1991:576

*Microschatia polita* Horn, 1893:141

*Microschatia punctata* Solier, 1836:475

*Microschatia rockefelleri* Pallister, 1954:15

*Microschatia robusta* Horn, 1893:142

*Microschatia solieri* Brown and Doyen, 1991:552

*Microschatia sulcipennis* LeConte, 1858:18

## *Pelecyphorus* Solier

*Pelecyphorus* Solier 1836:467. Type species: *Pelecyphorus mexicanus* Solier, 1836:469, by subsequent designation, Casey 1912:105. Lectotype (MNHN).

subgenus *Astrotus* LeConte 1858:19. Type species: *Microschatia contorta* LeConte, 1853:446, by original designation. **Revised Status.**

subgenus *Pelecyphorus* Solier 1836:467, *sensu stricto.*

subgenus *Stenosides* Solier 1836:484. Type species: *Stenosides graciliformis* Solier, 1836, by monotypy. **Revised Status.**

=*Pactostoma* LeConte 1858:19. Type species: *Asida anastomosis* Say, 1824, by original designation.

=*Ologlyptus* Lacordaire 1859:158 (unnecessary replacement name).

subgenus *Ucalegon* Champion 1884:65. Type species: *Ucalegon pulchellus* Champion, 1884. **Revised Status.**

subgenus *Pleisiasida* Smith, (=*Parasida* Casey 1912:126, junior homonym). Type species: *Parasida laciniata* Casey, 1912. **New Replacement Name.**

subgenus *Sicharbas* Champion 1884:67. Type species: *Sicharbas lobatus* Champion, 1884. **Revised Status.**

subgenus *Zaleucus* Champion 1892:491. Type species: *Zamolxis dilatatus* Champion, 1884. **Revised Status.**

**Redescription (see fig. 1.14).** Length: 6.0-22.9 mm, width: 2.3-11.1 mm; integument ferruginous to black; body obovate to elongate and nearly parallel sided; generally densely setose, occasionally setae inconspicuous; setae often modified, lanceolate, squamate, or stellate in shape. **Head:** Mentum variable, trapezoidal to broadly cordate; contacting postgenal processes or not, if tightly contacting postgenal processes then also reaching mandibles when closed; lateral margins straight or curved inward at apicies; anterior margin straight to weakly emarginate, medially notched or not. Ligula; sclerotized small, one-fourth to one-sixth mentum width, and thin, length approximately 5X width; slightly curved and partially visible above anterior margin of mentum or straight and concealed. Apical segment of maxillary palps enlarged, securiform to scalene in shape, more expanded in males. Submentum barely or distinctly projecting into buccal cavity; width two-thirds to equal that of buccal cavity, concealing or partially exposing maxillary cardos laterally. Postgena concealing mandibular protuberance; postgenal processes slightly to greatly swollen; produced, extending to middle of mentum or beyond, acute to broadly rounded. Labral margin straight or broadly emarginate, medially without setal brush; medial tormal process of labrum shorter than posterior tormal process; clypeal membrane concealed or rarely exposed. Clypeal margin straight or

emarginate. Eyes elongate, oval or reniform, partially concealed when head is retracted. Antenna weakly clavate; nearly moniliform; segments 10-11 rounded or laterally flattened , forming a slight club; tomentose sensilla absent on antennal segment 9; apical tomentose sensilla present on antennal segment 10, separated into two patches at lateral apices or coalesced into a single band; antennal segment 11 one-fourth to two-thirds size of segment 10, apical tomentose sensillum covering one-sixth to one-half of segment. **Prothorax:** Pronotal shape and sculpturing variable, with or without a median costa or paramedial fossae, lacking paramedial basal gibbosities; pronotal margin costate, medially acutely expanded or not; anterior apicies produced, acute or rounded, posterior apicies obtuse or acute, projecting over elytral humera or not; posterior margin straight, slightly convex, or weakly bisinuate, often with a medial tooth projecting posterad. Prosternal process thin, declivious behind procoxae or raised and projecting behind procoxal cavities, apex truncate, broadly rounded, or sagittate; if raised then received in shallow or moderate emargination between mesocoxae. **Pterothorax:** Apterous. Scutellum triangular, visible or mostly concealed underneath elytra, not raised above scutum; mesonotum with two faint or deep transverse depressions, often leaving a thin medial ridge between the scutellum and scutum. Elytral sculpturing variable, discal costae present or faintly indicated, marginal costae rarely lacking; epipleura indistinct. Metendosternite stem approximately as twice wide as tall. **Legs:** Ferruginous to nearly black, tarsal formula 5-5-4; pro- and mesocoxae globular, metacoxae more transverse; mesocoxal cavities open or externally closed by sternites; mesotrocantin small to minute, concealed or exposed; protibia with outer apical margin forming a spine; protibial outer lateral margin not carinate; inner apical margin of protibia with two spurs, posterior spur

shorter than anterior spur. **Abdomen:** Intercoxal process impressed around margin or not, rounded or truncate at apex. Female apical coxites ventrally flattened; three to twelve spermathecal branches present, emerging from apex of common duct; accessory gland short or long, with an enlarged chamber absent or rarely present near apex.

**Diagnosis.** *Pelecyphorus* is distinguished from all other asidine genera by a unique combination of the following characters: Ligula small, one-fourth to one-sixth mentum width, and thin, length approximately 5X width; partially visible above anterior margin of mentum or straight and concealed. Scutellum not raised above scutum; mesonotum with two faint or deep transverse depressions. Anterior protibial spur longer than posterior.

**Distribution.** Mexico: representatives are known from every state with the exceptions of Chiapas, Yucatan, Tabasco, and Baja California Norte. United States: Arizona, Colorado, Kansas, New Mexico, Texas.

### *Pelecyphorus* Species Checklist

*Pelecyphorus* (*Pelecyphorus*) *mexicanus* Solier, 1836:469

*Pelecyphorus* (*Ucalegon*) *pulchellus* (Champion, 1884:65), **NEW COMBINATION**

*Pelecyphorus* (*Zaleucus*) *dilatatus* (Champion, 1884:70), **NEW COMBINATION**

*Pelecyphorus* (*Zaleucus*) *platesthoides* (Champion, 1884:71), **NEW COMBINATION**

*Pelecyphorus* (*Sicharbas*) *lobatus* (Champion, 1884:67), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *alveolatus* (Casey 1912:83), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *contortus* (LeConte, 1853:446), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *debilis* (Champion 1884:66), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *erosus* (Champion 1892:504), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *fasciculatus* (Champion, 1892:495), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *guanajuatensis* (Champion, 1884:56), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *limosus* (Champion, 1884:66), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *nosodermoides* Champion), 1892:505, **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *regularis* (Horn, 1870:290), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *seticornis* (Champion, 1884:67), **NEW COMBINATION**

*Pelecyphorus* (*Astrotus*) *undatus* (Champion, 1892:504), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *asidoides* Solier, 1836:471, **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *bibasalis* (Casey, 1912:128), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *cristatus* (Pallister 1954:24), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *esperanzae* (Wilke, 1922:271), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *dissimilis* (Champion, 1884:59), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *fallax* (Champion, 1884:57), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *favosus* (Champion, 1884:58), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *similatus* (Champion, 1884:58), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *foveolatus* Solier, 1836:472, **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *indutus* (Champion, 1884:56), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *laciniatus* (Casey, 1912:128), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *laticollis* (Champion, 1884:58), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *liratus* (LeConte, 1854:223), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *longipennis* (Champion, 1884:56), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *mixtecae* (Wilke, 1922:271), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *obliviosus* (Wilke, 1922:270), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *purpusi* (Wilke, 1922:271), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *planatulus* (Casey, 1912:129), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *scutellaris* (Champion, 1884:57), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *sexcostatus* LeConte, 1861:337, **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *similata* (Champion, 1884:58), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *spinimanus* (Champion, 1892:494), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *tenebrosus* (Champion, 1892:495), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *tolucanus* Casey, 1912:130), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *tristis* (Champion, 1884:55), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *trisinuatus* (Pallister, 1954:22), **NEW COMBINATION**

*Pelecyphorus* (*Plesiasida*) *zacualpanicolus* (Wilke, 1922:272), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *anastomosis* (Say, 1824:256), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *bicarinatus* (Champion, 1884:69), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *bisinuatus* (Pallister, 1954:13), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *breviuscula* (Casey, 1912:87), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *canus* (Champion, 1884:68), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *exoleta* (Casey, 1912:87), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *graciliformis* (Solier, 1836:486), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *hebes* (Champion, 1892:506), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *luteotecta* (Casey, 1912:88), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *kulzeri* (Pallister, 1954:12), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *monticola* (Casey, 1912:88), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *obtecta* (Casey, 1912:89), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *planatus* (Champion, 1884:69), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *sigillata* (Casey, 1912:89), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *sinuaticollis* (Champion, 1884:69), **NEW COMBINATION**

*Pelecyphorus* (*Stenosides*) *texanus* (Wickham, 1903:72), **NEW COMBINATION**

## ***Philolithus* Lacordaire**

*Philolithus* Lacordaire 1858:18; Lacordaire 1859:157. Type species: *Pelecyphorus carinatus* LeConte, 1851:128, by subsequent designation, Casey 1912:105.

subgenus *Glyptasida* Casey, 1912:95. Type species: *Pelecyphorus sordidus* LeConte 1853:445, by original designation . **Revised Status.**

subgenus *Gonasida* Casey, 1912:117. Type species: *Pelecyphorus elatus* LeConte 1853:445, by original designation. **Revised Status.**

subgenus *Herthasida* Wilke, 1922:69. Type species: *Asida ingens* Champion 1892:503, by monotypy. **Revised Status.**

subgenus *Philolithus* Lacordaire, 1858:18, *sensu stricto.*

subgenus *Tisamenes* Champion, 1884:64. Type species: *Tisamenes truquii* Champion 1884:64, by monotypy. **Revised Status**.

**Redescription (see fig. 1.15);** [modified from Brown 1971b]. Length 10.8-35.0mm, width 5.9-13.0. Integument black to ferruginous. **Head:** Nearly hypognathous. Mentum transversely hexagonal to broadly cordate, not or barely contacting postgena, not reaching mandibles, anterior margin medially notched. Ligula small, approximately one-fifth mentum width, straight and concealed beneath apical margin of mentum. Apical segment of maxillary palps enlarged and scalene, much larger in males with proximal angle acute and prolonged. Submentum raised, apex straight, width less than four-fifths buccal cavity width, laterally exposing maxillary cardos. Postgenal processes not or slightly produced, rounded or acute. Labral margin broadly emarginate; medially without setal brush; labral medial tormal process equal or shorter than posterior tormal process; clypeal membrane exposed or concealed. Clypeal margin nearly straight or broadly emarginate. Frons sculpturing variable; median depression absent or faintly impressed; frontoclypeal suture obscured or faintly impressed; small dorsal sulcus present above apices of eyes or lacking . Eyes elongate, broadly oval, not emarginate. Antenna weakly clavate and laterally flattened; antennal segment 10 subquadrate with two tomentose sensilla at lateral apices, outer sensillum usually divided in females; antennal segment 11 approximately one-half or less size of segment 10; apical tomentose sensilla on antennal segment 11 small, asymmetrical or not. **Prothorax:** Pronotal shape and sculpturing variable; pronotal margin costate, medially acutely expanded or not; anterior apicies slightly produced and rounded, posterior apicies obtuse or acute, not projecting over

elytral humera, posterior margin straight to slightly bisinuate. Prosternal process broad, laterally impressed between procoxa, declivous behind procoxae and often expanded at base. **Pterothorax:** Apterous. Scutellum triangular, gradually raised above scutum; mesonotum without tomentose depressions. Elytral sculpturing variable; marginal and discal costa present or absent; glabrous or with simple setae, usually inconspicuous, rarely long and forming a contrasting color pattern. Epipleura thin and indistinct. Metendosternite stem approximately as twice wide as tall. **Legs:** Black to ferruginous; Ferruginous to nearly black, tarsal formula 5-5-4; procoxae large, length greater than anterior prosternal length, pro- and mesocoxae globular, metacoxae more transverse; mesocoxal cavities open, mesotrocantin large, exposed; protibial outer apical margin flared, forming a small setose spine; inner apical margin of protibia with two subequal spurs; tarsi venter with two lateral rows of stout spiniform setae, medially glabrous. **Abdomen:** Intercoxal process impressed around margin, rounded or truncate at apex. Female apical coxites ventrally rounded; ten or more spermathecal branches present, serially arranged along one side of common duct to apex, largest near accessory gland and decreasing in size to apex; accessory gland long, with an enlarged chamber medially.

**Diagnosis.** *Philolithus* species are distinguished from members of all other asidine genera by a unique combination of the following characters: Mentum transversely hexagonal to broadly cordate with a small median notch apically; ligula small and concealed; postgenal process not or barely produced; eyes broadly oval and not emarginate; head nearly hypognathous, prosternal process declivious behind procoxa; apical maxillary palps large and scalene, much more expanded in males.

**Distribution.** *Philolithus* species occur from central Mexico to southern Canada, from the west coast to western Kansas.

**Discussion.** The genera now reduced to subgeneric status under *Philolithus* (*Glyptasida*, *Gonasida*, *Herthasida*, and *Tisamenes*) are differentiated almost entirely by homoplasious dorsal characters, particularly pronotal shape. Brown (1971b) noted that the genera shared many derived characters between them; including a reduction of the urogomphi in the larvae, which is so far unique within the tribe. Brown also noted that many of the *Philolithus* species described by Casey are likely to be synonymized when the genus is revised.

### ***Philolithus*** **Species Checklist**

*Philolithus* (*Philolithus*) *abscissus* (Casey, 1912:109)

*Philolithus* (*Philolithus*) *aegrotus* (LeConte, 1861:337)

*Philolithus* (*Philolithus*) *corporalis* (Casey, 1912:107)

*Philolithus* (*Philolithus*) *fumosus* (Casey, 1912:109)

*Philolithus* (*Philolithus*) *morbillosus* (LeConte, 1858b:74)

*Philolithus* (*Philolithus*) *parvus* (Casey, 1912:110)

*Philolithus* (*Philolithus*) *piceus* (Casey, 1912:111)

*Philolithus* (*Philolithus*) *reptans* (Casey, 1912:108)

*Philolithus* (*Philolithus*) *snowi* (Casey, 1912:108)

*Philolithus* (*Philolithus*) *socer* (Casey, 1912:108)

*Philolithus* (*Philolithus*) *subtenuis* (Casey, 1912:112)

*Philolithus* (*Philolithus*) *carinatus* (LeConte, 1851:128)

*Philolithus* (*Philolithus*) *quadripennis* (Casey, 1912:113)

*Philolithus* (*Philolithus*) *sophistes* (Casey, 1912:113)

*Philolithus* (*Philolithus*) *actuosus* (Horn, 1870:284)

*Philolithus* (*Philolithus*) *adversus* (Casey, 1912:114)

*Philolithus* (*Philolithus*) *corrosus* (Casey, 1912:117)

*Philolithus* (*Philolithus*) *densicollis* (Horn, 1894:417)

*Philolithus* (*Philolithus*) *haruspex* (Casey, 1912:115)

*Philolithus* (*Philolithus*) *jaegeri* (Papp, 1961a:107)

*Philolithus* (*Philolithus*) *opimus* (Casey, 1912:115)

*Philolithus* (*Philolithus*) *pantex* (Casey, 1912:116)

*Philolithus* (*Philolithus*) *porcatus* (Papp, 1961b:109)

*Philolithus* (*Philolithus*) *reflexus* (Casey, 1912:114)

*Philolithus* (*Philolithus*) *rugosus* (Papp, 1961a:157)

*Philolithus* (*Philolithus*) *uteanus* (Casey, 1924:308)

*Philolithus* (*Glyptasida*) *aegra* (LeConte, 1858:19), **NEW COMBINATION**

*Philolithus* (*Glyptasida*) *rugosissima* (Champion, 1884:53), **NEW COMBINATION**

*Philolithus* (*Glyptasida*) *sordida* (LeConte, 1853:445), **NEW COMBINATION**

*Philolithus* (*Gonasida*) *alaticollis* (Casey, 1912:122), **NEW COMBINATION**

*Philolithus* (*Gonasida*) *aucta* (Casey, 1912:122), **NEW COMBINATION**

*Philolithus* (*Gonasida*) *compar* (Casy, 1912:120), **NEW COMBINATION**

*Philolithus* (*Gonasida*) *elata* (LeConte, 1853:445), **NEW COMBINATION**

*Philolithus* (*Gonasida*) *inferna* (Casey, 1912:119), **NEW COMBINATION**

*Philolithus* (*Gonasida*) *gravida* (Casey, 1912:119), **NEW COMBINATION**

*Philolithus* (*Herthasida*) *ingens* (Champion, 1892:503), **NEW COMBINATION**

*Philolithus* (*Tisamenes*) *truquii* (Champion 1884:64), **NEW COMBINATION**

## ***Stenomorpha*** **Solier**

*Stenomorpha* Solier 1836:487. Type species: *Stenomorpha costata* Solier 1836:490 (MNHN), by subsequent designation, Casey 1912:78.

subgenus *Asidina* Casey 1912:169. Type species: *Pelecyphorus parallela* LeConte, 1851:128, by original designation. **Revised Status**.

subgenus *Asidopsis* Casey 1912:185. Type species: *Asida opaca* Say, 1824:254, by original designation. **Revised Status**.

subgenus *Bothrasida* Casey 1912:122. Type species: *Asida clathrata* Champion, 1884:54, by original designation. **Revised Status**.

subgenus *Megasida* Casey 1912:202. Type species: *Asida obliterata* Champion, 1892:497, by original designation. **Revised Status**.

subgenus *Notiasida* Casey 1912:124. Type species: *Notiasida abstrusa* Casey, 1912:125, by original designation. **Revised Status**.

subgenus *Platasida* Casey 1912:182. Type species: *Asida embaphionides* Horn, 1894:419, by original designation. **Revised Status**.

subgenus *Pycnomorpha* Motschulsky 1870:398. Type species: *Pycnomorpha californica* Motschulsky 1870: 399, by monotypy. **Revised Status**.

subgenus *Stenomorpha* Solier 1836:487, *sensu stricto*.

subgenus *Stethasida* Casey 1912:203. Type species: *Pelecyphorus muricatulus* LeConte 1851:129, by original designation. **Revised Status**.

subgenus *Trichiasida* Casey 1912:172. Type species: *Pelecyphorus hirsutus* LeConte 1851:127, by original designation. **Revised Status**.

**Redescription (see fig. 1.16).** Length: 9.4-27.0 mm, width: 4.6-14.9 mm; integument ferruginous to black; body obovate to elongate and nearly parallel sided; generally glaberous or setae inconspicous, occasionally setose; setae simple or, rarely, lanceolate in shape. **Head:** Mentum variable, trapezoidal to cordate; laterally reaching postgena or not, never contacting mandibles when closed; lateral margins straight or curved outward at apicies; anterior margin emarginate medially. Ligula; sclerotized, prominent and tumid; width one-fourth or more mentum width, length approximately 3X width; strongly curved or notched and raised above anterior margin of mentum. Apical segment of maxillary palps enlarged, isotriangular to scalene in shape, more expanded in males.

Submentum distinctly projecting into buccal cavity; width four-fifths or less that of buccal cavity, completely or partially exposing maxillary cardos laterally. Postgena exposing mandibular protuberance; postgenal processes not or slightly produced, extending to middle of mentum or less, acute to broadly rounded. Labral margin broadly emarginate, medially without setal brush; length of medial tormal process of labrum variable, greater to less than posterior tormal process length; clypeal membrane exposed or rarely concealed; clypeal margin broadly emarginate. Eyes elongate, oval or reniform; median depression on frons absent or faintly indicated. Antenna weakly clavate, laterally flattened or not, segments 8-11 always flattened; length of segment 3 2.5X or more width; tomentose sensilla absent on antennal segment 9; apical tomentose sensilla present on antennal segment 10, separated into two patches at lateral apices or meeting on one side; antennal segment 11 one-third size of segment 10 to nearly equal, apical tomentose sensillum covering one-third or more of segment. **Prothorax:** Pronotal shape and sculpturing variable, with or without a median costa or paramedial fossae, lacking paramedial basal gibbosities; pronotal margin costate, medially acutely expanded or not; anterior apicies produced, acute or rounded, posterior apicies obtuse or acute, projecting over elytral humera or not; posterior margin straight, slightly convex, or weakly bisinuate, often with a medial tooth projecting posterad. Prosternal process declivious behind procoxae, rarely raised and projecting behind procoxal cavities. **Pterothorax:** Apterous. Scutellum triangular, visible or mostly concealed underneath elytra, gradually raised above scutum; mesonotum with two rounded paramedial depressions, shallow or deep. Elytral sculpturing variable, discal and marginal costae present or absent; epipleura indistinct. Metendosternite stem approximately as wide as tall. **Legs:** Ferruginous to

nearly black, tarsal formula 5-5-4; pro- and mesocoxae globular, metacoxae more transverse; mesocoxal cavities open or externally closed by sternites; mesotrocantin large and exposed; protibia with outer apical margin forming a spine; protibial outer lateral margin not carinate; inner apical margin of protibia with two subequal spurs. **Abdomen:** Intercoxal process impressed around margin or not, rounded or truncate at apex. Female apical coxites ventrally rounded; eight or more spermathecal branches present, serially arranged along one side of common duct to apex or rarely emerging only from the apex; accessory gland long, with an enlarged chamber medially.

**Diagnosis.** *Stenomorpha* is distinguished from all other asidine genera by a unique combination of the following characters: Ligula large and tumid, width one-fourth or more mentum width, length approximately 3X width; strongly curved or notched and raised above anterior margin of mentum. Scutellum raised above scutum; mesonotum with two faint or deep rounded depressions. Protibial spurs subequal. Mesotrocantin large and exposed.

**Distribution.** *Stenomorpha* species occur from central Mexico to southern Canada, from the west coast to western Kansas, Nebraska, etc.

## *Stenomorpha* Species Checklist

*Stenomorpha* (*Stenomorpha*) *advena* (Casey, 1912:143)

*Stenomorpha* (*Stenomorpha*) *amplicollis* (Casey, 1912:153)

*Stenomorpha* (*Stenomorpha*) *angulata* (LeConte, 1851:127)

*Stenomorpha* (*Stenomorpha*) *blanda (*Champion, 1884:63)

*Stenomorpha* (*Stenomorpha*) *blapsoides* Solier, 1836:491

*Stenomorpha* (*Stenomorpha*) *brevimargo* (Casey, 1912:134)

*Stenomorpha* (*Stenomorpha*) *caliginosus* (Casey, 1912:137)

*Stenomorpha* (*Stenomorpha*) *captiosa* (Horn, 1870:287)

*Stenomorpha* (*Stenomorpha*) *clarissae* (Wilke, 1821:273)

*Stenomorpha* (*Stenomorpha*) *compressa* (Horn, 1870:287)

*Stenomorpha* (*Stenomorpha*) *congruens* (Casey, 1912:164)

*Stenomorpha* (*Stenomorpha*) *consobrina* (Horn, 1870:287)

*Stenomorpha* (*Stenomorpha*) *consors* (Casey, 1912:162)

*Stenomorpha* (*Stenomorpha*) *consueta* (Casey, 1912:161)

*Stenomorpha* (*Stenomorpha*) *convexa* (LeConte, 1859:14)

*Stenomorpha* (*Stenomorpha*) *convexicollis* (LeConte, 1854:223)

*Stenomorpha* (*Stenomorpha*) *corrugans* (Casey, 1912:143)

*Stenomorpha* (*Stenomorpha*) *costata* Solier, 1836:490

*Stenomorpha* (*Stenomorpha*) *costipennis* (LeConte, 1859:76)

*Stenomorpha* (*Stenomorpha*) *crassa* (Casey, 1912:154)

*Stenomorpha* (*Stenomorpha*) *cressoni* (Blaisdell, 1933:191)

*Stenomorpha* (*Stenomorpha*) *cribratus* (Casey, 1912:140)

*Stenomorpha* (*Stenomorpha*) *crinita* (Casey, 1912:148)

*Stenomorpha* (*Stenomorpha*) *deceptor* (Casey, 1912:154)

*Stenomorpha* (*Stenomorpha*) *directa* (Casey, 1912:141)

*Stenomorpha* (*Stenomorpha*) *evanescens* (Casey, 1912:146)

*Stenomorpha* (*Stenomorpha*) *facilis* (Casey, 1912:165)

*Stenomorpha* (*Stenomorpha*) *fastigiosa* (Casey, 1912:157)

*Stenomorpha* (*Stenomorpha*) *globicollis* (Casey, 1912:158)

*Stenomorpha* (*Stenomorpha*) *gracilior* (Casey, 1912:160)

*Stenomorpha* (*Stenomorpha*) *gravidipes* (Casey, 1912:155)

*Stenomorpha* (*Stenomorpha*) *huachucae* (Casey, 1912:162)

*Stenomorpha* (*Stenomorpha*) *inhabilis* (Casey, 1912:156)

*Stenomorpha* (*Stenomorpha*) *integer* (Casey, 1912:153)

*Stenomorpha* (*Stenomorpha*) *lecontei* (Horn 1866:12)

*Stenomorpha* (*Stenomorpha*) *lecontella* (Blaisdell 1936:227)

*Stenomorpha* (*Stenomorpha*) *luctata* (Horn, 1870:286)

*Stenomorpha* (*Stenomorpha*) *marginata* (LeConte, 1851:128)

*Stenomorpha* (*Stenomorpha*) *maritima* (Casey, 1912:151)

*Stenomorpha* (*Stenomorpha*) *mckittricki* (Pierce, 1954)

*Stenomorpha* (*Stenomorpha*) *montezuma* (Wilke, 1921:272)

*Stenomorpha* (*Stenomorpha*) *musiva* (Wilke, 1921:273)

*Stenomorpha* (*Stenomorpha*) *neutralis* (Casey, 1912:146)

*Stenomorpha* (*Stenomorpha*) *oblonga* (Casey, 1924:309)

*Stenomorpha* (*Stenomorpha*) *obovata* (LeConte, 1851:127)

*Stenomorpha* (*Stenomorpha*) *oregonensis* (Casey, 1924:309)

*Stenomorpha* (*Stenomorpha*) *orizabae* (Wilke, 1921:273)

*Stenomorpha* (*Stenomorpha*) *papagoana* (Casey, 1912:163)

*Stenomorpha* (*Stenomorpha*) *pollens* (Casey, 1912:134)

*Stenomorpha* (*Stenomorpha*) *procurrens* (Casey, 1912:137)

*Stenomorpha* (*Stenomorpha*) *puncticollis* (LeConte, 1866:111)

*Stenomorpha* (*Stenomorpha*) *rimata* (LeConte, 1854:223)

*Stenomorpha* (*Stenomorpha*) *rudis* (Casey, 1912:139)

*Stenomorpha* (*Stenomorpha*) *rugata* (Casey, 1912:138)

*Stenomorpha* (*Stenomorpha*) *rustica* (Casey, 1912:135)

*Stenomorpha* (*Stenomorpha*) *satiata* (Casey, 1912:138)

*Stenomorpha* (*Stenomorpha*) *semirufa* (Casey, 1912:140)

*Stenomorpha* (*Stenomorpha*) *severa* (Casey, 1912:144)

*Stenomorpha* (*Stenomorpha*) *socialis* (Casey, 1912:162)

*Stenomorpha* (*Stenomorpha*) *speculatus* (Blaisdell, 1936:225)

*Stenomorpha* (*Stenomorpha*) *sponsor* (Casey, 1912:135)

*Stenomorpha* (*Stenomorpha*) *spurcans* (Casey, 1912:145)

*Stenomorpha* (*Stenomorpha*) *strigulosa* (Casey, 1912:163)

*Stenomorpha* (*Stenomorpha*) *subcruenta* (Casey, 1912:140)

*Stenomorpha* (*Stenomorpha*) *subcylindrica* (Horn, 1870:288)

*Stenomorpha* (*Stenomorpha*) *subelegans* (Casey, 1912:152)

*Stenomorpha* (*Stenomorpha*) *tetrica* (Casey, 1912:149)

*Stenomorpha* (*Stenomorpha*) *tularensis* (Casey, 1912:152)

*Stenomorpha* (*Stenomorpha*) *uhdei* (Wilke, 1921:273)

*Stenomorpha* (*Stenomorpha*) *umbrosa* (Champion 1884:62)

*Stenomorpha* (*Stenomorpha*) *vigens* (Casey 1912:159)

*Stenomorpha* (*Asidina*) *confluens* (LeConte, 1851:128), **NEW COMBINATION**

*Stenomorpha* (*Asidina*) *furcata* (Champion, 1892:499), **NEW COMBINATION**

*Stenomorpha* (*Asidina*) *parallela* (LeConte, 1851:128), **NEW COMBINATION**

*Stenomorpha* (*Asidina*) *rugicollis* (Triplehorn and Brown, 1971:76), **NEW COMBINATION**

*Stenomorpha* (*Asidina*) *semilaevis* (Horn, 1870:284), **NEW COMBINATION**

*Stenomorpha* (*Asidina*) *wickhami* (Horn, 1894:420), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *abbreviata* (Casey, 1912:198), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *cochisensis* (Casey, 1912:188), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *coenosa* (Casey, 1912:199), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *collega* (Casey, 1912:198), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *consentanea* (Casey 1912:192), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *divaricata* (Blaisdell 1923:255), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *dolosa* (Casey 1912:194), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *durangoensis* (Casey 1912:201), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *eximia* (Casey 1912:187), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *gracilipes* (Casey 1912:189), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *humeralis* (Triplehorn and Flores 2002:288), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *immunda* (Casey 1912:199), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *macra* (Horn) 1882:304), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *mancipata* (Horn) 1878:56), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *collaris* (Champion, 1892:499), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *nitidula* (Casey, 1912:196), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *obsidiana* (Casey, 1912:193), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *olsoni* (Triplehorn and Flores, 2002:286), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *opaca* (Say, 1824:254), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *pinalica* (Casey, 1912:190), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *planata* (Horn, 1894:415), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *polita* (Say, 1824:255), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *quadricollis* (Horn, 1880:151), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *servilis* (Casey, 1912:193), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *suavis* (Casey, 1912:189), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *tensa* (Casey, 1912:197), **NEW COMBINATION**

*Stenomorpha* (*Asidopsis*) *woodgatei* (Casey, 1912:197), **NEW COMBINATION**

*Stenomorpha* (*Bothrasida*) *baroni* (Casey 1912:124), **NEW COMBINATION**

*Stenomorpha* (*Bothrasida*) *clathrata* (Champion) 1884:54 (Casey, 1912:76), **NEW COMBINATION**

*Stenomorpha* (*Bothrasida*) *funesta* (Champion, 1884:53), **NEW COMBINATION**

*Stenomorpha* (*Bothrasida*) *mucorea* (Wilke 1922:270), **NEW COMBINATION**

*Stenomorpha* (*Bothrasida*) *sanctae-agnae* (Wilke, 1922:270), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *foeda* (Champion, 1892:498), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *latissima* (Champion, 1892:500), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *magnifica* (Pallister, 1954:30), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *moricoides* (Champion, 1892:497), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *obliterata* (Champion, 1892:497), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *rufipes* (Champion, 1884:62), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *segregata* (Champion, 1892:497), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *tarda* (Champion, 1892:498), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *tenuicollis* (Triplehorn, 1967:40), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *zacatecensis* (Pallister, 1954:32), **NEW COMBINATION**

*Stenomorpha* (*Megasida*) *tenebrosa* (Champion, 1892:495), **NEW COMBINATION**

*Stenomorpha* (*Notiasida*) *abstrusa* (Casey, 1912:125), **NEW COMBINATION**

*Stenomorpha* (*Notiasida*) *evertissima* (Casey, 1912:125), **NEW COMBINATION**

*Stenomorpha* (*Notiasida*) *intricata* (Champion, 1892:493), **NEW COMBINATION**

*Stenomorpha* (*Notiasida*) *lata* (Champion, 1884:60), **NEW COMBINATION**

*Stenomorpha* (*Notiasida*) *lugubris* (Wilke, 1922:269), **NEW COMBINATION**

*Stenomorpha* (*Notiasida*) *geminata* (Champion, 1892:492), **NEW COMBINATION**

*Stenomorpha* (*Notiasida*) *suturalis* (Champion, 1884:55), **NEW COMBINATION**

*Stenomorpha* (*Platasida*) *embaphionides* (Horn, 1894:419), **NEW COMBINATION**

*Stenomorpha* (*Platasida*) *flaccida* (Horn, 1897:379), **NEW COMBINATION**

*Stenomorpha* (*Pycnomorpha*) *californica* (Motschulsky, 1870: 399), **NEW COMBINATION**

*Stenomorpha* (*Pycnomorpha*) *gibbicollis* (Horn, 1870: 288), **NEW COMBINATION**

*Stenomorpha* (*Pycnomorpha*) *tumidicollis* (Blaisdell, 1943: 226), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *adumbrata* (Casey, 1912:208), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *angustula* (Casey, 1890: 370), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *brevipes* (Casey, 1912:206), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *convergens* (Casey, 1912:207), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *discreta* (Casey, 1912:207), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *longula* (Casey, 1912:207), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *muricatula* (LeConte, 1851:129), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *obsoleta* (LeConte, 1851:128), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *occulta* (Casey, 1912:208), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *pertinax* (Casey, 1912:211), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *socors* (Casey, 1912:212), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *stricta* (Casey, 1912:210), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *tarsalis* (Casey, 1912:208), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *tenax* (Casey, 1912:213), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *torpida* (Casey, 1912:206), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *unica* (Casey, 1912:209), **NEW COMBINATION**

*Stenomorpha* (*Stethasida*) *vergrandis* (Casey, 1912:213), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *acerba* (Horn, 1878:56), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *difficilis* (Champion, 1884:61), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *duplex* (Casey, 1912:178), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *eremica* (Wilke, 1922:274), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *hirsuta* (LeConte, 1851:127), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *hispidula* (LeConte, 1851:127), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *horrida* (Champion, 1892:500), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *idahoensis* (Boddy, 1957:187), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *ignava* (Casey, 1912:180), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *impetrata* (Horn, 1894:418), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *impotens* (Casey, 1912:180), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *lineatopilosa* (Casey, 1912:175), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *lutulenta* (Doyen, 1988:225), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *palmeri* (Champion, 1884:59), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *pubescens* (Champion, 1884:61), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *subpilosa* Solier, 1836:490, **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *tenella* (Casey, 1912:177), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *thoracica* (Champion, 1884:62), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *unicostata* (Champion, 1892:501), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *villosa* (Champion, 1884:60), **NEW COMBINATION**

*Stenomorpha* (*Trichiasida*) *spinimana* (Champion, 1892:494), **NEW COMBINATION**

*Stenomorpha* (*incertae sedis*) *subvittata* (Horn, 1894:416), **NEW COMBINATION**

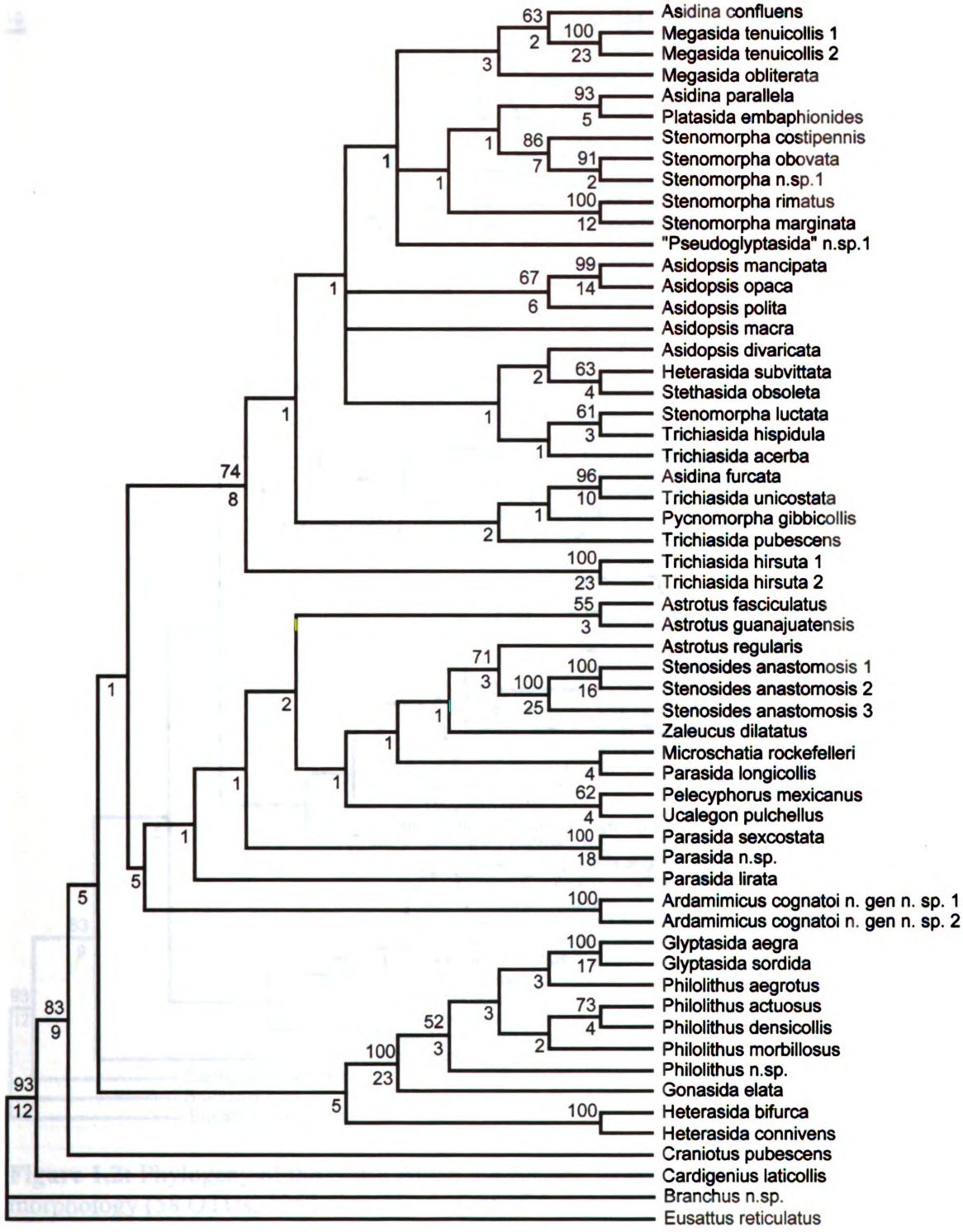


**Figure 1.1:** Phylogeny of the North American Asidini based on 28S, COI, and adult morphology (58 OTUs, 1252 characters). The strict consensus of four most parsimonious trees (L=3615, CI=0.22, RI=0.47) is shown bootstrap values above the branches and average partitioned Bremer support values below.

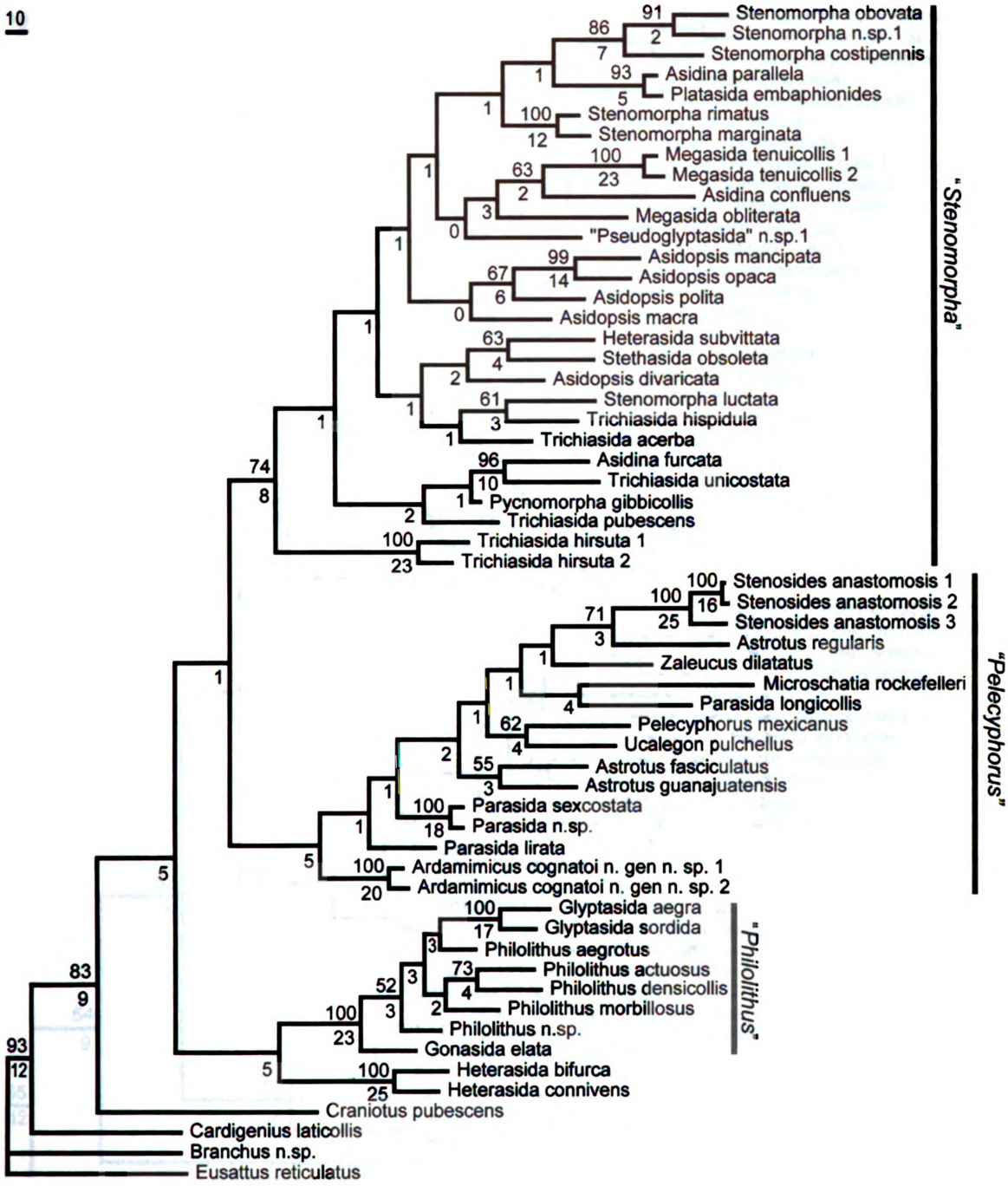


**Figure 1.2:** Phylogeny of the North American Asidini based on 28S, COI, and adult morphology (58 OTUs, 1252 characters). One of four most parsimonious trees (L=3615, CI=0.22, RI=0.47) is shown with bootstrap values above the branches and average partitioned Bremer support values below.

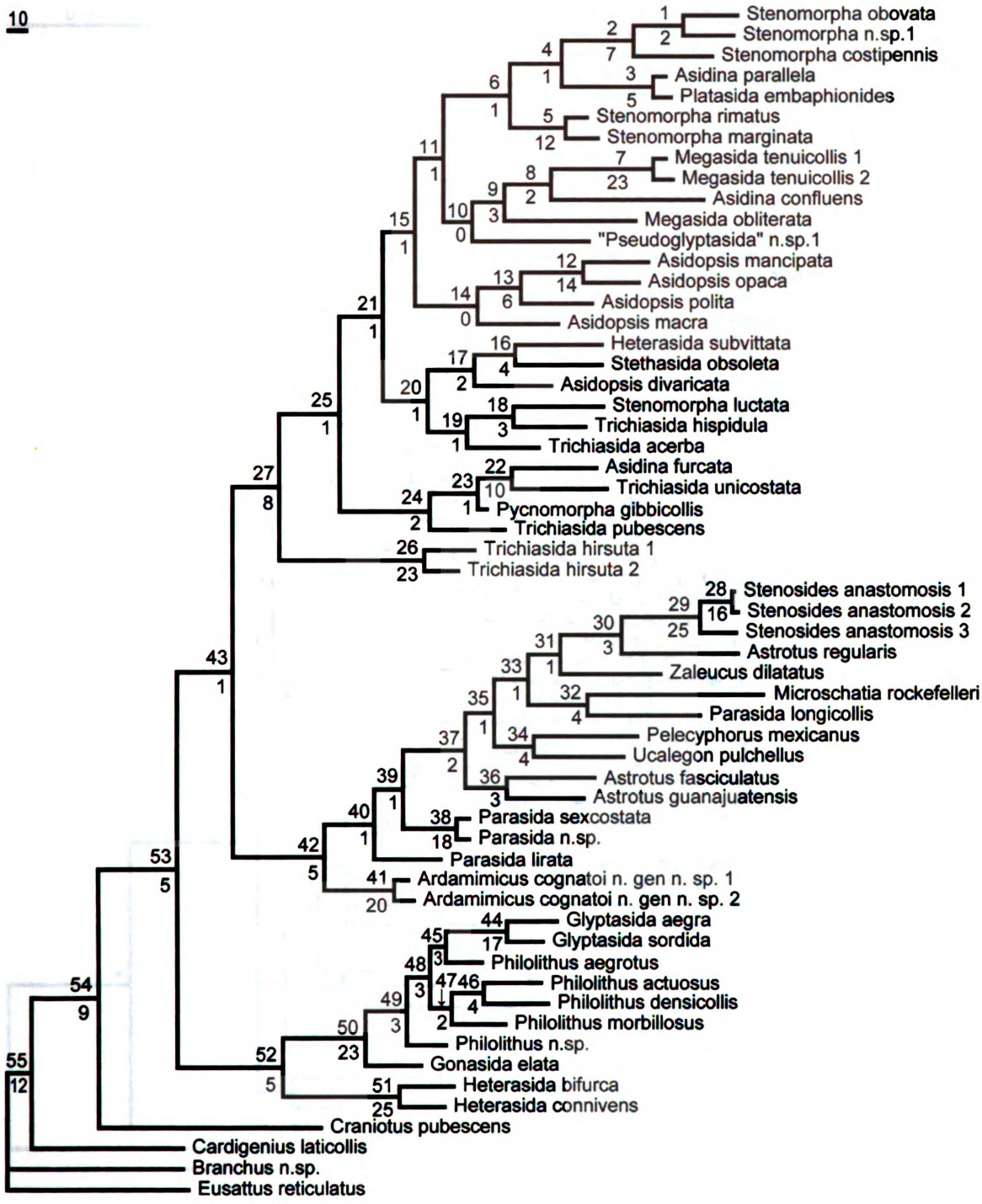


**Figure 1.3:** Phylogeny of the North American Asidini based on 28S, COI, and adult morphology (58 OTUs, 1252 characters). One of four most parsimonious trees (L=3615, CI=0.22, RI=0.47) is shown with node numbers above the branches and average partitioned Bremer support values below.

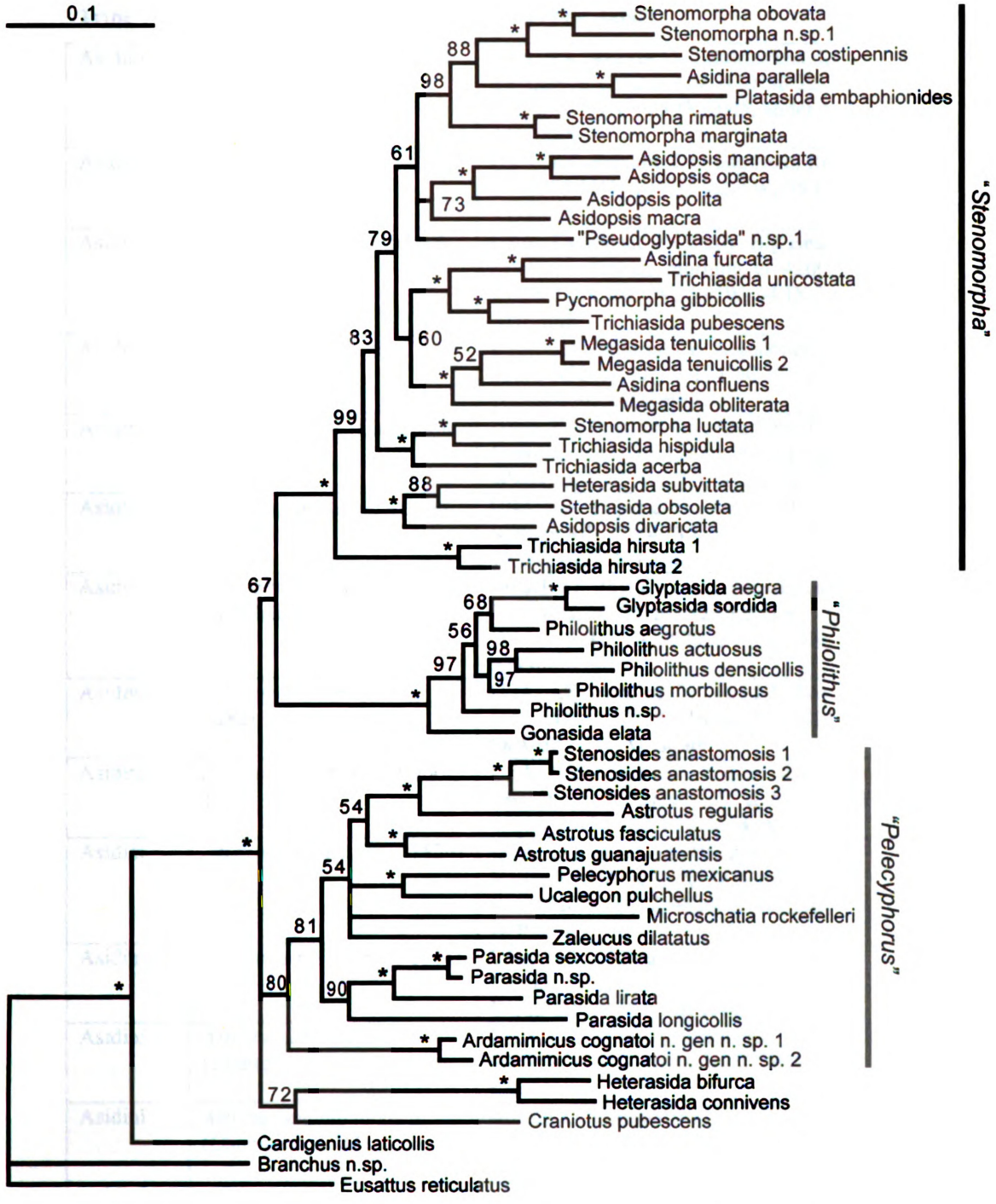


**Figure 1.4:** Phylogeny of the North American Asidini based on 28S, COI, and adult morphology (58 OTUs, 1252 characters). The Bayesian majority rule consensus tree is shown (GTR+I+Γ model; 6,000 sampled trees from 5,000,000 generations, -LogL = 16,269) with posterior probability values above the branches (* = 100% p.p.).

| Tribe | Species | Collection data |
|---|---|---|
| Asidini | *"Ardamimicus cognatoi"*; 1 | USA: TX: Reeves Co., Balmorhea, Lake Balmorhea Co. Rd. 319, N30°58'22.7", W102°33'01.1", 05.IX.2005, under rocks, ADSmith |
| Asidini | *"Ardamimicus cognatoi"*; 2 | USA: TX: Presidio Co., Big Bend Ranch SP, 29°32'58.80"N 104°10'7.23"W, 05.IX.2005, ADSmith |
| Asidini | *"Pseudoglyptasida" n.sp.1* | USA: TX: Presidio County, Big Bend Ranch SP, Cinco Tinajas, morning, el. 4200ft, 29°28'27"N 103°58'35.9"W, 04.IX.2005, ADSmith |
| Asidini | *Asidina confluens* (LeConte, 1851) | USA: CA: Imperial Co, Algodones dunes, el 300ft, N32°45'40", W114°46'29", dusk, 10.XII.2007, ADSmith |
| Asidini | *Asidina furcata* (Champion, 1892) | USA: TX: Presidio Co., Big Bend Ranch SP, Ojitro Adentro, el. 1281m, N29.4922 W104.0591, 25.V.2005, ADSmith |
| Asidini | *Asidina parallela* (LeConte, 1851) | USA: CA: Imperial Co, I-8 mm80, Moutain Springs Rd., 32°40'30.70"N 116° 6'1.51"W, 10.XII.2007, K.Kanda |
| Asidini | *Asidopsis divaricata* Blaisdell, 1923 | MEXICO: Baja Cal. Sur, San Miguel Comondú, el. 255m, N26°02.204' W111°49.91', BCS#20, 24.VII.2009, ADSmith |
| Asidini | *Asidopsis macra* (Horn, 1882) | USA: AZ: Cochise Co., 1mi NE Rustler Park, N31°54'54.1" W109°16'08.5", el. 8210', night, 08.VIII.2006, ADSmith |
| Asidini | *Asidopsis mancipata* (Horn, 1878) | USA: NM: Grant Co., Airport rd. off Hwy 180, 5mi S Hurley, el 5355 ft, N32°37'48" W108°08'22", 22.VIII.2006, ADSmith |
| Asidini | *Asidopsis opaca* (Say, 1824) | USA: CO: Weld Co., Pawnee NG, Crow Valley Rec. Area, N40°38'43.0" W104°20'34.2", el. 4834', 05.VIII.2006, ADSmith |
| Asidini | *Asidopsis polita* (Say, 1824) | USA: ND: Billings Co., Painted Canyon Center, under old cow dung, N46°53'42" W103°22'56", 03.VIII.2006, ADSmith |
| Asidini | *Astrotus fasciculatus* (Champion, 1892) | MEXICO: Morelos, Quilamula, N18°30'37.1" W99°00'10.7", 1167m, 20.V.2007, P. Cifuentes |
| Asidini | *Astrotus guanajuatensis* (Champion, 1884) | MEXICO: Guanajuato, Guanajuato, N21°00'12", W101°14'12", el. 3424', 20.V.2006, ADSmith |
| Asidini | *Astrotus regularis* Horn, 1870 | USA: TX: Val Verde Co., Seminole Cyn SP, under rocks, el. 1320 ft, N29°42'2" W101°18'42", 03.II.2006, ADSmith |

**Table 1.1 (continued on following pages):** Specimens sequenced and collecting data

| Tribe | Species | Collection data |
|---|---|---|
| Branchini | *Branchus* n.sp. 1 | GUATEMALA: El Progreso: San Agustin Acasaguatlán, Rancho El Limonar. 308m, N14°55.408 W90°02.406, 3.VII.2009; MJ Paulsen |
| Asidini | *Cardigenius laticollis* Solier, 1836 | ARGENTINA: Córdoba, Alpha Corral, Ea. Eloiea. 32°37'52"S 64°43'26"W. 1042m. 5-7/II/09. UV light. F.C. Ocampo, K. Sheldon |
| Asidini | *Craniotus pubescens* LeConte 1851 | USA: AZ: Pinal Co., rest area off I-8 mm151, 17.XII.2007, ADSmith |
| Coniontini | *Eusattus reticulatus* (Say, 1824) | USA: TX: El Paso Co., roadside I-10E mm46, 07.X.2005, ADSmith |
| Asidini | *Glyptasida aegra* (LeConte, 1858) | USA: TX: Presidio County, Big Bend Ranch SP, Cinco Tinajas, morning, el. 4200ft, 29°28'27"N 103°58'35.9"W, 25.V.2005, ADSmith |
| Asidini | *Glyptasida sordida* (LeConte, 1853) | USA: TX: El Paso Co., 2mi W Fabens, roadside I-10E, 22.VIII.2005, ADSmith |
| Asidini | *Gonasida elata* (LeConte, 1853) | USA: NM: Doña Ana Co., Jornada rd. 3mi N Hwy 70, N32°25'19" W106°43'36", on Pogonomyrmex nest, 03.X.2005, ADSmith |
| Asidini | *Heterasida bifurca* (LeConte, 1861) | MEXICO: Baja Cal. Sur, 22km NW of C.San Lucas, el. 30m, N23°01.538' W110°04.895', BCS#04, 21.VII.2009, ADSmith |
| Asidini | *Heterasida connivens* (LeConte, 1866) | MEXICO: Baja Cal. Sur, 12km E Todos Santos, el. 314m, N23°26.790' W110°06.31', BCS#37, 28.VII.2009, ADSmith |
| Asidini | *Heterasida subvittata* (Horn, 1894) | MEXICO: Baja Cal. Sur, Sier. de la Laguna trail, el 1573m, N23°32.78' W110°00.83',BCS#43, 28.VII.2009, ADSmith |
| Asidini | *Megasida obliterata* (Champion, 1892) | USA: TX: Culberson Co., 2mi E Van Horn off I-10E, 05.IX.2005, ADSmith |
| Asidini | *Megasida tenuicollis* Triplehorn, 1967; 1 | USA: TX: Brewster Co., roadside, 04.IX.2005, Jhulcr |
| Asidini | *Megasida tenuicollis* Triplehorn, 1967; 2 | USA: TX: Culberson Co., Guadalupe Mts, N31°53' W104°49', 20.VIII.2006, ADSmith |
| Asidini | *Microschatia rockefelleri* Pallister, 1954 | USA: TX: Hudspeth Co., Rest Area off I-10E mm 98, 31°12'47.9"N 105°29'37.1"W, el 4640ft, 13.VIII.2006, ADSmith |
| Asidini | *Parasida lirata* (LeConte, 1854) | USA: AZ: Pima County, Madera Canyon, Elephant Head trail, mid-afternoon, 31°44'21"N, 110°53'30"W, el. 4376ft, 13.VIII.2006, ADSmith |

**Table 1.1 (cont.):** Specimens sequenced and collecting data

| Tribe | Species | Collection data |
|---|---|---|
| Asidini | *Parasida longicollis* (Champion, 1884) | MEXICO: Puebla, Cacaloapan, elev. 6175', N18°34'44" W97°35'3"W, 11.VII.2008, ADSmith |
| Asidini | *Parasida sexcostata* (LeConte, 1861) | MEXICO: Baja Cal. Sur, 13km S of La Paz, el. 191m, N23°59.768' W110°16.24', BCS#12, 22.VII.2009, ADSmith |
| Asidini | *Parasida* n.sp. 1 | MEXICO: Baja Cal. Sur, Sier. de la Laguna trail, el 1573m, N23°32.78' W110°00.83',BCS#43, 28.VII.2009, ADSmith |
| Asidini | *Pelecyphorus mexicanus* Solier, 1836 | MEXICO: Puebla, Hwy150,3 km N Azumbilla, N18°39'58" W97°22'33", 10.VII.2008, ADSmith |
| Asidini | *Philolithus actuosus* (Horn, 1870) | USA: NV: Clark Co., Walking Box Cyn Rd., 35°29'56.67"N 115° 2'13.36"W, 15.XII.2007, ADSmith |
| Asidini | *Philolithus aegrotus* (LeConte, 1861) | MEXICO: Baja Cal. Sur, 52km W of La Paz, el. 265m, N24°09.164' W110°49.91', BCS#27, 25.VII.2009, ADSmith |
| Asidini | *Philolithus densicollis* (Horn, 1894) | USA: WA: Benton Co., Badger Cyn, nr Kennewick, N46°11'51" W119°21'59", 11X.2008, H. Lippold |
| Asidini | *Philolithus morbillosus* (LeConte, 1858) | USA: AZ: Cochise Co., Rest Area off I-10W mm 321, 32°03'41.5"N 110°04'40.7"W, el 4920ft, 03.X.2005, ADSmith |
| Asidini | *Philolithus* n.sp. 1 | MEXICO: Baja Cal. Norte, Sierra Libertad, El Rancho, 28.49060°N 113.59583°W, 1143m, 09.X.2009, William H. Clark, collector #12,270 |
| Asidini | *Platasida embaphionides* (Horn, 1894) | MEXICO: Baja Cal. Sur, 22km NW of C.San Lucas, el. 30m, N23°01.538' W110°04.895', BCS#04, 21.VII.2009, ADSmith |
| Asidini | *Pycnomorpha gibbicollis* (Horn, 1870) | MEXICO: Baja Cal. Sur, 4km W of La Paz, el. 29m, N24°08.525' W110°27.91', BCS#28, 25.VII.2009, ADSmith |
| Asidini | *Stenomorpha costipennis* (LeConte, 1859) | USA: CA: Kings Co., off Hwy 41, N35°56.8' W120°00.4', 08.III.2008, ADSmith |
| Asidini | *Stenomorpha luctata* (Horn, 1870) | USA: NV: Clark Co., Boulder City, Bootleg Cyn bike trail, 35°58'58.56"N 114°51'29.09"W, 16.XII.2007, ADSmith |
| Asidini | *Stenomorpha rimatus* (LeConte, 1854) | USA: AZ: Cochise Co., Rest Area off I-10W mm 321, 32°03'41.5"N 110°04'40.7"W, el 4920ft, 03.X.2005, ADSmith |
| Asidini | *Stenomorpha marginata* (LeConte, 1851) | Arizona: Pima County, Madera Canyon, Elephant Head trail, 31°44'21"N, 110°53'30"W, el. 4376ft, 05.X.2005, ADSmith |

**Table 1.1 (cont.):** Specimens sequenced and collecting data

| Tribe | Species | Collection data |
|---|---|---|
| Asidini | *Stenomorpha obovata* (LeConte, 1851) | USA: New Mexico: Luna County, Rest Area off I-10W mm61, at night, N32°13'29.4" W108°07'23.6", el. 4560ft, 21.VIII.2006, ADSmith |
| Asidini | *Stenomorpha* n.sp.1 | USA: NV: Clark Co., Boulder City, Bootleg Cyn bike trail, 35°58'58.56"N 114°51'29.09"W, 16.XII.2007, ADSmith |
| Asidini | *Stenosides anastomosis* (Say, 1824); 1 | USA: TX: Presidio Co., ZH Canyon, 11.7mi W Valentine, N30.5438 W104.6856, 19-23.V.2005, ADSmith |
| Asidini | *Stenosides anastomosis* (Say, 1824); 2 | USA: TX: Culberson Co., Guadalupe Mts, N31°53' W104°49', 20.VIII.2006, ADSmith |
| Asidini | *Stenosides anastomosis* (Say, 1824); 3 | USA: AZ: Graham County, Pinaleño Mnts, off Hwy 366, el.5220ft, N32°39'54.6" W109°47'45.5", 07.VI.2008, ADSmith |
| Asidini | *Stethasida obsoleta* (LeConte, 1851) | USA: CA: Riverside Co., Riverside, el. 721 ft, 33°58'5.13"N 117°25'24.84"W, 30.XII.2006, ADSmith |
| Asidini | *Trichiasida acerba* (Horn, 1878) | USA: NV: Clark Co., Warm Springs Rd., 36°43'04.23"N 114°43'04.74W, 16.XII.2007, ADSmith |
| Asidini | *Trichiasida hirsuta* (LeConte, 1851); 1 | USA: CA: Imperial Co, Algodones dunes, el 300ft, N32°45'40", W114°46'29", dusk, 10.XII.2007, ADSmith |
| Asidini | *Trichiasida hirsuta* (LeConte, 1851); 2 | USA: California: Riverside Co., Palm Desert, el 115ft, 33°46'19.46"N 116°18'25.72"W, 13.XII.2007, ADSmith |
| Asidini | *Trichiasida hispidula* (LeConte, 1851) | USA: CA: San Diego Co., Anza Borrega desert, N32°52.492' W116°13.100', 824ft KK09_03, 28-30.ii.2009 , K. Kanda |
| Asidini | *Trichiasida pubescens* (Champion, 1884) | MEXICO: Hidalgo, Pachuca, Hotel La Paz, el.~7800', walls at night, 08.VII.2008, ADSmith |
| Asidini | *Trichiasida unicostata* (Champion, 1892) | MEXICO: Guerrero, Jonathan Amith #592 |
| Asidini | *Ucalegon pulchellus* Champion, 1884 | MEXICO: Oaxaca, Yagul Ruins, el. ~5600', N16°57'32" W96°26'54", 12.VII.2008, ADSmith |
| Asidini | *Zaleucus dilatatus* (Champion, 1884) | MEXICO: Oaxaca, Hwy 190, ~53 km SE Huajuapan de Leon, N17°35'41" W97°26'5"W, 11.VII.2008, ADSmith |

**Table 1.1 (cont.):** Specimens sequenced and collecting data

| | Partition | | | |
|---|---|---|---|---|
| **Node** | **Morphology** | **COI** | **28S** | **Total** |
| 1 | 0.33 | 1.67 | 0.00 | 2 |
| 2 | 12.50 | -6.50 | 1.00 | 7 |
| 3 | 1.00 | 5.00 | -1.00 | 5 |
| 4 | -1.75 | 2.75 | 0.00 | 1 |
| 5 | 7.33 | 6.67 | -2.00 | 12 |
| 6 | -4.00 | 5.00 | 0.00 | 1 |
| 7 | 1.33 | 23.66 | -2.00 | 23 |
| 8 | 1.17 | 3.83 | -3.00 | 2 |
| 9 | 6.50 | -1.50 | -2.00 | 3 |
| 10 | 0.00 | 0.00 | 0.00 | 0 |
| 11 | -4.00 | 7.00 | -2.00 | 1 |
| 12 | 0.00 | 13.00 | 1.00 | 14 |
| 13 | -2.50 | 8.50 | 0.00 | 6 |
| 14 | 0.50 | -0.50 | 0.00 | 0 |
| 15 | -4.00 | 5.00 | 0.00 | 1 |
| 16 | 6.00 | -1.00 | -1.00 | 4 |
| 17 | 4.00 | -1.00 | -1.00 | 2 |
| 18 | 2.50 | -0.50 | 1.00 | 3 |

**Table 1.2 (cont. following pages):** Partitioned Bremer support values from TreeRot v.3

| | Partition | | | |
|---|---|---|---|---|
| **Node** | **Morphology** | **COI** | **28S** | **Total** |
| 19 | -4.00 | 5.67 | -0.67 | 1 |
| 20 | -4.00 | 5.67 | -0.67 | 1 |
| 21 | -3.50 | 5.00 | -0.50 | 1 |
| 22 | 4.00 | 5.00 | 1.00 | 10 |
| 23 | 0.43 | 2.43 | -1.86 | 1 |
| 24 | 2.00 | 0.00 | 0.00 | 2 |
| 25 | -4.00 | 5.00 | 0.00 | 1 |
| 26 | 13.33 | 6.67 | 3.00 | 23 |
| 27 | 4.00 | 5.00 | -1.00 | 8 |
| 28 | 0.50 | 18.75 | -3.25 | 16 |
| 29 | 9.00 | 14.00 | 2.00 | 25 |
| 30 | 9.00 | -7.00 | 1.00 | 3 |
| 31 | 12.75 | -9.75 | -2.00 | 1 |
| 32 | 0.53 | 2.18 | 1.29 | 4 |
| 33 | 8.50 | -6.50 | -1.00 | 1 |
| 34 | -3.50 | 8.50 | -1.00 | 4 |
| 35 | 12.75 | -9.75 | -2.00 | 1 |
| 36 | 9.00 | -7.00 | 1.00 | 3 |
| 37 | -1.50 | 2.50 | 1.00 | 2 |

**Table 1.2 (cont.):** Partitioned Bremer support values from TreeRot v.3

| | Partition | | | |
|---|---|---|---|---|
| **Node** | **Morphology** | **COI** | **28S** | **Total** |
| 38 | 2.50 | 15.00 | 0.50 | 18 |
| 39 | -4.00 | 5.67 | -0.67 | 1 |
| 40 | 12.25 | -9.25 | -2.00 | 1 |
| 41 | 3.60 | 16.40 | 0.00 | 20 |
| 42 | 0.00 | 1.00 | 4.00 | 5 |
| 43 | 6.71 | -4.57 | -1.14 | 1 |
| 44 | 17.25 | -1.25 | 1.00 | 17 |
| 45 | -0.95 | 3.90 | 0.05 | 3 |
| 46 | 19.00 | -16.00 | 1.00 | 4 |
| 47 | -1.00 | 1.00 | 2.00 | 2 |
| 48 | -0.58 | 4.42 | -0.83 | 3 |
| 49 | 10.67 | -8.67 | 1.00 | 3 |
| 50 | 1.00 | 14.00 | 8.00 | 23 |
| 51 | 26.00 | 1.00 | -2.00 | 25 |
| 52 | -0.80 | 3.40 | 2.40 | 5 |
| 53 | 2.00 | 2.00 | 1.00 | 5 |
| 54 | 0.00 | 1.00 | 8.00 | 9 |
| 55 | 19.50 | -11.50 | 4.00 | 12 |
| **Total** | **205.35** | **134.98** | **11.66** | **352** |

**Table 1.2 (cont.):** Partitioned Bremer support values from TreeRot v.3

| Clade | Parsimony (bootstrap / Bremer) | Bayesian (posterior probability %) |
|---|---|---|
| N. American Asidini | 83 / 9 | 100 |
| "*Stenomorpha*" | 74 / 8 | 100 |
| "*Philolithus*" | 100 / 23 | 100 |
| "*Pelecyphorus*" | < 50 / 5 | 80 |
| "*Pelecyphorus*" + "*Stenomorpha*" | < 50 / 1 | N/A |
| "*Philolithus*" + "*Stenomorpha*" | N/A | 67 |
| *H. bifurca* + *H. connivens* | 100 / 5 | 100 |
| "*Philolithus*" (*H. bifurca* + *H. connivens*) | < 50 / 5 | N/A |
| *Craniotus* (*H. bifurca* + *H. connivens*) | N/A | 72 |
| | | |

**Table 1.3:** Support for selected clades from parsimony and Bayesian analyses. Numbers represent bootstrap/Bremer supports for parsimony analysis or posterior probabilities for Bayesian analysis. N/A = not applicable or not found in the resulting tree(s)

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** |
| *Ardamimicus cognatoi* 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Ardamimicus cognatoi* 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Asidina confluens* | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 |
| *Asidina furcata* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 0 |
| *Asidina parallela* | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Asidopsis mancipata* | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Asidopsis polita* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Asidopsis opaca* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Asidopsis macra* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Asidopsis divaricata* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Astrotus fasciculatus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 9 | 1 | 1 | 2 | 3 | 1 | 1 | 2 | 0 | 0 |
| *Astrotus guanajuatensis* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 9 | 1 | 1 | 2 | 3 | 1 | 1 | 2 | 0 | 0 |
| *Astrotus regularis* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Branchus n.sp. 1* | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 6 | 4 | 1 | 1 | 1 | 0 | 3 | 4 | 0 | 0 |
| *Cardigenius laticollis* | 1 | 0 | 1 | 3 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 6 | 4 | 0 | 1 | 2 | 0 | 3 | 1 | 1 | 0 |
| *Craniotus pubescens* | 2 | 0 | 1 | 3 | 1 | 0 | 0 | 2 | 3 | 1 | 1 | 1 | 0 | 2 | 0 | 3 | 2 | 1 | 0 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Eusattus reticulatus* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 6 | 4 | 1 | 1 | 1 | 0 | 3 | 4 | 1 | 0 |
| *Glyptasida aegra* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 3 | 4 | 1 | 2 | 0 | 1 | 0 |
| *Glyptasida sordida* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 3 | 4 | 1 | 2 | 0 | 1 | 0 |

**Table 1.4 (continued on following pages):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** |
| *Gonasida elata* | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 3 | 4 | 1 | 2 | 1 | 1 | 0 |
| *Heterasida bifurca* | 1 | 0 | 1 | 3 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 0 | 0 |
| *Heterasida connivens* | 1 | 0 | 1 | 3 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 0 | 0 |
| *Heterasida subvittata* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Megasida obliterata* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 |
| *Megasida tenuicollis* 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 |
| *Megasida tenuicollis* 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 |
| *Microschatia rockefelleri* | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 3 | 1 | 0 | 1 | 0 | 1 | 8 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 0 |
| *Parasida lirata* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 9 | 1 | 1 | 2 | 3 | 1 | 2 | 2 | 1 | 0 |
| *Parasida longicollis* | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 9 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 0 | 0 |
| *Parasida sexcostata* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 9 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 0 | 0 |
| *Parasida* n.sp. 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 0 | 1 | 1 | 0 | 9 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 0 | 0 |
| *Pelecyphorus mexicanus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 9 | 1 | 1 | 2 | 3 | 1 | 1 | 1 | 0 | 0 |
| *"Pseudoglyptasida" n.sp.*1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Philolithus actuosus* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | ? | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 4 | 1 | 2 | 0 | 1 | 0 |
| *Philolithus aegrotus* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 4 | 1 | 2 | 0 | 1 | 0 |
| *Philolithus densicollis* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 2 | 4 | 1 | 2 | 0 | 1 | 0 |
| *Philolithus morbillosus* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 4 | 1 | 2 | 0 | 1 | 0 |
| *Philolithus* n.sp. 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 4 | 1 | 2 | 0 | 1 | 0 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** |
| *Platasida embaphionides* | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | ? | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Pycnomorpha gibbicollis* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 0 |
| *Stenomorpha costipennis* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Stenomorpha rimatus* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 4 | 1 | 2 | 1 | 1 | 0 |
| *Stenomorpha marginata* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 4 | 1 | 2 | 1 | 1 | 0 |
| *Stenomorpha luctata* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Stenomorpha obovata* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 3 | 4 | 1 | 2 | 1 | 1 | 0 |
| *Stenomorpha* n.sp.1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | ? | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3/4 | 1 | 2 | 1 | 1 | 0 |
| *Stenosides anastomosis* 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 0 |
| *Stenosides anastomosis* 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 0 |
| *Stenosides anastomosis* 3 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 5 | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 0 |
| *Stethasida obsoleta* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 0 |
| *Trichiasida acerba* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Trichiasida hirsuta* 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Trichiasida hirsuta* 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Trichiasida hispidula* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 |
| *Trichiasida pubescens* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 0 |
| *Trichiasida unicostata* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 4 | 2 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 0 |
| *Ucalegon pulchellus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 9 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 0 | 0 |
| *Zaleucus dilatatus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 9 | 1 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 1 |

**Table 1.4 (cont.):** Morphological character matrix of 43 characters for 73 species. Characters are their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **26** | **27** | **28** | **29** | **30** | **31** | **32** | **33** | **34** | **35** | **36** | **37** | **38** | **39** | **40** | **41** | **42** | **43** | **44** | **45** | **46** | **47** | **48** | **49** | **50** |
| *Ardamimicus cognatoi* 1 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| *Ardamimicus cognatoi* 2 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| *Asidina confluens* | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Asidina furcata* | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 |
| *Asidina parallela* | 4 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Asidopsis mancipata* | 4 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| *Asidopsis polita* | 4 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 1 | 0 |
| *Asidopsis opaca* | 4 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| *Asidopsis macra* | 3 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| *Asidopsis divaricata* | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| *Astrotus fasciculatus* | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 4 | 0 | 0 | 2 | 1 | 0 | 1 | 2 | 2 | 0 | 0 | 1 | 0 |
| *Astrotus guanajuatensis* | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 0 | 0 | 1 | 0 |
| *Astrotus regularis* | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 4 | 0 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 0 | 0 | 1 | 0 |
| *Branchus n.sp. 1* | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 |
| *Cardigenius laticollis* | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Craniotus pubescens* | 0 | 2 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Eusattus reticulatus* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 0 |
| *Glyptasida aegra* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Glyptasida sordida* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| Species | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 |
| *Gonasida elata* | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 1 | 0 | 1 | 1 |
| *Heterasida bifurca* | 2 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Heterasida connivens* | 2 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 4 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Heterasida subvittata* | 3 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Megasida obliterata* | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Megasida tenuicollis* 1 | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Megasida tenuicollis* 2 | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Microschatia rockefelleri* | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 |
| *Parasida lirata* | 2 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 2 | 4 | 0 | 0 | 2 | 1 | 0 | 1 | 3 | 0 | 1 | 0 | 1 | 0 |
| *Parasida longicollis* | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Parasida sexcostata* | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| *Parasida* n.sp. 1 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Pelecyphorus mexicanus* | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 1 | 0 |
| *"Pseudoglyptasida" n.sp.*1 | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 1 | 0 |
| *Philolithus actuosus* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Philolithus aegrotus* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Philolithus densicollis* | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Philolithus morbillosus* | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Philolithus* n.sp. 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **26** | **27** | **28** | **29** | **30** | **31** | **32** | **33** | **34** | **35** | **36** | **37** | **38** | **39** | **40** | **41** | **42** | **43** | **44** | **45** | **46** | **47** | **48** | **49** | **50** |
| *Platasida embaphionides* | 4 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| ***Pycnomorpha gibbicollis*** | **3** | **2** | **0** | **0** | **1** | **0** | **0** | **0** | **0** | **0** | **2** | **2** | **3** | **1** | **0** | **0** | **0** | **0** | **0** | **1** | **0** | **0** | **0** | **1** | **0** |
| ***Stenomorpha costipennis*** | 4 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| ***Stenomorpha rimatus*** | 2 | 1/2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| ***Stenomorpha marginata*** | 2 | 1/2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| ***Stenomorpha luctata*** | **0** | **2** | **1** | **0** | **1** | **0** | **0** | **0** | **0** | **0** | **1** | **1** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **3** | **0** | **1** | **0** | **1** | **0** |
| ***Stenomorpha obovata*** | 4 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| ***Stenomorpha*** n.sp.1 | 4 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | ? | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| ***Stenosides anastomosis*** 1 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| ***Stenosides anastomosis*** 2 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| ***Stenosides anastomosis*** 3 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| ***Stethasida obsoleta*** | 4 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 1 | 0 |
| ***Trichiasida acerba*** | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| ***Trichiasida hirsuta*** 1 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| ***Trichiasida hirsuta*** 2 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| ***Trichiasida hispidula*** | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 |
| ***Trichiasida pubescens*** | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 |
| ***Trichiasida unicostata*** | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 |
| ***Ucalegon pulchellus*** | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 |
| ***Zaleucus dilatatus*** | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **51** | **52** | **53** | **54** | **55** | **56** | **57** | **58** | **59** | **60** | **61** | **62** | **63** | **64** | **65** | **66** | **67** | **68** | **69** | **70** | **71** | **72** | **73** | **74** | **75** |
| *Ardamimicus cognatoi* 1 | 0 | 3 | 0 | 1 | 1 | 1 | 5 | 3 | 3 | 0 | 1 | 0 | 1 | 1 | **0** | 0 | 3 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Ardamimicus cognatoi* 2 | 0 | 3 | 0 | 1 | 1 | 1 | 5 | 3 | 3 | 0 | 1 | 0 | 1 | 1 | **0** | 0 | 3 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Asidina confluens* | 0 | 1 | 0 | 0 | 1 | 1 | 7 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | **0** | **0** | **2** | **0** | **0** | **0** | **1** | **1** | **0** | **0** | **0** |
| *Asidina furcata* | 1 | 1 | 0 | 1 | 1 | 1 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | **0** | **0** | **2** | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Asidina parallela* | 0 | 0 | 0 | 1 | 1 | 1 | 6 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | **0** | **0** | **2** | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Asidopsis mancipata* | 1 | 0 | 0 | 0 | 1 | 1 | 7 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | **0** | **0** | **2** | 3 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |
| *Asidopsis polita* | 0 | 0 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | **0** | **0** | **0** | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Asidopsis opaca* | 1 | 0 | 0 | 0 | 1 | 1 | 7 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | **0** | **0** | **1** | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| ***Asidopsis macra*** | **0** | 3 | **0** | **0** | **1** | **1** | **7** | **0** | **2** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| ***Asidopsis divaricata*** | **0** | 3 | **0** | **0** | **1** | **1** | 6 | **0** | **1** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| ***Astrotus fasciculatus*** | **0** | **1** | **0** | **1** | **1** | **0** | **2** | **1** | **4** | **0** | **1** | **2** | **1** | **0** | **0** | 0 | **3** | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| ***Astrotus guanajuatensis*** | 0 | **1** | **0** | **1** | **1** | **0** | **2** | **1** | **4** | **0** | **1** | **2** | **1** | **0** | **0** | **0** | **3** | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| ***Astrotus regularis*** | 1 | 2 | 1 | 1 | 1 | 0 | 9 | 1 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| ***Branchus n.sp. 1*** | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1/3 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 4 | 5 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| ***Cardigenius laticollis*** | 0 | 3 | 0 | 1 | 0 | 2 | 8 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| ***Craniotus pubescens*** | **0** | 3 | **0** | **0** | **1** | **1** | **6** | **0** | **2** | **0** | **0** | **3** | **0** | **2** | **0** | **0** | **0** | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| ***Eusattus reticulatus*** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **1** | **0** | **0** | **0** | **0** | **0** | **0** | **1** | **1** | **4** | 5 | 0 | 3 | 1 | 1 | 0 | 0 | 0 |
| ***Glyptasida aegra*** | **0** | **1** | **0** | **0** | **1** | **1** | **0** | **1** | **4** | **0** | **0** | **0** | **0** | **2** | **0** | **0** | **1** | 1 | 0 | 3 | 1 | 0 | 0 | 0 | 0 |
| ***Glyptasida sordida*** | **0** | **1** | **0** | **0** | **1** | **1** | **0** | **1** | **4** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **1** | 2 | 0 | 3 | 1 | 0 | 0 | 0 | 0 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **51** | **52** | **53** | **54** | **55** | **56** | **57** | **58** | **59** | **60** | **61** | **62** | **63** | **64** | **65** | **66** | **67** | **68** | **69** | **70** | **71** | **72** | **73** | **74** | **75** |
| *Gonasida elata* | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Heterasida bifurca* | 0 | 2 | 0 | 1 | 1 | 1 | 5 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Heterasida connivens* | 0 | 2 | 0 | 1 | 1 | 1 | 5 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Heterasida subvittata* | 0 | 1 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Megasida obliterata* | 0 | 3 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Megasida tenuicollis* 1 | 0 | 3 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Megasida tenuicollis* 2 | 0 | 3 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Microschatia rockefelleri* | 1 | 1 | 0 | 0 | 1 | 2 | 8 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 4 | 5 | 0 | 3 | 1 | 1 | 0 | 0 | 0 |
| *Parasida lirata* | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 3 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Parasida longicollis* | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Parasida sexcostata* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Parasida* n.sp. 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Pelecyphorus mexicanus* | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 1/3 | 1 | 1 | 0 | 0 | 0 |
| *"Pseudoglyptasida" n.sp.*1 | 0 | 3 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |
| *Philolithus actuosus* | 1 | 1 | 0 | 0 | 1 | 1 | 0 | ? | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Philolithus aegrotus* | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 1 | 1 | 0 | 0 | 0 |
| *Philolithus densicollis* | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Philolithus morbillosus* | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 1 | 1 | 0 | 0 | 0 |
| *Philolithus* n.sp. 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 1 | 1 | 0 | 0 | 0 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **51** | **52** | **53** | **54** | **55** | **56** | **57** | **58** | **59** | **60** | **61** | **62** | **63** | **64** | **65** | **66** | **67** | **68** | **69** | **70** | **71** | **72** | **73** | **74** | **75** |
| *Platasida embaphionides* | 0 | 0 | 0 | 1 | 1 | 1 | 6 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Pycnomorpha gibbicollis* | 0 | 2 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Stenomorpha costipennis* | 0 | 3 | 0 | 0 | 1 | 1 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Stenomorpha rimatus* | 0 | 3 | 0 | 0 | 1 | 1 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Stenomorpha marginata* | 0 | 3 | 0 | 0 | 1 | 1 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Stenomorpha luctata* | 0 | 3 | 0 | 0 | 1 | 1 | 7 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Stenomorpha obovata* | 0 | 0 | 0 | 0 | 1 | 1 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Stenomorpha* n.sp.1 | 0 | 3 | 0 | 0 | 1 | 1 | 6 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Stenosides anastomosis* 1 | 0 | 2 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 3 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Stenosides anastomosis* 2 | 0 | 2 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 3 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Stenosides anastomosis* 3 | 0 | 2 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 3 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Stethasida obsoleta* | 0 | 1 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Trichiasida acerba* | 0 | 3 | 0 | 0 | 1 | 0 | 7 | 1 | 2 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Trichiasida hirsuta* 1 | 0 | 3 | 0 | 1 | 1 | 1 | 7 | 0 | 2 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Trichiasida hirsuta* 2 | 0 | 3 | 0 | 1 | 1 | 1 | 7 | 0 | 2 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Trichiasida hispidula* | 0 | 3 | 0 | 0 | 1 | 1 | 7 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Trichiasida pubescens* | 0 | 3 | 0 | 0 | 1 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Trichiasida unicostata* | 1 | 1 | 0 | 1 | 1 | 1 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Ucalegon pulchellus* | 1 | 3 | 0 | 1 | 1 | 0 | 2 | 1 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 |
| *Zaleucus dilatatus* | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **76** | **77** | **78** | **79** | **80** | **81** | **82** | **83** | **84** | **85** | **86** | **87** | **88** | **89** | **90** | **91** | **92** | **93** | **94** | **95** | **96** | **97** | **98** | **99** | **100** |
| *Ardamimicus cognatoi* 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | ? | ? | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| *Ardamimicus cognatoi* 2 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | ? | ? | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| *Asidina confluens* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | ? | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 3 |
| *Asidina furcata* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 1 | 4 |
| *Asidina parallela* | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | ? |
| *Asidopsis mancipata* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | ? |
| *Asidopsis polita* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | 3 |
| *Asidopsis opaca* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | 3 |
| *Asidopsis macra* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | ? |
| *Asidopsis divaricata* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | 3 |
| *Astrotus fasciculatus* | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | ? |
| *Astrotus guanajuatensis* | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 3 |
| *Astrotus regularis* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Branchus n.sp. 1* | 2 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 3 | 3 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | ? |
| *Cardigenius laticollis* | 2 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 3 | 3 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | ? |
| *Craniotus pubescens* | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | ? |
| *Eusattus reticulatus* | 2 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 8 | 0 | 0 | 0 | 5 |
| *Glyptasida aegra* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 7 | 0 | 0 | 1 | 3 |
| *Glyptasida sordida* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 7 | 0 | 0 | 0 | 3 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **76** | **77** | **78** | **79** | **80** | **81** | **82** | **83** | **84** | **85** | **86** | **87** | **88** | **89** | **90** | **91** | **92** | **93** | **94** | **95** | **96** | **97** | **98** | **99** | **100** |
| *Gonasida elata* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 7 | 0 | 0 | 2 | 4 |
| *Heterasida bifurca* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | ? | ? | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | ? |
| *Heterasida connivens* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | ? | ? | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | ? |
| *Heterasida subvittata* | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 3 |
| *Megasida obliterata* | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 4 |
| *Megasida tenuicollis* 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 4 |
| *Megasida tenuicollis* 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 4 |
| *Microschatia rockefelleri* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 |
| *Parasida lirata* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 3 |
| *Parasida longicollis* | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | ? |
| *Parasida sexcostata* | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 0 |
| *Parasida* n.sp. 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 1 | 3 |
| *Pelecyphorus mexicanus* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | ? |
| *"Pseudoglyptasida" n.sp.*1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 3 |
| *Philolithus actuosus* | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | ? | 0 | 0 | 1 | ? |
| *Philolithus aegrotus* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 7 | 0 | 0 | 0 | 2 |
| *Philolithus densicollis* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 7 | 0 | 0 | 1 | 2 |
| *Philolithus morbillosus* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 7 | 0 | 0 | 0 | ? |
| *Philolithus* n.sp. 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 7 | 0 | 0 | 0 | ? |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **76** | **77** | **78** | **79** | **80** | **81** | **82** | **83** | **84** | **85** | **86** | **87** | **88** | **89** | **90** | **91** | **92** | **93** | **94** | **95** | **96** | **97** | **98** | **99** | **100** |
| *Platasida embaphionides* | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | ? |
| *Pycnomorpha gibbicollis* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 3 |
| *Stenomorpha costipennis* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | ? |
| *Stenomorpha rimatus* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 4 |
| *Stenomorpha marginata* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 4 |
| *Stenomorpha luctata* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | ? |
| *Stenomorpha obovata* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 4 |
| *Stenomorpha* n.sp.1 | ? | ? | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | 1 | ? | 0 | 0 | 1 | ? |
| *Stenosides anastomosis* 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 1 |
| *Stenosides anastomosis* 2 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 1 |
| *Stenosides anastomosis* 3 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 1 |
| *Stethasida obsoleta* | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | ? |
| *Trichiasida acerba* | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | ? |
| *Trichiasida hirsuta* 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 6 | 0 | 0 | 0 | 3 |
| *Trichiasida hirsuta* 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 6 | 0 | 0 | 0 | 3 |
| *Trichiasida hispidula* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | ? |
| *Trichiasida pubescens* | 1 | 1 | 1 | 2 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | ? | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | ? |
| *Trichiasida unicostata* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 1 | ? |
| *Ucalegon pulchellus* | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 3 |
| *Zaleucus dilatatus* | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 1 |

**Table 1.4 (cont.):** Morphological character matrix of 100 characters for 58 OTUs. Characters and their scores in Materials and Methods.

**Figure 1.5:** Dorsal habitus of *Ardamimicus cognatoi* Smith, **n. gen.** and **n.sp.**, ♀ (L=12.1mm)

**Figure 1.6:** Dorsal habitus of *Craniotus pubescens* LeConte, ♀ (L=8.9mm)

**Figure 1.7:** Dorsal habitus of *Ferveoventer browni* Smith, **n. gen.** and **n.sp.** (L=9.4mm)

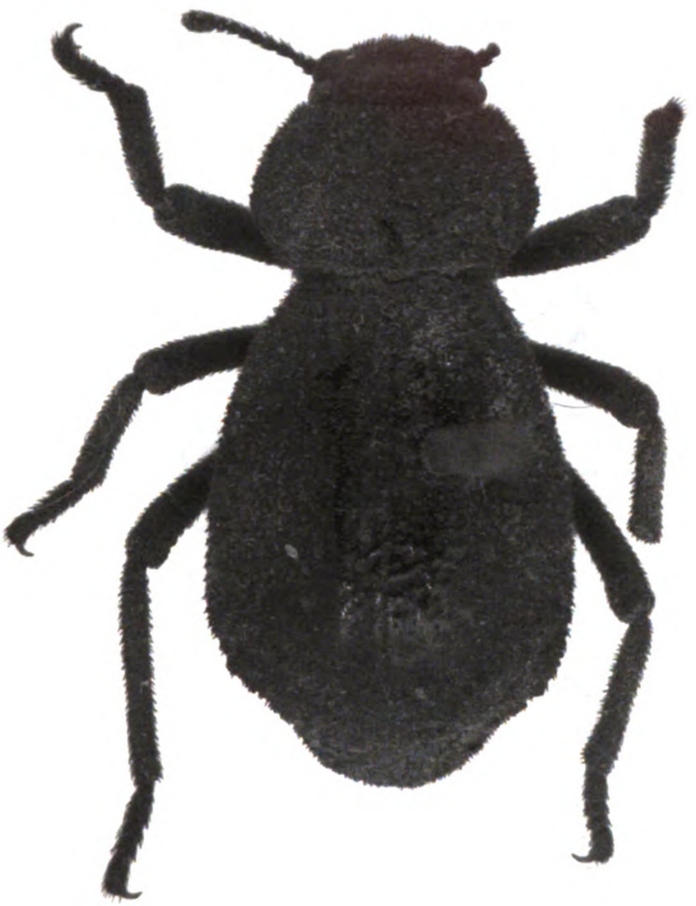

**Figure 1.8:** Dorsal habitus of *Ferveoventer planatus* (Champion), (L=7.9mm)

**Figure 1.9:** Dorsal habitus of *Heterasida bifurca* (LeConte), ♂ (L=9.6mm)

**Figure 1.10:** Dorsal habitus of *Heterasida connivens* (LeConte), ♀ (L=9.4mm)

**Figure 1.11:** Dorsal habitus of *Litasida townsendi* Casey, ♂ (L=11.0mm)

**Figure 1.12:** Dorsal habitus of *Micrasida obiernorum* Smith, **n. gen.** and **n.sp.**, (L=5.9mm)

**Figure 1.13:** Dorsal habitus of *Microschatia rockefelleri* Pallister, (L=14.0mm)

**Figure 1.14:** Dorsal habitus of *Pelecyphorus mexicanus* Solier, (L=16.3mm)

**Figure 2.15:** Dorsal habitus of *Philolithus aegrotus* (LeConte), (L=14.1mm)

**Figure 1.16:** Dorsal habitus of *Stenomorpha obovata* (LeConte), ♂ (L=19.6mm)

# CHAPTER TWO

## Revision of the genus *Pelecyphorus* Solier, 1836

## (Coleoptera: Tenebrionidae: Asidini)

## ABSTRACT

A taxonomic revision of the North American genus *Pelecyphorus* Solier is presented. Eight subgenera are erected and described. Seven are based on the existing Asidini genera *Pelecyphorus* Solier *sensu stricto*, *Astrotus* LeConte, *Stenosides* Solier, *Ucalegon* Champion, *Zaleucus* Champion, *Plesiasida* Smith (=Parasida Casey), and *Sicharbas* Champion. One **new subgenus**, *Variodorsus*, is described.

Forty species of *Pelecyphorus* are recognized as valid, including seven **new species** described herein: *P. cavatus*, *P. cifuentesi*, *P. crypticus*, *P. deaztlani*, *P. doyeni*, *P. oaxacensis*, and *P. triplehorni*. All valid species are described or redescribed, along with diagnoses, distributions, and images of each. An illustrated key to the subgenera and species is also provided.

Twenty-four previously described species are presented as **new synonyms**: *P. anastomosis* (Say) (=*P. breviuscula* (Casey); =*P. exoleta* (Casey); =*P. luteotecta* (Casey); =*P. monticola* (Casey); =*P. obtecta* (Casey); =*P. sigillata* (Casey)), *P. graciliformis* (Solier) (=*P. canus* (Champion); = *P. sinuaticollis* (Champion)), *P. erosus* (Champion) (=*P. nosodermoides* (Champion)), *P. guanajuatensis* (Champion) (=*Stenomorpha mucorea* (Wilke)), *P. dispar* (Champion) (=*P. bisinuatus* (Pallister); =*P. kulzeri* (Pallister); =*P. trisinuatus* (Pallister)), *P. liratus* (LeConte) (=*laciniatus* (Casey); = *P. cristatus* (Pallister)), *P. asidoides* Solier (=*zacualpanicolus* (Wilke)), *P. fallax* (Champion) (=*P. favosus* (Champion); = *P. similatus* (Champion)), *P. laticollis* (Champion) (=*P. planatulus* (Casey)), P. *scutellaris* (Champion) (=*P. tolucanus* (Casey)), *P. longipennis* (Champion) (=*P. mixtecae* (Wilke); =*P. esperanzae* (Wilke)), P. *tristis* (Champion) (=*P. purpusi* (Wilke)), P. *indutus* (Champion) (=*P. bicarinatus* (Champion)).

## INTRODUCTION

*Pelecyphorus* Solier is a large morphologically diverse genus of asidine darkling beetles (Tenebrionidae: Asidini) endemic to Mexico and the southwestern United States. Like all asidines, *Pelecyphorus* species are flightless detritivores that lack defensive glands and spend much of their lives as subterranean larvae. Solier (1836) erected the genus to hold four new species, three from Mexico (*P. mexicanus*, *P. foveolatus*, and *P. asidoides*) and one from South Africa (*P. capensis*), the last of which was subsequently removed from the genus (Lacordaire 1859). *Pelecyphorus* was originally defined based on the following characters: apical segment of the maxillary palp enlarged, antennal segments 3-9 cylindrical, and distal tarsomere on the hind leg longer than the three preceding segments. However, these characters are present in a majority of the nearly 300 species of North American Asidini, only three of which had been described before Solier's publication. Because of the overly generalized original description, nearly all of the asidines described over thirty-four years by LeConte, were placed in *Pelecyphorus*.

In his revision of the Tenebrionidae north of Mexico, Horn (1870) synonymized *Pelecyphorus* and several other North American asidine genera with the Mediterranean genus *Asida*, citing the lack of clear boundaries separating them. During the next forty years over 100 additional asidine species were described from Mexico and the southwestern United States, with most placed directly into *Asida*. Then Casey (1912) revised the North American asidine fauna and resurrected *Pelecyphorus* along with nearly all of the previously described genera. Casey designated *Pelecyphorus mexicanus* Solier as the type species for the genus based on the illustrations in Solier (1836). It is worth noting that he had never actually examined a specimen of *P. mexicanus*. Casey

redefined the genus based on a combination of homoplastic characters and characters that previously had delimited the genus *Philolithus* Lacordaire, 1859. All of the former *Philolithus* species were added to *Pelecyphorus*, while two of the original *Pelecyphorus* species (*P. foveolatus*, and *P. asidoides*) were moved into Casey's new genus *Parasida*. Brown (1971b) studied the type series of *P. mexicanus* and determined that it was far removed from the species added to *Pelecyphorus* by Casey. Brown resurrected *Philolithus* and restricted the genus *Pelecyphorus* to the type species pending further study.

A phylogenetic analysis of the North American Asidini genera (Smith 2010, Chapter 1) determined that *P. mexicanus* belonged within a larger clade of asidine species, which included the other two North American *Pelecyphorus* species descibed by Solier (*P. foveolatus* and *P. asidoides*) and six previously described genera (*Astrotus* LeConte, *Stenosides* Solier, *Ucalegon* Champion, *Zaleucus* Champion, *Plesiasida* Smith (=Parasida Casey), and *Sicharbas* Champion). In order to maintain stability and recognize the morphological diversity represented within this group of species, an expanded definition of *Pelecyphorus* was presented and the other genera within the clade were assigned subgeneric status within *Pelecyphorus sensu lato*.

In this study I revise the genus *Pelecyphorus*. Eight subgenera and 40 species are described, including one new subgenus and seven new species. A key to the species is provided along with diagnoses, distributions, and images of each.

## METHODS AND MATERIALS

The results of this study are based on an examination of approximately 1,654 *Pelecyphorus* specimens, including type material from all but two species. Type specimens for *P. anastomosis* and *P. graciliformis* are lost and presumed to be destroyed. Neotypes were designated for both species based on their original descriptions, illustrations, and ranges.

Only morphological characters drawn from adult specimens were used in this study and the phylogenetic species concept as defined in Wheeler and Platnick (2000) was employed to delimit taxa. The morphological characters and methodology used in this revision follow those presented in Chapter 1.

## RESULTS

### Taxonomy of *Pelecyphorus* Solier

#### *Pelecyphorus* Solier

*Pelecyphorus* Solier, 1836:467. Type species: *Pelecyphorus mexicanus* Solier, 1836:469, by subsequent designation, Casey 1912:105. Lectotype (MNHN).

subgenus *Pelecyphorus* Solier, 1836:467, *sensu strictu.*

subgenus *Astrotus* LeConte, 1858:19. Type species: *Microschatia contorta* LeConte, 1858, by original designation.

subgenus *Stenosides* Solier, 1836:484. Type species: *Stenosides graciliformis* Solier, 1836, by monotypy.

=*Pactostoma* LeConte, 1858:19. Type species: *Asida anastomosis* Say, 1824, by original designation.

=*Ologlyptus* Lacordaire, 1859:158 (unnecessary replacement name).

subgenus *Ucalegon* Champion, 1884:65. Type species: *Ucalegon pulchellus* Champion, 1884.

subgenus *Pleisiasida* Smith, (=*Parasida* Casey 1912:126, junior homynym). Type species: *Parasida laciniata* Casey, 1912. **New Replacement Name.**

subgenus *Sicharbas* Champion, 1884:67. Type species: *Sicharbas lobatus* Champion, 1884.

subgenus *Variodorsus* Smith. Type species: *Asida guanajuatensis* Champion, 1884. **New Subgenus.**

subgenus *Zaleucus* Champion, 1892:491. Type species: *Zamolxis dilatatus* Champion, 1884.

**Redescription.** Length: 6.0-22.9 mm, width: 2.3-11.1 mm; integument ferruginous to black; body obovate to elongate and nearly parallel sided; densely setose or sparsely setose, occasionally setae inconspicuous; setae often modified, lanceolate, squamate, or stellate in shape. **Head:** Mentum variable, trapezoidal to broadly cordate; contacting

postgenal processes or not, if tightly contacting postgenal processes then also reaching mandibles when closed; lateral margins straight or curved inward at apicies; anterior margin straight to weakly emarginate, medially notched or not. Ligula; sclerotized small, one-fourth to one-sixth mentum width, and thin, length approximately 5X width; slightly curved and partially visible above anterior margin of mentum or straight and concealed. Apical segment of maxillary palps enlarged, securiform to scalene in shape, more expanded in males. Submentum barely or distinctly projecting into buccal cavity; width two-thirds to equal that of buccal cavity, concealing or partially exposing maxillary cardos laterally. Postgena concealing mandibular protuberance; postgenal processes slightly to greatly swollen; produced, extending to middle of mentum or beyond, acute to broadly rounded. Labral margin straight or broadly emarginate, medially without setal brush; medial tormal process of labrum shorter than posterior tormal process; clypeal membrane concealed or rarely exposed. Clypeal margin straight or emarginate. Eyes elongate, oval or reniform, partially concealed when head is retracted. Antenna weakly clavate; nearly moniliform; segments 10-11 rounded or laterally flattened , forming a slight club; tomentose sensilla absent on antennal segment 9; apical tomentose sensilla present on antennal segment 10, separated into two patches at lateral apices or coalesced into a single band; antennal segment 11 one-fourth to two-thirds size of segment 10, apical tomentose sensillum covering one-sixth to one-half of segment. **Prothorax:** Pronotal shape and sculpturing variable, with or without a median costa or paramedial fossae, lacking paramedial basal gibbosities; pronotal margin costate, medially acutely expanded or not; anterior apicies produced, acute or rounded, posterior apicies obtuse or acute, projecting over elytral humera or not; posterior margin straight, slightly convex, or

weakly bisinuate, often with a medial tooth projecting posterad. Prosternal process thin, declivious behind procoxae or raised and projecting behind procoxal cavities, apex truncate, broadly rounded, or sagittate; if raised then received in shallow or moderate emargination between mesocoxae. **Pterothorax:** Apterous. Scutellum triangular, visible or mostly concealed underneath elytra, not raised above scutum; mesonotum with two faint or deep transverse depressions, often leaving a thin medial ridge between the scutellum and scutum. Elytral sculpturing variable, discal costae present or faintly indicated, marginal costae rarely lacking; epipleura indistinct. Metendosternite stem approximately as twice wide as tall. **Legs:** Ferruginous to nearly black, tarsal formula 5-5-4; pro- and mesocoxae globular, metacoxae more transverse; mesocoxal cavities open or externally closed by sternites; mesotrocantin small to minute, concealed or exposed; protibia with outer apical margin forming a spine; protibial outer lateral margin not carinate; inner apical margin of protibia with two spurs, posterior spur shorter than anterior spur. **Abdomen:** Punctation and setation variable; intercoxal process impressed around margin or not, rounded or truncate at apex. Female apical coxites ventrally flattened; three to twelve spermathecal branches present, emerging from apex of common duct; accessory gland short or long, with an enlarged chamber absent or rarely present near apex.

**Diagnosis.** *Pelecyphorus* is distinguished from all other asidine genera by a unique combination of the following characters: Ligula small, one-fourth to one-sixth mentum width, and thin, length approximately 5X width; partially visible above anterior margin of mentum or straight and concealed. Scutellum not raised above scutum; mesonotum with two faint or deep transverse depressions. Anterior protibial spur longer than posterior.

**Distribution.** Mexico: representatives are known from every state with the exceptions of Chiapas, Yucatan, Tabasco, and Baja California Norte. United States: Arizona, Colorado, Kansas, New Mexico, Texas.

## Key to the Species of *Pelecyphorus* Solier

1 Mentum completely filling buccal cavity, tightly contacting postgenal processes and contacting or nearly contacting mandibles at apex; submentum wide, more than 4/5 buccal cavity width, reaching postgena or laterally exposing a minute space.....2

- Mentum not filling buccal cavity, if contacting postgenal processes then not reaching mandibles at apex; submentum narrower, 4/5 buccal cavity width or less, laterally exposing a large space .....19

2(1) Anterior apicies of mentum expanded and curved inward towards mandibles; mesotrocantin concealed; large tubercle present on hypomeron margin behind eye; *Astrotus*-type stellate setae present; dorsal surface evenly, thickly encrusted with debris; (subgenus *Astrotus* LeConte).....4

- Anterior apicies of mentum straight or slightly curved inward, not significantly expanded; mesotrocantin usually exposed; large tubercle absent on hypomeron; *Astrotus*-type stellate setae absent; dorsal surface encrusted with debris or not; ...3

3(2') Ligula small, straight, and concealed underneath mentum; postgenal processes broadly rounded and swollen; pronotum without tubercles; (subgenus *Stenosides* Solier) .....8

- Ligula larger, curved, and usually exposed above anterior margin of mentum; postgenal processes acute, not swollen; pronotum tuberculate; (subgenus *Sicharbas* Champion) ..... 14

4(2) Elytral humera carinate and reflexed; pronotum with a longitudinal medial depression; elytra with transverse costae or nodules ..... 5

- Elytral humera obtuse; pronotum without a longitudinal medial depression; elytra lacking transverse costae or nodules ..... ***P. (A.) hebes* (Champion)**

5(4) Lateral margin of elytra with large or small projections..... 6

- Lateral margin of elytra tuberculate, but lacking projections..... 7

6(5) 8-10 large lateral projections on elytron margin; prosternal process raised behind procoxa ..... ***P. (A.) contortus* (LeConte)**

- 12 or more small lateral projections on elytron margin; prosternal process deflexed behind procoxa..... ***P. (A.) alveolatus* (Casey)**

7(5') Pronotum broadly sinuate; sutural costa not raised ..... ***P. (A.) regularis* (Horn)**

- Pronotum acutely sinuate, sharply dilated near middle; sutural costa raised ..... ***P. (A.) crypticus* Smith, n. sp.**

8(3) Median ridge on pronotum strongly raised and triangularly expanded in basal half, forming a large bifurcate process projecting past basal pronotal margin; elytral humera prominent and reflexed; south Texas..... ***P. (S.) texanus* (Wickham)**

- Median ridge on pronotum absent or slightly raised, never triangularly expanded or forming a large process; elytral humera small or oblique, not reflexed..... 9

9(8') Frontoclypeal suture deeply, transversely excavated; pronotal marginal costa absent or faintly indicated over most of length; Mexico: Coahuila.....

..... ***P. (S.) cavatus* Smith, n. sp.**

- Frontoclypeal suture weakly or strongly depressed, not forming a deep excavation; pronotal marginal costa raised and distinct over entire length .....10

10(9') Pronotal disc confluently foveate; antennal segment 11 small and deeply amplected into segment 10..... ***P. (S.) limosus* (Champion)**

- Pronotal disc densely, but not confluently foveate; antennal segment 11 larger and barely amplected into segment 10.....11

11(10') Elytral marginal costa densely tuberculate and setose, submentum not transversely depressed .....12

- Elytral marginal costa not tuberculate or setose, submentum deeply transversely depressed; Mexico, Nuevo Leon..... ***P. (S.) deaztlani* Smith, n. sp.**

12(11) Pronotal marginal costa crenulate and reflexed; elytra without transverse costae .... ..... ***P. (S.) graciliformis* (Solier)**

- Pronotal marginal costa punctate, not reflexed; elytra with irregular transverse costae.....13

13(12') Transverse costae on elytra absent between discal costa and elytral suture; crests of elytral costae densely tuberculate and setose ..... ***P. (S.) anastomosis* (Say)**

- Transverse costae on elytra present between discal costa and elytral suture; crests of elytral costae sparsely setose and smooth..... ***P. (S.) triplehorni* Smith, n. sp.**

14 (3') Tomentose sensilla on antennal segment 10 coalesced into a broad continuous band.....15

- Tomentose sensilla on antennal segment 10 not forming a broad continuous band, separate or meeting on one side .....17

15(14) Pronotum medially longitudinally depressed, apical protibial spine small and setose to apex .....16

- Pronotum medially tuberculate, not longitudinally depressed, apical protibial spine large and glabrous.....***P.* (*S.*) *seticornis* (Champion)**

16(15) Pronotum angularly sinuate, dilated before middle and forming a triangular flange, posterior apicies projecting over elytra.....***P.* (*S.*) *lobatus* (Champion)**

- Pronotum sinuate, dilated before middle and forming a broadly rounded flange, posterior apicies not projecting over elytra.....***P.* (*S.*) *oaxacensis* Smith, n. sp.**

17(14') Pronotal disc foveate, fovea subtended by tubercles; elytra clothed with squamate and lanceolate erect setae, elytral humera not reflexed .....18

- Pronotal disc foveate, lacking tubercles; elytra clothed with lanceolate decumbent setae, elytral humera reflexed; Mexico, Durango.....***P.* (*S.*) *undatus* (Champion)**

18(17) Elytral discal costa absent; pronotal margin strongly sinuate; dark coalesced patches of erect setae present on posterior half of elytra; Mexico, Puebla.....
.....***P.* (*S.*) *debilis* (Champion)**

- Elytral discal costa present in basal half or throughout; pronotal margin arctuate or slightly sinuate; dark coalesced patches of erect setae absent on elytra ; Mexico, Hidalgo.....***P.* (*S.*) *erosus* (Champion)**

19(1') Dense tomentose fringe present on abdominal ventrites 1-4; elytra costae confused, coarsely reticulate, whitish *Pelecyphorus*-type stellate setae densely packed into elytral depressions ..... ***P.* (*Pelecyphorus*) *mexicanus* Solier**

- Tomentose fringe absent on all abdominal ventrites ; elytra costae variable; setation variable, but never with *Pelecyphorus*-type stellate setae.....20

20(19') Squamate and erect lanceolate setae present on elytra, squamate setae white, black, or reddish, forming a distinctive contrasting pattern with two dense black triangular patches halfway down elytral length; pronotum usually with a broad median depression.....***P.(Ucalegon) pulchellus* (Champion)**

- Setae variable, but lanceolate setae never erect and squamate setae, if present, not forming a distinctive pattern; pronotum never broadly medially depressed.....21

21(20') Elytral humera oblique; setae sparse, hair-like or narrowly lanceolate; pronotum lacking fossae; (subgenus *Zaleucus* Champion) .....22

- Elytral humera planate, often reflexed; setae dense, squamate or lanceolate, or absent; pronotum with two or four fossae.....25

22(21) Pronotal margin arctuate, posterior apicies obtuse; prosternal process deflexed behind procoxae. .....23

- Pronotal margin sinuate, posterior apicies acute, projecting or not; prosternal process raised behind procoxae .....24

23(22) Pronotum dilated; postgenal processes greatly swollen and projecting nearly to anterior margin of mentum; intercostal spaces on elytra smooth of weakly rugose; Oaxaca and Puebla .....***P. (Z.) dilatatus* (Champion)**

- Pronotum not dilated; postgenal processes slightly swollen and not projecting nearly to anterior margin of mentum; intercostal spaces on elytra strongly rugose; Coahuila, Nuevo Leon, or Zacatecas .....***P. (Z.) doyeni* Smith, n. sp.**

24(22') Posterior apicies of pronotum not projecting, apex of prosternal process rounded; elytral marginal carina crenulate in apical third; intercostal spaces on elytra smooth.....***P. (Z.) platesthoides* (Champion)**

- Posterior apicies of pronotum projecting, apex of prosternal process acute; elytral marginal carina smooth in apical third; intercostal spaces on elytra rugose ..... ***P. (Z.) foveolatus*** **Solier**

25(21') Mentum reaching postgenal processes; antennal segment 11 one-fourth size of segment 10; (subgenus *Variodorsus*, **n. sub. gen.**) .....26

- Mentum not reaching postgenal processes; antennal segment 11 approximately one-half size of segment 10; (subgenus *Plesiasida*, nomen novem, =*Parasida* Casey) .....27

26(25) Pronotumwith a raised medial ridge; elytra with discal costae present and bifurcate, inner branch eroded after basal third, densely clothed in multicolored erect squamate and lanceolate scales, forming irregular darker points and lines across surface. ..... ***P. (V.) fasciculatus*** **(Champion)**

- Pronotumlacking a raised medial ridge; elytra with a ntework of raised carinate costae, densely clothed with short pale squamate scales ..... ..... ***P. (V.) guanajuatensis*** **(Champion)**

27(25') Pronotal posterior apicies produced and projecting over elytral humera; pronotal posterior margin with a tomentose fringe .....28

- Pronotal posterior apicies not or weakly produced, not projecting over elytral humera; pronotal posterior margin without a tomentose fringe.....36

28(27) Elytral base depressed and tomentose.....29

- Elytral base not depressed or tomentose.....31

29(28) Discal costa branches not meeting at base; abdominal punctures minute; medial tooth present on pronotal posterior margin.....30

- Discal costa branches meeting at base; abdominal punctures minute; medial tooth absent on pronotal posterior margin ..... ***P. (P.) dispar* (Champion)**

30(29) Pseudoepiplura punctate and tuberculate, lanceolate setae emerging from tubercles; USA: NM, AZ, or Mexico: Chihuahua ..... ***P. (P.) liratus* (LeConte)**

- Pseudoepiplura nearly impunctate and not tuberculate, lanceolate setae nearly absent; Mexico: Durango ..... ***P. (P.) bibasalis* (Casey)**

31(28') Elytral costae raised and straight, intercostal regions with longitudinal lines of squamate setae ..... 32

- Elytral costae barely indicated or weakly raised and reticulate, intercostal regions setose or not, never forming longitudinal lines of squamate setae ..... 35

32(31) Elytral costae thick and strongly raised, sides and crests of costae smooth rounded and impunctate, elytra broadly convex ..... 33

- Elytral costae thin and weakly raised, tubercles and scales covering sides and occasionally crests; elytra nearly planate..... ***P. (P.) laticollis* (Champion)**

33(32) Elytral costae sharply raised, transverse costae common, usually with one to six; median row of dark intercostal scales wide, nearly reaching costae; pronotum with brown squamate scales..... ***P. (P.) fallax* (Champion)**

- Elytral costae broadly rounded, transverse costae rare, usually absent or with no more than two; median row of dark intercostal scales thinner than lateral rows of white scales; pronotum with pale squamate or lanceolate scales ..... 34

34(33') Pronotum arctuate, narrowest at apex, widening to middle, nearly parallel sided to base; psedoepiplura tuberculate and densely clothed with squamate scales..... ..... ***P. (P.) obliviosus* (Wilke)**

- Pronotum weakly sinuate, widest near middle; pseudoepipleura punctate and sparsely clothed with short acuminate setae ..... ***P. (P.) scutellaris* (Champion)**

35(31') Elytral discal costa low and reticulate; pronotal medial ridge absent or faintly indicated; combined protarsal segments approximately two-thirds length of protibia ..... ***P. (P.) asidoides* Solier**

- Elytral discal costa indistinct among confused network of low costae; pronotal medial ridge present and raised; combined protarsal segments subequal to length of protibia; Jalisco ..... ***P. (P.) intricatus* (Champion)**

36 (27') Elytral discal costa distinctly divided, inner branch raised; central continental Mexico ..... 37

- Elytral discal costa absent or inner branch not raised; Baja California Sur ..... 39

37(36) Elytra glossy black, setae minute and inconspicuous; legs ferruginous; crests of costae smooth and impunctate ..... ***P. (P.) tristis* (Champion)**

- Elytra dull black or ferruginous, densely setose; legs variable; crests of costae setose, punctate or tuberculate ..... 38

38(37') Labral margin emarginate; elytral costae tuberculate with erect acuminate setae; setae on tarsal venter short and spiniform ..... ***P. (P.) indutus* (Champion)**

- Labral margin truncate; elytral costae punctate with thin decumbent setae; setae on tarsal venter long acuminate and golden ..... ***P. (P.) longipennis* (Champion)**

39(36') Elytral discal and marginal costae absent; pronotal margin strongly reflexed; elevation 4500' or more ..... ***P. (P.) cifuentesi* Smith, n. sp.**

- Elytral discal and marginal costae present; pronotal margin straight or weakly reflexed; elevation 1500' or less ..... ***P. (P.) sexcostatus* LeConte**

## subgenus *Astrotus* LeConte, 1858

*Astrotus* LeConte 1858:19. Type species: *Microschatia contorta* LeConte, 1853:446, by original designation.

**Description.** Length 8.7 - 22.9mm, width 4.7 - 11.1mm. Integument black or ferruginous; densely covered in Astrotus-type stellate setae raised on small tubercles. **Head:** Retractable into pronotum past eyes. Mentum large, completely filling buccal cavity, sub-trapezoidal; anterior margin broadly emarginate or nearly straight; lateral margins curved inward at apicies. Ligula small, less than one-fifth mentum width, straight or slightly curved, concealed or barely visible. Apical segment of maxillary palps securiform to triangular. Submentum broad, laterally contacting postgena, concealing maxillary cardos. Postgenal process produced, swollen, broadly rounded. Labrum with apical margin emarginate; clypeal membrane concealed. Clypeal margin straight. Frons shallowly foveate and tuberculate, median pit deeply to faintly depressed; frontoclypeal suture deeply to faintly depressed; dorsal sulcus absent above apices of eyes; eyes elongate and slightly reniform. Antenna compact, weakly clavate; antennal segments 3-9 rounded, moniliform; segments 10 and 11 slightly flattened, forming a club; antennal segment 10 subquadrate, two tomentose sensory patches present at lateral apices; antennal segment 11 with a small apical tomentose sensory patch, amplected into segment 10. **Prothorax:** Pronotum widest at middle, sinuate or sharply angulate; median

longitudinal depression present, often with a faint carina visible at over part of length and forming a small tooth at base; lateral costae present. Large nodule projecting from anterior margin of hypomeron. Prosternal process raised and thickened behind procoxal cavities; apex broadly rounded or sagittate. **Pterothorax:** Scutellum triangular, straight and not reaching height of scutum; mesonotum with two transverse glaberous depressions, open at base, between the scutellum and scutum or laterally eroded. Elytral sculpturing variable; eltral humera planate or reflexed. Marginal costa present, crenulate with tubercles or larger projecting nodules; generally divided, inner branch reduced to nodules. Discal costa present, reticulate or straight, serrated or not. Sutural costa present or absent. Transverse ridges between elytral costae present or absent, position variable. **Legs:** Mesotrocantin small to minute, concealed or exposed; femura and tibia shallowly nearly confluently foveolate, both densely clothed with stellate setae. **Abdomen:** tuberculate with stellate setae; intercoxal process width equal to mesosternal apex, anterior margin nearly straight.

**Diagnosis.** The species in the subgenus *Astrotus* are distinguished from all other *Pelecyphorus* species based on a unique combination of the following characters: body densely covered in *Astrotus*-type stellate setae raised on tubercles and usually evenly coated with debris; mentum completely filling buccal cavity, sub-trapezoidal, anterior margin broadly arctuate and reaching base of mandibles when closed, lateral apicies expanded and strongly bent inward towards mandibles; ligula less than one-fifth mentum width, concealed; apical segment of maxillary palps securiform or triangular; labral margin straight; postgenal process produced, slightly swollen, broadly rounded; large projecting nodule present on anterior margin of hypomeron.

**Distribution.** Arid habitats from central and southern Mexico to the western United States. The states where they are currently known to occur are MEXICO: Coahuila, Durango, Nuevo Leon, Tamaulipas; USA: Texas, Kansas.

**Biology.** Species from this subgenus have been collected from underneath rocks or plant debris and from the area surrounding *Pogonomyrmex* ant nests. Specimens have been observed feeding on plant debris in *Pogonomyrmex* midden heaps (Marion Smith, pers. comm.).

## Species Descriptions

### *Pelecyphorus* (*Astrotus*) *alveolatus* (Casey)

*Astrotus alveolatus* Casey 1912:83

*Pelecyphorus* (*Astrotus*) *alveolatus* (Casey). Smith, 2010

**Type Material.** HOLOTYPE, by monotypy, (male) labeled: a) "Tex."; b) on red paper, "HOLOTYPE / *Astrotus* / *alveolatus* ♂ / T.L. Casey, 1912" (NMNH).

**Additional Material Examined** (50 specimens). Texas: Brooks, Dimmit, Hidalgo, Starr, Webb Counties.

**Redescription (see fig. 2.1).** Length 9.8-13.6mm, width 4.7-7.1mm. Body generally evenly thickly coated with debris. **Head:** Densely, shallowly foveate; fovea subtended by *Astrotus*-type stellate setae, primary seta squamate; frontoclypeal suture and medial

depression on frons weakly impressed; epistoma broadly rounded, epistomal suture obscured and not indented at margin; eye reniform, nearly flat, and surrounded by a black callus; labrum nearly parallel sided; apical segment of maxillary palp securiform in both sexes, slightly larger in males; mentum with erect pale spiniform setae and densely foveate, minute tomentum coating surface between fovea. Tomentose sensilla on antennal segment 10 broad and wrapping around apex, nearly meeting medially; apical tomentose sensillum on antennal segment 11 covering one-third to one-half of segment. **Prothorax:** Lateral margin acutely sinuate, dilated at middle and forming a triangular flange, apex of flange reflexed; anterior apicies produced and acute, posterior apicies acute and barely projecting over elytral humera, posterior margin nearly straight, occasionally with a minute medial tooth. Pronotal disc densely, foveate; fovea subtended by *Astrotus*-type stellate setae on small tubercles, primary seta squamate; longitudinal medial depression usually distinct and glabrous; two elongate paramedial fossae present and glabrous. Prosternal process broadly rounded, medially impressed, and deflexed behind procoxae. **Pterothorax:** Elytra gradually widening to apical third, before sharply sloping and tapering caudad; marginal costa present as an irregular row of small laterally projecting tuberculate crests or nodules; elytral humera carinate and reflexed. Scutellum glabrous, mesonotum smooth between scutellum and raised, shelf-like, scutum. Elytral disc moderately punctate, clothed in stellate setae, and costate; sutural costa strongly raised at base and partially covering scutellum, gradually eroding posterad and absent in apical third; Discal costa not reaching elytral base and present as an elevated irregular row of tuberculate crests and nodules, densely crowned with *Astrotus*-type stellate setae, primary setae erect and squamate; transverse costa and nodules present between sutural costa,

discal costa, and marginal costae, variable in density and placement. **Legs:** Mesotrocantin minute, concealed. Femora and tibia densely clothed in *Astrotus*-type stellate setae, primary setae simple, decumbent and nearly clear; tarsi venter with long pale spiniform setae; protarsal segments combined approximately two-thirds length of protibia; anterior protibial spur subequal to basitarsi. **Abdomen:** Densely shallowly foveate, fovea subtended by *Astrotus*-type stellate setae, arising from minute tubercles.

**Diagnosis.** *P. alveolatus* can be separated from the other members of the *Astrotus* subgenus based on the following character combination: tomentose sensilla on antennal segment 10 large, curved around apex and nearly meeting; prosternal process declivious behind procoxa; pronotal lateral margin acutely medially dilated and flanged, flange reflexed; elytral marginal carinae with small laterally projecting crests and nodules.

**Distribution.** southern Texas.

**Biology.** Unknown. Collected in pitfall traps or from underneath cut yucca left out for 16-17 months on sandy soil.

### ***Pelecyphorus* (*Astrotus*) *contortus* (LeConte)**

*Microschatia contorta* LeConte, 1853:446

*Astrotus contortus* (LeConte). LeConte, 1858:19

*Pelecyphorus* (*Astrotus*) *contortus* (LeConte). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (sex undetermined) labeled: a) red disc = Texas; b) "Type / 4524"; c) "Astrotus / contortus LeC.". (MCZ).

**Additional Material Examined** (36 specimens). Texas: Cameron, Dimmit, Jim Hogg, Kenedy, Kleberg, San Patricio, and Willacy Counties.

**Redescription (see fig. 2.2).** Length 8.7-13.6mm, width 4.4-7.2mm. Body generally evenly thickly coated with debris. **Head:** Densely clothed with *Astrotus*-type stellate setae, primary seta short and spiniform, arising from small tubercles; frontoclypeal suture and medial depression on frons deeply impressed; epistoma broadly rounded, epistomal suture obscured and not indented at margin; eye reniform, nearly flat, and surrounded by a black callus; labrum nearly parallel sided; apical segment of maxillary palp securiform in female, slightly larger and isotriangular in males; mentum with erect pale spiniform setae and densely foveate, minute tomentum coating surface between fovea. Tomentose sensilla on antennal segment 10 small and oval, not wrapping around apex; apical tomentose sensillum on antennal segment 11 small, barely visible laterally. **Prothorax:** Lateral margin acutely sinuate, dilated at middle and forming a triangular flange, apex of flange straight or slightly reflexed; anterior apicies slightly produced and broadly rounded, posterior apicies acute and barely projecting over elytral humera, posterior margin nearly straight with a minute medial tooth. Pronotal disc densely, foveate; fovea subtended by *Astrotus*-type stellate setae on small tubercles, primary seta squamate; longitudinal medial depression usually distinct, glabrous in basal fourth; two elongate paramedial fossae present and setose, occasionally divided into four rounded fossae. Prosternal process raised behind procoxae, apex broadly rounded. **Pterothorax:** Densely, evenly coated with *Astrotus*-type stellate setae arising from minute tubercles, primary setae absent or short and spiniform. Elytra gradually widening to apical third, before

sharply sloping and tapering caudad; cauda slightly or strongly reflexed; marginal costa present as an irregular row of 8-10 large lateral projections; elytral humera carinate and reflexed. Scutellum small and glabrous, mesonotum tuberculate between scutellum and raised, shelf-like, scutum. Elytral disc moderately punctate and costate; sutural costa strongly raised at base and partially covering scutellum, gradually eroding posterad and absent in apical third; discal costa present and not reaching elytral base, with irregular projections increasing in size posterad; transverse costa present between sutural and discal costae, absent between discal and marginal costae. **Legs:** Mesotrocantin minute, concealed. Femora and tibia densely clothed in *Astrotus*-type stellate setae, primary setae simple, decumbent and nearly clear; tarsi venter with long pale spiniform setae; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur subeqaul to basitarsi. **Abdomen:** Densely clothed with *Astrotus*-type stellate setae, arising from minute tubercles.

**Diagnosis.** *P. contortus* can be separated from the other members of the *Astrotus* subgenus based on the following character combination: tomentose sensilla on antennal segment 10 small, oval; prosternal process raised behind procoxa, apex rounded; pronotal lateral margin acutely medially dilated and flanged, flange straight or barely reflexed; elytral marginal carinae with 8-10 large lateral projections.

**Distribution.** southern Texas along the Gulf coast.

**Biology.** Unknown. Collected in pitfall traps set in sandy soil or from around *Pogonomyrmex* nests.

## *Pelecyphorus* (*Astrotus*) *regularis* (Horn)

*Astrotus regularis* Horn, 1870:290

*Pelecyphorus* (*Astrotus*) *regularis* (Horn). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (sex undetermined) labeled: a) "Tex"; b) "Type No. 3941" [old ANSP number]; c) "A. / regularis / Horn"; d) "MCZ TYPE / 7191". (MCZ).

**Additional Material Examined** (48 specimens). USA: Texas (Atascosa, Brewster, Kinney, Pecos, Terrell, Uvalde, Val Verde Counties). MEXICO: Coahuila, Durango, and Nuevo Leon.

**Redescription (see fig. 2.3).** Length 9.7-15.4mm, width 5.0-8.1mm. Body generally evenly thickly coated with debris. **Head:** Densely clothed with *Astrotus*-type stellate setae arising from small tubercles, primary seta long, pale, spiniform, and decumbent; frontoclypeal suture laterally impressed, medial depression faintly or deeply impressed; epistoma broadly rounded, epistomal suture obscured and not indented at margin; eye reniform, nearly flat, and surrounded by a black callus; labrum narrowing towards apex; apical segment of maxillary palp securiform in both sexes; mentum with erect pale spiniform setae and densely foveate, minute tomentum coating surface between fovea. Tomentose sensilla on antennal segment 10 small and oval, not wrapping around apex; apical tomentose sensillum on antennal segment 11 small, barely visible laterally. **Prothorax:** Lateral margin broadly sinuate, dilated near middle, but not forming an acute

flange; anterior apicies slightly produced and broadly rounded, posterior apicies acute and barely projecting over elytral humera, posterior margin nearly straight, occasionally with a minute medial tooth. Pronotal disc densely clothed with *Astrotus*-type stellate setae arising from large tubercles, primary setae short and spiniform or longer and lanceolate; longitudinal medial depression usually glabrous throughout, apical third with a low carina; two elongate paramedial fossae present or faintly indicated and setose. Prosternal process broadly rounded, medially impressed or not, gradually deflexed behind procoxae. **Pterothorax:** Densely, evenly coated with *Astrotus*-type stellate setae arising from minute tubercles, primary setae short and spiniform or longer and lanceolate. Elytra gradually widening to apical third, before sharply sloping and tapering caudad; cauda not reflexed; marginal costa present and tuberculate, lacking lateral projections; elytral humera carinate and reflexed. Scutellum small and glabrous, mesonotum glabrous and impunctate between scutellum and raised, shelf-like, scutum. Elytral disc moderately punctate and costate; sutural costa not raised; discal costa present and reaching elytral base, irregular projections occassionaly present near posterior edge of costa; transverse costa short, often connecting sutural and discal costae, never connecting discal and marginal costae. **Legs:** Mesotrocantin minute, concealed. Femora and tibia densely clothed in *Astrotus*-type stellate setae, primary setae simple, decumbent and nearly clear; tarsi venter with short pale spiniform setae; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi. **Abdomen:** Densely shallowly punctate, punctures subtended by *Astrotus*-type stellate setae, arising from minute tubercles.

**Diagnosis.** *P. regularis* can be separated from the other members of the *Astrotus* subgenus based on the following character combination: tomentose sensilla on antennal segment 10 small, oval; prosternal process gradually declivios behind procoxa; pronotal lateral margin sinuate and broadly rounded; elytral marginal carinae without lateral projections; elytral discal costa reaching anterior elytral margin.

**Distribution.** Known from western Texas and northeastern Mexico.

**Biology.** Unknown. Collected in pitfall traps set in sandy soil, under rocks, walking on surface, or from around *Pogonomyrmex* nests.

**Variation.** *Astrotus*-type stellate setae on specimens from Mexico have a long lanceolate seta as the primary setae and larger projections on the elytral discal costa posterad. Mexican specimens may represent an undescribed sister species to *P. regularis*, but further study and increased taxon sampling are needed before any definitive determination can be made.

### *Pelecyphorus* (*Astrotus*) *hebes* (Champion), New Combination

*Ologlyptus hebes* Champion, 1892:506

*Stenosides hebes* (Champion). Wilke, 1922:268

*Pelecyphorus* (*Astrotus*) *hebes* (Champion). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (sex undetermined) labeled: a) Orange bordered white circle reading "Type"; b) "Villa Lerdo, / Durango. / Hoge."; c) "Ologlyptus / hebes, Ch."; d) "Sp. figured."; d) "B.C.ACol.IV.1. / Ologlyptus / hebes.".

(BNMH). PARALECTOTYPES [all bearing the label "PARALECTOTYPE / *Ologlyptus* / hebes / Champion, 1892 / det. ADSmith" on yellow paper]: 6 specimens (BMNH) all bearing the same locality data as the lectotype.

Additional Material Examined. Three specimens (ZMHB), two labeled: "Mexico / J.Flohr G.", one labeled: "Coy".

**Redescription (see fig. 2.4).** Length 18.8-22.9mm, width 9.5-11.1mm. Body generally evenly thickly coated with debris. **Head:** Densely shallowly foveate, minute tomentum coating surface between fovea, each fovea subtended by a decumbent, pale, squamate setae; frontoclypeal suture laterally impressed, medial depression faintly or deeply impressed; epistoma broadly rounded, epistomal suture obscured and not indented at margin; eye reniform, nearly flat, and surrounded by a black callus; labrum laterally rounded; apical segment of maxillary palp securiform in both sexes; mentum with erect pale spiniform setae and densely foveate, minute tomentum coating surface between fovea. Tomentose sensilla on antennal segment 10 small and oval, not wrapping around apex; apical tomentose sensillum on antennal segment 11 small, barely visible laterally. **Prothorax:** Lateral margin broadly sinuate, dilated near middle, but not forming an acute flange; anterior apicies produced and rounded, posterior apicies acute, not projecting over elytral humera, posterior margin nearly straight, lacking a minute medial tooth. Pronotal disc densely shallowly foveate, minute tomentum coating surface between fovea, each fovea subtended by a short, decumbent, squamate setae; longitudinal medial depression and paramedial fossae absent. Prosternal process medially impressed and deflexed behind procoxae. **Pterothorax:** Densely, evenly coated with *Astrotus*-type stellate setae arising

from minute tubercles, primary setae short and nearly squamate. Elytra broadly ovate, widest near middle; and tapering caudad; cauda not reflexed; marginal costa present and tuberculate, lacking lateral projections, inner branch present as a short distinct ridge on disc between margin and discal costa; elytral humera obtuse and not reflexed. Scutellum glabrous and impunctate, mesonotum with a faint costa between scutellum and raised, shelf-like, scutum. Elytral discal costa present, evenly raised and lacking projections; sutural costa not raised; transverse costa absent. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely shallowly foveate, minute tomentum coating surface between fovea, each fovea subtended by a decumbent, pale, squamate setae; tarsi venter medially glabrous with two lateral rows of short pale spiniform setae; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi. **Abdomen:** Densely clothed with *Astrotus*-type stellate setae, arising from minute tubercles.

**Diagnosis.** *P. hebes* can be separated from the other members of the *Astrotus* subgenus based on the following character combination: tomentose sensilla on antennal segment 10 small, oval; prosternal process gradually deflexed behind procoxa; pronotal lateral margin sinate and broadly rounded; pronotum lacking longitudinal medial depression; elytral marginal carinae without lateral projections; elytral humera obsolete, not reflexed; irregular transverse costa and projections lacking on elytra; mesotrocantin exposed.

**Distribution.** Known only from the region of Villa Lerdo in Durango, Mexico.

**Biology.** Unknown.

**Discussion.** *P. hebes* is currently known from only 12 specimens, all collected prior to 1892.

## *Pelecyphorus* (*Astrotus*) *crypticus* Smith, New Species

**Type Material.** HOLOTYPE (female) labeled: a) "TEX. Dickens Co. / 2 mi. SW Dickens / X-17-1971 pitfall / trap E. Zukauckas"; b) green paper circle denoting the KWBC; c) on red paper, "HOLOTYPE / *Pelecyphorus* / (*Astrotus*) / *crypticus* ♀ / Aaron D. Smith" (CASC). PARATYPES (64 specimens) [all bearing the label "PARATYPE / *Pelecyphorus* / (*Astrotus*) / *crypticus* / Aaron D. Smith" on yellow paper] with the following locality data: same as holotype (2-KWBC); "Texas, Dickens Co. / 9mi. SE. Dickens / Sept 3 1969" (1-KWBC); "1 Sep 70 / Lubb Co. Tx / J. Carroll" (1-TTUZ); "12 mi SW / Post TX. / Garza Co. / 3-IX-1973" (1-TTUZ); "20 Sept 70 / Lubbock Co / Tex D.F. Pruner" (1-TTUZ); "5 mi. S / Kermit Texas / Winkler Co. / VII.29.1979" (1-TTUZ); "Aug 13 / Lubbock / Brunson" (1-TTUZ); "Lubbock Tex / X-10-48 / R. W." (2-KWBC); "Plainview T. / 10-1-31" (1-TAMU); "Robert Lee / TEX. Geococcyx / calif. 142460" (2-NMNH); "TEX. : Armstrong Co., / N. rim of Palo Duro / Cyn., 14 mi. S. of / Claude 3400 '. / 29-VIII-1971 leg. / K. Brown & P. Petrulia" (2-KWBC); "TEX. : Hall Co., / 6 mi. SE Turkey / 18-VI-1970 pitfalls / C.W. O'Brien" (2-KWBC); "TEX. Dickens Co. / 2 mi. SW Dickens / X-3-1971 pitfall / E. Zukauckas" (1-TTUZ); same as holotype, except date "X.1.1971" (1-KWBC); same as holotype, except date "X.3.1971" (1-KWBC); "TEX. Dickens Co. / 4mi. SW. Dickens / IV.17.1972 pitfall / trap E. Zukauckas" (1-KWBC); same as last, except date "X.10-1971" (2-KWBC); same as last, except date "X.7.1971" (1-KWBC); same as last, except date "XI-14-1971" (3-KWBC); same as last, except date "XI-18-1971" (1-KWBC); same as last, except date "XI-21-1971" (1-KWBC); same as last, except date "XII-9-1971" (1-KWBC); "TEX. Gaines Co., / abt. 18

mi SW / Seminole / 3-IX-1969" (1-KWBC); "TEX. Howard Co. / 10 mi. S. Big Spring / Hwy 33, VI-13-1971 / O'Brien & Marshall" (1-KWBC, 1-RLAC); same as last, except date "VI-5-1971" (3-KWBC); "TEX. Lubbock / X-17-1971 / C.W. O'Brien / pitfall trap" (9-KWBC); same as last, except date "X-29-1971" (1-KWBC); same as last, except date "X-3-6-1971" (5-KWBC); same as last, except date "XII-30-1971" (2-KWBC); "TEX. Reagan Co. / 16 mi. N. BigLake / VI-13-1971 / C. W. O'Brien" (1-KWBC); "TEX. Scurry Co. 4 / mi. N. Polar Rd. Hwy. 84 13-XI-1970 / MD. Merritt Pitfall" (5-KWBC); "Tex: Howard Co., / 10 mi. S. Big Spring on Hwy. 33 III-25-1973", b) "C.W. O'Brien, dead under stones and dung" (1-KWBC); "Texas, 10 mi. N / Dickens / Dickens Co. / 9-6. 1972" (1-TTUZ); a) "Aug 7", b) "Clark Co / Kansas" (1-NMNH).

**Description (see fig. 2.5).** Length 8.7-12.0mm, width 4.3-6.9mm. Body generally evenly thickly coated with debris. **Head:** Densely, shallowly foveate; fovea subtended by tubercles with *Astrotus*-type stellate setae at apex, primary seta squamate, primary seta short, pale, squamate or spiniform, and decumbent; frontoclypeal suture impressed, medial depression on frons faint or deep; epistoma broadly rounded, epistomal suture mostly obscured and not indented at margin; eye slightly reniform and surrounded by a black callus; labrum narrowing towards apex; apical segment of maxillary palp securiform in female, larger and isotriangular in male; mentum with erect pale spiniform setae and densely foveate, minute tomentum coating surface between fovea. Tomentose sensilla on antennal segment 10 small, slightly wrapping around apex; apical tomentose sensillum on antennal segment 11 covering one-third or less of segment. **Prothorax:** Lateral margin sinuate, dilated at middle and forming a broad triangular flange, apex of

flange straight or slightly reflexed; anterior apicies produced and acute, posterior apicies acute and barely projecting over elytral humera, posterior margin nearly straight, occasionally with a minute medial tooth. Pronotal disc densely, foveate; fovea subtended by *Astrotus*-type stellate setae on nearly confluent tubercles, primary seta squamate; longitudinal medial depression usually glabrous throughout, with a low carina near apical and posterior margins; two elongate paramedial fossae present or faintly indicated and setose. Prosternal process broadly rounded, medially impressed or not, raised behind procoxae. **Pterothorax:** Elytra costate; sutural costa strongly raised at base and partially covering scutellum, gradually eroding posterad and absent in apical third; discal costa present and reaching elytral base; marginal costa present and tuberculate, lacking lateral projections; elytral humera carinate and reflexed; transverse costa numerous, connecting sutural, discal, and marginal costae, giving the elytra a honeycombed appearance. *Astrotus*-type stellate setae densely clustered along crests of costae and arising from small tubercles, primary setae short and spiniform or squamate; stellate setae and punctures sparse between costa. Elytra gradually widening to apical third, before sharply sloping and tapering caudad; cauda not reflexed; Scutellum small and glabrous, mesonotum tuberculate and occasionally costate between scutellum and raised, shelf-like, scutum. **Legs:** Mesotrocantin minute, concealed. Femora and tibia densely clothed in *Astrotus*-type stellate setae, primary setae simple, decumbent and nearly clear; tarsi venter with short pale spiniform setae; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur subequal to basitarsi. **Abdomen:** Densely shallowly punctate, punctures subtended by *Astrotus*-type stellate setae, arising from minute tubercles.

**Diagnosis.** *P. crypticus* can be separated from the other members of the *Astrotus* subgenus based on the following character combination: prosternal process raised behind procoxa, apex broadly rounded; pronotal lateral margin acutely sinuate and dilated at middle; elytral marginal carinae without lateral projections; numerous transverse costae present on elytra, creating an irregular pattern of cells.

**Distribution.** Known from northwestern Texas and Kansas.

**Biology.** Unknown.

## subgenus *Stenosides* Solier, 1836

*Stenosides* Solier 1836:484. Type species: *Stenosides graciliformis* Solier, 1836, by monotypy.

=*Pactostoma* LeConte 1858:19. Type species: *Stenosides anastomosis* (Say), 1824, by original designation.

=*Ologlyptus* Lacordaire 1859:158 (unnecessary replacement name).

**Description.** Length 7.5-13.5mm, width 3.6-6.7 wide. Integument black to ferruginous; densely to sparsely clothed in decumbent flattened yellowish-white lanceolate or acuminate setae. **Head:** Mentum large, completely filling buccal cavity, sub-trapezoidal; anterior margin straight to weakly emarginate, occasionally with a minute median notch; lateral margins straight or weakly curved inward at apicies. Ligula small, less than one-fifth mentum width, straight or slightly curved, concealed or barely visible. Apical segment of maxillary palps securiform to triangular. Submentum broad, laterally contacting postgena or leaving at most a minute space between them. Postgenal process

produced, slightly swollen, broadly rounded. Labrum with apical margin straight; medial tormal process shorter than posterior tormal process; clypeal membrane concealed. Clypeal margin straight or broadly emarginate. Dorsal sulcus present above apices of eyes; eyes broadly oval to slightly reniform. Antenna weakly clavate; antennal segments 3-8 rounded, slightly moniliform; segments 9-11 flattened, forming a weak club; antennal segment 10 subquadrate or widest at apicies; two tomentose sensory patches present at lateral apices; antennal segment 11 with a broad apical tomentose sensory patch, amplected into segment 10. **Prothorax:** Pronotum with or without distinct lateral costae; foveate, with the anterior margin of each fovea bearing a single decumbent yellowish-white setae. Prosternum medially flat, sharphly rising at base of procoxal cavites to form prosternal process; prosternal process declivous behind procoxae. **Pterothorax:** Scutellum triangular; mesonotum with two transverse setae lined depressions leaving a thin medial ridge between the scutellum and scutum. Elytra broadly convex; sculpturing variable. Marginal costa present, generally divided in posterior one-half to one-third of elytron, inner branch strong, faintly indicated, or reduced to a row of tubercles. Discal costa present, divided near elyron base, inner branch strong to faintly indicated, branches meeting in distal third of elytron. Sutural costa slightly raised or absent. Transverse ridges between elytron costae present or absent, position variable. Epipleuron mostly obscured, costate from abdominal ventrite 3 or 4 to elytron apex. **Legs:** Setose; mesotrocantin small, visible.

**Diagnosis.** The subgenus *Stenosides* is distinguished from other *Pelecyphorus* subgenera by a unique combination of the following characters: mentum completely filling buccal cavity, sub-trapezoidal, anterior margin straight or weakly emarginate, lateral apicies not

strongly bent inward; ligula less than one-fifth mentum width, concealed to barely visible; apical segment of maxillary palps securiform or triangular; labral margin straight; postgenal process produced, slightly swollen, broadly rounded; eyes broadly oval to slightly reniform; prosternal process declivous behind procoxae; transverse setose depressions on mesonotum; mesotrocantin small.

**Distribution.** Arid habitats from central and southern Mexico to the western United States. The states where they are currently known to occur are MEXICO: Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Nuevo Leon, Mexico, Mexico D.F., Oaxaca, Puebla, San Luis Potosi, Tlaxcala, Zacatecas; USA: Arizona, Colorado, Kansas, New Mexico, Texas.

## Species Descriptions

### *Pelecyphorus* (*Stenosides*) *anastomosis* (Say)

*Asida anastomosis* Say, 1824:256

*Pelecyphorus anastomo*sis (Say). LeConte 1851:33

*Microschatia anastomosis* (Say). LeConte 1853:446

*Pactostoma anastomosis* (Say). LeConte, 1858:19

*Ologlyptus anastomosis* (Say). Lacordaire, 1859:159

*Pactostoma anastomosis* (Say). Casey, 1912:86

*Stenosides anastomosis* (Say). Wilke, 1922:268

*Pelecyphorus* (*Stenosides*) *anastomosis* (Say). Smith, 2010

=*Stenosides anastomosis salebrosa* Casey, 1912:87, **New Synonym**

=*Stenosides breviuscula* Casey, 1912:87, **New Synonym**

=*Stenosides exoleta* Casey, 1912:87, **New Synonym**

=*Stenosides luteotecta* Casey, 1912:88), **New Synonym**

=*Stenosides monticola* (Casey, 1912:88), **New Synonym**

=*Stenosides obtecta* (Casey, 1912:89), **New Synonym**

=*Stenosides sigillata* (Casey, 1912:89), **New Synonym**

**Type Material.** NEOTYPE, designated here, (female) labeled: a) "Kan. / Snow"; b) "Coll Hubbard / & Schwarz"; c) on red paper, "NEOTYPE / *Asida* / *anastomosis* / Say, 1824 / det. Aaron D. Smith". (NMNH).

**Additional Material Examined.** (151 specimens). USA: Arizona, Colorado, Kansas, New Mexico, Texas. MEXICO: Chihuahua.

**Redescription (see fig. 2.6).** Length 8.1-13.5mm, width 3.8-6.7mm. Integument black to ferruginous, often coated with debris; setae pale, yellowish-white to golden; elytra wider than pronotum. **Head:** Densely foveate, each fovea subtended by a decumbent, lanceolate setae; frontoclypeal suture and medial depression on frons faintly or deeply impressed; epistoma broadly rounded, epistomal suture obscured and not indented at margin; eye elongate, oval or slightly reniform; apical segment of maxillary palp securiform in female, isotriangular in male. Mentum foveate with decumbent lanceolate setae, becoming erect and acuminate apically, anterior margin with or without a minute median

notch. Antenna moderately clothed in erect acuminate setae; antennal segment 10 widest at apicies, approximately 2X larger than segment 11. **Prothorax:** Pronotum weakly sinuate, widest near middle; marginal costa present, not reflexed, and gradually widening anteriorly; anterior apicies barely produced and rounded, posterior apicies acute, not projecting over elytral humera, posterior margin nearly straight, rarely with a minute medial tooth. Pronotal disc densely foveate, each fovea subtended by a decumbent lanceolate setae, often arising from a minute tubercle; medially longitudinally impunctate and glabrous in most specimens, rarely with a faint costa. Prosternal process sharply raised from prosternum anteriorly, deflexed behind procoxae. **Pterothorax:** Moderately clothed with decumbent lanceloate setae arising from minute tubercles, denser along crests of costae. Elytra ovate, broadly convex, and costate; marginal costa present and tuberculate, inner branch present as a short distinct ridge on disc or reduced to a row of tubercles; elytral humera distinct and not or slightly reflexed; discal costa present, bifurcating near base and reunited in apical third, inner branch often eroded and barely visible; sutural costa feebly raised or not; transverse costae present and confused between discal and marginal costa. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely shallowly foveate and setose, setae short and acuminate, with stouter darker colored setae also present along inner margins of tibia; tarsi venter with pale acuminate setae, and stouter darker setae along lateral margins, medially nearly glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi. **Abdomen:** Moderately punctate, punctures small and subtended by decumbent acuminate setae.

**Diagnosis.** *P. anastomosis* can be separated from the other members of the *Stenosides* subgenus based on the following character combination: Pronotum weakly sinuate, marginal costa present and not reflexed; frontoclypeal suture faintly or deeply impressed; elytra with transverse anastomizing ridges present and restricted to space between elytral and marginal costae.

**Distribution.** USA: Arizona, Colorado, Kansas, New Mexico, Texas. MEXICO: Chihuahua.

**Biology.** Collected from underneath rocks, plant debris, and dung.

**Discussion.** Thomas Say's original specimen(s) were presumably destroyed along with most of his collection, hence the need for a neotype. The *Stenosides* species synonymized under *P. anastomosis* were all described by Casey (1912) from one or two specimens each taken from disparate localities. All of the characters used to separate them vary within any given population of *P. anastomosis* throughout their range.

### *Pelecyphorus* (*Stenosides*) *cavatus* Smith, New Species

**Type Material.** HOLOTYPE, (sex undetermined) labeled: a) "Mexico: Coahuila / 20 mi N of Conception / del Oro 5800' / 10 August 1993 / Collector Unknown / Cal. Acad Sci. Collection"; b) "California Academy / of Sciences / collection"; c) on red paper, "HOLOTYPE / *Pelecyphorus* / (*Stenosides*) / *cavatus* / Aaron D. Smith" (CASC). PARATYPES (3-CASC) [all bearing the label "PARATYPE / *Pelecyphorus* / (*Stenosides*) / *cavatus* / Aaron D. Smith" on yellow paper]: with same label data as holotype.

**Description (see fig. 2.7).** Length 10.0-12.5mm, width 4.9-6.1mm (holotype length: 11.1mm, width: 5.6mm). Integument black; setae pale yellowish-white unless otherwise noted; elytra wider than pronotum. **Head:** Densely foveate, each fovea with a decumbent acuminate or lanceolate setae arising from margin or side; frontoclypeal suture deeply transversely excavated; clypeus swollen and sloping towards labrum, anterior margin of clypeus broadly emarginate; medial depression on frons absent or faintly impressed; epistoma broadly rounded, epistomal suture mostly obscured and not indented at margin; broad sulcus present around apex of eye; eye broadly oval to slightly reniform; apical segment of maxillary palp securiform in both sexes. Mentum foveate with erect acuminate setae, more numerous near anteriorly, anterior margin nearly straight and without a minute median notch. Antenna moderately clothed in erect acuminate setae; antennal segment 10 subquadrate, approximately 1.5X larger than segment 11. **Prothorax:** Pronotum nearly parallel sided, weakly sinuate, widest near middle; marginal costa eroded and absent or nearly absent over most of length; anterior apicies barely produced and rounded, posterior apicies acute, not projecting over elytral humera, posterior margin straight, lacking a medial tooth. Pronotal disc densely foveate, each fovea with a decumbent acuminate or lanceolate setae arising from margin or side. Prosternal process sharply raised from prosternum anteriorly, medially longitudinally impressed, and deflexed behind procoxae. **Pterothorax:** Sparsely and irregularly punctate and setose, setae decumbent and acuminate. Elytra ovate, nearly planate on disc, and costate; marginal costa slightly raised and broadly rounded, bifurcate in apical third; elytral humera small, obtuse, and not reflexed; discal costa present, broadly rounded and

slightly raised, bifurcating near base and reunited in apical third, inner branch eroded and barely visible; sutural costa not raised; transverse costae absent or present and slightly raised in between discal and marginal carinae in apical third. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely shallowly foveate and setose, setae short and acuminate, with stouter darker colored setae also present along inner margins of tibia; tarsi venter with pale acuminate setae, and stouter darker setae along lateral margins, medially nearly glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi. **Abdomen:** Moderately punctate, punctures small and subtended by acuminate setae.

**Diagnosis.** *P. cavatus* can be separated from the other members of the *Stenosides* subgenus based on the following character combination: Frontoclypeal suture deeply transversely excavate; pronotum weakly sinuate, marginal costa absent or faintly indicated over most of length.

**Distribution.** Known only from the type locality.

**Etymology.** The specific epithet is Latin and means "hollowed out", referring to the deeply excavated head.

**Biology.** Unknown.

### *Pelecyphorus* (*Stenosides*) *deaztlani* Smith, New Species

**Type Material.** HOLOTYPE, (sex undetermined) labeled: a) "MEXICO. Nuevo / Leon: Hwy 58, 13 km / E of junction with Hwy / 57, 2000 m / 5 Jun 1993."; b) on red paper, "HOLOTYPE / *Pelecyphorus* / (*Stenosides*) / *deaztlani* / Aaron D. Smith" (CASC).

PARATYPES (2-CASC, 1-KWBC) [all bearing the label "PARATYPE / *Pelecyphorus* / (*Stenosides*) / *deaztlani* / Aaron D. Smith" on yellow paper]: with same label data as holotype.

**Description (see fig. 2.8).** Length 9.3-10.5mm, width 4.9-5.6mm (holotype length: 9.3mm, width: 5.4mm). Integument black; setae pale yellowish-white unless otherwise noted; elytra slightly wider than pronotum. **Head:** Densely foveate, each fovea with a decumbent acuminate or lanceolate setae arising from margin or side; frontoclypeal suture impressed; anterior margin of clypeus slightly emarginate; medial depression on frons faintly impressed; epistoma broadly rounded, epistomal suture mostly obscured and not indented at margin; broad sulcus present around apex of eye; eye broadly oval to slightly reniform; apical segment of maxillary palp securiform in both sexes. Mentum foveate with erect acuminate setae, more numerous near anteriorly, anterior margin nearly straight and without a minute median notch; submentum deeply transversely impressed posteriorly, anterior margin broadly emarginate. Antenna moderately clothed in erect acuminate setae; antennal segment 10 subquadrate, approximately 1.5-2X larger than segment 11. **Prothorax:** Pronotum weakly sinuate, widest near middle; marginal costa present , expanded, and not reflexed; anterior apicies barely produced and rounded, posterior apicies acute, not projecting over elytral humera, posterior margin straight, lacking a medial tooth. Pronotal disc densely foveate, each fovea with a decumbent acuminate or lanceolate setae arising from margin or side. Prosternal process sharply raised from prosternum anteriorly, medially longitudinally impressed, and deflexed behind procoxae. **Pterothorax:** Moderately setose, setae decumbent and lanceolate, and

irregularly punctate and. Elytra ovate, broadly convex, and costate; marginal costa slightly raised and broadly rounded, bifurcate in apical third; elytral humera small, obtuse, and not reflexed; discal costa present, broadly rounded and slightly raised, bifurcating near base and reunited in apical third, inner branch eroded and barely visible; sutural costa not raised; transverse costae absent or present and slightly raised in between discal and marginal carinae in apical third. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely shallowly foveate and setose, setae short, acuminate, and arising from small tubercles on tibia, with stouter darker colored setae also present along inner margins of tibia; tarsi venter with pale acuminate setae, and stouter darker setae along lateral margins, medially nearly glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi. **Abdomen:** Moderately punctate, punctures small and subtended by acuminate setae.

**Diagnosis.** *P. deaztlani* can be separated from the other members of the *Stenosides* subgenus based on the following character combination: Frontoclypeal suture regularly impressed; pronotum weakly sinuate, marginal costa present, expanded, and not reflexed; elytral costae broadly rounded, not tuberculate; submentum deeply transversely impressed.

**Distribution.** Known only from the type locality.

**Etymology.** The species is named in honor of Tonantzin Deaztlan for supporting the author throughout his graduate education.

**Biology.** Unknown.

## *Pelecyphorus* (*Stenosides*) *triplehorni* Smith, New Species

**Type Material.** HOLOTYPE, (male) labeled: a) "MEXICO: Dgo., 2 mi / NW Nombre de Dios / VII-12-1975"; b) "CA, WE, BW / Triplehorn"; c) on red paper, "HOLOTYPE / *Pelecyphorus* / (*Stenosides*) / *triplehorni* ♂/ Aaron D. Smith" (OSUC). PARATYPES (15-OSUC) [all bearing the label "PARATYPE / *Pelecyphorus* / (*Stenosides*) / *triplehorni* / Aaron D. Smith" on yellow paper]: with same label data as holotype.

**Description (see fig. 2.9).** Length 10.3-12.6mm, width 5.0-6.4mm (holotype length: 11.0mm, width: 5.3mm). Integument black to ferruginous, often coated with debris; setae yellowish-white to light brown; elytra wider than pronotum. **Head:** Densely foveate, each fovea subtended by a decumbent, lanceolate setae; frontoclypeal suture faintly impressed, medial depression on frons faintly impressed or absent; epistoma broadly rounded, epistomal suture obscured and not indented at margin; broad sulcus present around apex of eye; eye elongate and broadly oval; apical segment of maxillary palp securiform in female, isotriangular in male. Mentum foveate with erect acuminate setae, anterior margin without a minute median notch. Antenna moderately clothed in erect acuminate setae; antennal segment 10 widest at apicies, approximately 2X larger than segment 11. **Prothorax:** Pronotum weakly sinuate, widest near middle; marginal costa present, not reflexed; anterior apicies barely produced and acute, posterior apicies acute, not projecting over elytral humera, posterior margin nearly straight, occasionally with a minute medial tooth. Pronotal disc densely foveate, each fovea subtended by a decumbent acuminate setae; medially longitudinally impunctate, glabrous, and slightly raised in most

specimens. Prosternal process sharply raised from prosternum anteriorly, deflexed behind procoxae. **Pterothorax:** Moderately clothed with decumbent lanceloate or acuminate setae, sparser along rounded crests of costae. Elytra ovate, broadly convex, and costate; marginal costa present; elytral humera distinct and not reflexed; discal costa present and confused, forming a reticulating network of longitudinal and transverse costae, crests of costae rounded, smooth, and predominately glabrous; sutural costa not raised. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely shallowly foveate and setose, setae short and acuminate, with stouter darker colored setae also present along on tibia; tarsi venter with pale acuminate setae, and stouter darker setae along lateral margins, medially nearly glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi. **Abdomen:** Moderately punctate, punctures small and subtended by decumbent acuminate setae.

**Diagnosis.** *P. triplehorni* can be separated from the other members of the *Stenosides* subgenus based on the following character combination: Pronotum weakly sinuate, marginal costa present and not reflexed; frontoclypeal suture faintly impressed; elytra with a reticulated network of rounded costae, crests of costae rounded, smooth, and nearly glaberous.

**Distribution.** MEXICO: Durango.

**Etymology.** The species is named in honor of Charles A. Triplehorn, collector of the type series and tenebrionid taxonomist extraordinaire.

**Biology.** Unknown.

## *Pelecyphorus* (*Stenosides*) *limosus* (Champion), New Combination

*Astrotus limosus* Champion 1884:66

*Pelecyphorus* (*Stenosides*) *limosus* (Champion). Smith, 2010

**Type Material.** HOLOTYPE, by monotypy, (sex undetermined) labeled: a) Orange bordered white circle reading "Type"; b) "Mexico. / Salle Coll.";c) "Astrotus / limosus / Champ"; d) "Sp. figured." ; e) "B.C.ACol.IV.1. / Astrotus / limosus". (BMNH).

**Redescription (see fig. 2.10).** Length 7.8mm, width 3.3mm. Integument black and coated with debris; setae predominately pale, yellowish-white; elytra slightly wider than pronotum and approximately 2.6X longer. **Head:** Densely foveate, each fovea subtended by a decumbent, lanceolate setae; frontoclypeal suture and medial depression on frons deeply impressed; epistoma broadly rounded, epistomal suture obscured and not indented at margin; eye slightly reniform. Mentum anterior margin without a minute median notch. Antenna moderately clothed in erect acuminate setae; antennal segment 11 deeply amplected into segment 10; antennal segment 10 subquadrate and much larger than segment 11. **Prothorax:** Pronotum weakly sinuate, widest near middle; marginal costa present, expanded, and slightly reflexed; anterior apicies barely produced and rounded, posterior apicies acute, not projecting over elytral humera, posterior margin nearly straight. Pronotal disc confluently foveate, giving surface a rough uneven appearance, with short lanceolate setae. Prosternal process sharply raised from prosternum anteriorly, deflexed behind procoxae. **Pterothorax:** Sparsely clothed with short lanceloate setae,

denser along crests of costae. Elytra ovate, broadly convex, and costate; marginal costa broadly rounded and reticulate, confluent with discal costa in apical third; elytral humera small and not reflexed; discal costa present broadly rounded and reticulate, bifurcating near base, branches not connected or reaching elytral base anteriorly, reunited in apical third, with a small additional outer branch present behind middle, not confluent with other costae posteriorly; sutural costa not raised. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely setose and coated with debis, setae short, acuminate, and arising from small tubercles on tibia; tarsi venter with pale acuminate setae along lateral margins, medially nearly glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi. **Abdomen:** Surface obscured by debris, moderately clothed in acuminate setae.

**Diagnosis.** *P. limosus* can be separated from the other members of the *Stenosides* subgenus based on the following character combination: Pronotum weakly sinuate, marginal costa present and not reflexed, pronotal disc confluently foveate; antennal segment 11 small and deeply amplected into segment 10.

**Distribution.** Mexico.

**Biology.** Unknown.

**Discussion.** The exact type locality is unknown. Three additional specimens labeled a) "Mexico / Tehuautc"; b) "Fry Coll. / 1905. 100.", were placed with Champion's *P. anastomosis* specimens in the BMNH, and may be conspecific with the *P. limosus* type based on their size, pronotal sculpturing and antennal configuration. However, they vary from *P. limosus* in elytral sculpturing. Additional specimens are needed to ascertain whether or not they are *P. limosus* or an undescribed species.

***Pelecyphorus* (*Stenosides*) *graciliformis* (Solier)**

*Stenosides graciliformis* Solier, 1836:486

*Ologlyptus graciliformis* (Solier). LaCordaire, 1859:159

*Stenosides graciliformis* Solier. Casey, 1912:84

*Pelecyphorus* (*Stenosides*) *graciliformis* (Solier). Smith, 2010

=*Stenosides canus* (Champion, 1884:68), **New Synonym**

=*Stenosides sinuaticollis* (Champion, 1884:69), **New Synonym**

**Type Material.** NEOTYPE, designated here, (female) labeled: a) "Oaxaca, / Mexico. / Hoege." ; b) "Ologlyptus / graciliformis / Sol."; c) "B.C.A. Col.IV.1. / Ologlyptus / graciliformis."; d) on red paper, "NEOTYPE / *Stenosides* / *graciliformis* / Solier, 1836 / det. Aaron D. Smith". (BMNH).

**Additional Material Examined.** (46 specimens). MEXICO: Durango, Guanajuato, Hidalgo, Mexico, Mexico D.F., Oaxaca, Puebla, San Luis Potosi, Tlaxcala, Zacatecas.

**Redescription (see fig. 2.11).** Length 8.0-12.1mm, width 4.3-6.2mm (neotype length: 11.7mm, width: 6.0mm). Integument black to ferruginous, and setose; setae pale, yellowish-white to golden, acuminate to slightly lanceolate, and decumbent unless otherwise noted; elytra wider than pronotum, pronotum base wider than elytral base; often coated with debris. **Head:** Densely foveate, each fovea subtended by a setae; frontoclypeal suture and medial depression on frons faintly or deeply impressed;

epistoma broadly rounded, epistomal suture obscured and not indented at margin; eye broadly oval; apical segment of maxillary palp securiform in both sexes. Mentum foveate and setose, anterior margin without a minute median notch. Antenna moderately clothed in erect setae; antennal segment 10 widest at apicies, approximately 2X larger than segment 11. **Prothorax:** Pronotum sinuate, widest near middle; marginal costa expanded, crenulate, and reflexed; anterior apicies slightly produced and acute, posterior apicies acute, not projecting over elytral humera, posterior margin nearly straight, without a minute medial tooth. Pronotal disc densely foveate, each fovea subtended by a setae. Prosternal process sharply raised from prosternum anteriorly, deflexed behind procoxae. **Pterothorax:** Moderately setose, setae denser along crests of costae, with scattered fovea. Elytra ovate, broadly convex, and costate; marginal costa present and tuberculate, inner branch present as a short separate carina on posterior half of disc, not confluent with discal carina; elytral humera obtuse; discal costa carinate, confluent with marginal carina caudally; sutural costa not raised; transverse costae absent. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely shallowly foveate and setose; tarsi venter with long pale setae; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur shorter than basitarsi; outer apical spine of protibia large, length approximately equal to protibial width, and acute. **Abdomen:** Densely punctate and setose.

**Diagnosis.** *P. graciliformis* can be separated from the other members of the *Stenosides* subgenus based on the following character combination: Pronotum sinuate, marginal costa expanded, crenulate and reflexed; elytra without transverse costae; protibial spine large.

**Distribution.** MEXICO: Durango, Guanajuato, Hidalgo, Mexico, Mexico D.F., Oaxaca, Puebla, San Luis Potosi, Tlaxcala, Zacatecas.

**Biology.** Unknown.

**Discussion.** *P. graciliformis* was originally described by Solier (1836), probably from a single specimen. A specimen previously considered to be the type is housed in the MNHN and bears the following labels: a) "TYPE"; b) "Ologlyptus / graciliformis / [illegible, possibly Mex.] / [illegible looks like dupl.]"; c) "Mexique"; d) "Stenosides / graciliformis / Solier / Type de Solier / Col. de Marseul / C. Girard vid. 1979". Upon examination it was clear that this specimen did not fit Solier's original description or illustrations. It was identified as a specimen of *P.* (*Sicharbas*) *debilis* (Champion). MNHN staff could not find another specimen labeled Stenosides graciliformis, nor any specimens matching automontaged images of *P. graciliformis* sent to the museum. Given the possibility that Champion may have seen the original type, a specimen matching Solier's description and labeled *Ologlyptus graciliformis* by Champion was selected from the BMNH as the neotype.

### ***Pelecyphorus* (*Stenosides*) *texanus* (Wickham)**

*Ologlyptus texanus* Wickham, 1903:72

*Stenosides texanus* (Wickham). Casey, 1912:84

*Pelecyphorus* (*Stenosides*) *texanus* (Wickham). Smith, 2010

**Type Material.** HOLOTYPE (male) labeled: a) "Cameron Co. Tex. IX" ; b) "HOLOTYPE / *Ologlyptus* / *texanus* / Wickham, 1836". (NMNH).

**Additional Material Examined.** (11 specimens). Texas: Cameron and Starr Counties.

**Redescription (see fig. 2.12).** Length 7.4-10.1mm, width 3.9-5.3mm. Integument black to ferruginous, and setose; setae pale, yellowish-white to light brown, lanceolate, and decumbent unless otherwise noted; elytra wider than pronotum and approximately 3X longer; often coated with debris. **Head:** Densely foveate, each fovea subtended by a setae; frontoclypeal suture and medial depression on frons faintly impressed; epistoma broadly rounded, epistomal suture obscured and indented at margin; eye elongate, slightly reniform oval; apical segment of maxillary palp securiform in female, isotriangular in male. Mentum foveate and setose, anterior margin without or without a minute median notch. Antenna moderately clothed in erect acuminate setae; antennal segment 10 widest at apicies, approximately 2X larger than segment 11. **Prothorax:** Pronotum strongly sinuate, widest near middle, then constricted in basal third before expanding at posterior apicies; marginal costa tuberculate, not reflexed; anterior apicies produced and rounded, posterior apicies acute, slightly divergently produced, not projecting over elytral humera, posterior margin nearly straight, medially with a large bifurcating process emerging from disc; pronotal disc densely foveate, each fovea subtended by a setae; longitudinal medial ridge present near apex, then strongly raised and triangular from midline to past pronotal base, forming a large bifurcate process. Prosternal process deflexed behind procoxae. **Pterothorax:** Moderately foveate and setose, setae denser along crests of costae. Elytra slightly ovate, widest behind middle,

and costate; marginal costa present and tuberculate, elytral humera prominent and reflexed; discal costa divided, not meeting at tips and parallel over entire length, not reaching elytral base; sutural costa not or slightly raised; broadly rounded low transverse costa present and connecting longitudinal costae or not. **Legs:** Mesotrocantin minute, exposed or concealed. Femora and tibia clothed in white decumbent lanceolate setae, anterior margins of tibia also with stouter dark brown spiniform setae; tarsi venter with stout brown spiniform setae; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length subequal to basitarsi. **Abdomen:** Densely punctate and setose.

**Diagnosis.** *P. texanus* can be separated from the other members of the *Stenosides* subgenus based on the following character combination: Pronotum strongly sinuate, widest near middle, then constricted in basal third before expanding at posterior apicies; Median ridge on pronotum strongly raised and triangularly expanded in basal half, forming a large bifurcate process projecting past basal pronotal margin.

**Distribution.** Only known from the southern tip of Texas (Cameron and Starr Counties).

**Biology.** Unknown.

### subgenus *Sicharbas* Champion, 1884

*Sicharbas* Champion, 1884:67. Type species: *Sicharbas lobatus* Champion, 1884:67, by monotypy.

**Redescription.** Length 6.0-12.3mm, width 2.3-5.7. Integument black to ferruginous; densely to sparsely setose, setae simple, lanceolate, or squamate. **Head:** Mentum large,

completely filling buccal cavity, sub-trapezoidal; anterior margin straight to weakly emarginate, occasionally with a shallow median notch; lateral margins straight or weakly curved inward at apicies. Ligula small, one-fourth or less mentum width, straight or slightly curved, concealed or visible beyond anterior margin of mentum. Apical segment of maxillary palps securiform in both sexes. Submentum broad, laterally contacting postgena or leaving at most a minute space between them. Postgenal process produced, acute or rounded. Labrum with apical margin straight; medial tormal process shorter than posterior tormal process; clypeal membrane concealed. Clypeal margin straight. Dorsal sulcus absent or faint above apices of eyes; eyes broadly oval to slightly reniform. Antenna weakly clavate; antennal segments rounded, nearly moniliform; antennal segment 10 conical or flattened, widest at apicies, two tomentose sensilla present at lateral apices or coalesced into a continuous band; apex of antennal segment 11 with a broad tomentose sensillum, base of segment deeply or slightly amplected into segment 10 (Fig.). **Prothorax:** Pronotum with a distinct marginal costa, angulate or not, reflexed or not; pronotal disc tuberculate, with or without paramedial fossae or longitudinal medial depression, setation and punctation variable. Prosternal process medially impressed and declivous behind procoxae. **Pterothorax:** Scutellum triangular, mostly concealed beneath elytra; mesonotum with two transverse glabrous or setae lined depressions leaving a thin medial ridge between the scutellum and scutum. Elytra elongate-ovate, nearly parallel sided or widest behind middle; sculpturing variable, often with irregular crests or protrusions. Marginal costa present. Discal costa usually distinct near base or eroded and confused Sutural costa present or absent. Transverse ridges between elytron costae

present or absent, position variable. **Legs:** Setose; mesotrocantin small, exposed or concealed.

**Diagnosis.** The subgenus *Sicharbas* is distinguished from other *Pelecyphorus* subgenera by a unique combination of the following characters: mentum completely filling buccal cavity, sub-trapezoidal, anterior margin straight or weakly emarginate, lateral apicies not strongly bent inward; ligula slightly curved, width one-fourth or less mentum width, concealed or visible; apical segment of maxillary palps securiform; labral margin straight; postgenal process produced, acute or rounded; prosternal process declivous behind procoxae; pronotum tuberculate; elytra elongate and nearly parallel sided.

**Distribution.** MEXICO: Guerrero, Hidalgo, Michoacán, Mexico, Mexico D.F., Morelos, Oaxaca, Puebla. All known species appear to be restricted to high elevation localities (above 6000') in central and southern Mexico.

## Species Descriptions

### *Pelecyphorus* (*Sicharbas*) *lobatus* (Champion), New Combination

*Sicharbas lobatus* Champion, 1884:67

*Pelecyphorus* (*Sicharbas*) *lobatus* (Champion). Smith, 2010

**Type Material.** HOLOTYPE, by monotypy, (male) labeled: a) Orange bordered white circle reading "Type"; b) "1741"; c) "Truqui / Mexico."; d) "Mexico. / Salle Coll.";

"Sicharbas / lobatus / Champ"; e) "Sp. figured."; f) "B.C.ACol.IV.1. / Sicharbas / lobatus". (BMNH).

**Additional Material Examined.** (35 specimens). MEXICO: Guerrero, Mexico D.F., and Morelos.

**Redescription (see fig. 2.13).** Length 10.2-12.3mm, width 3.9-5.5 (holotype length: 10.6mm, width: 4.2mm). Integument black or ferruginous, often densely coated with debris; setae pale, yellowish-white to light brown, acuminate to slightly lanceolate, and decumbent unless otherwise noted; elytra slightly wider than pronotum and approximately 3X longer. **Head:** Confluently foveate with short erect setae emerging from sides or margins of fovea; frontoclypeal suture slightly impressed, clypeus elongate, epistomal suture indented at margin; medial depression on frons deeply broadly impressed; eye broadly oval. Mentum anterior margin straight or with a shallow median emargination. Antenna sparsely clothed in erect acuminate setae; antennal segment 10 conical, widest at apicies, tomentose sensilla coalesced into a broad continuous band around apical half; antennal segment 11 deeply amplected into segment 10, exposing only the broad tomentose sensillum on apex. **Prothorax:** Pronotum margin costate and angularly sinuate, dilated before middle and forming a triangular flange, apex of flange straight or reflexed; anterior apicies slightly produced and rounded; posterior apicies produced, straight or slightly divergent, projecting over elytral humera, rounded at tip; posterior margin convex with a rounded emargination on each side near apicies. Pronotal disc densely shallowly foveate; anterior margins of fovea raised, forming rounded tubercles, each with a single seta; longitudinal medial depression usually distinct; two or

four rounded paramedial fossae present. **Pterothorax:** Elytra densely clothed with long decumbent lanceloate or acuminate scales, erect along crests of costae; margin nearly parallel sided, slightly widening caudad; marginal costa tuberculate, slightly reflexed, and often with broken up into a series of irregular crests and protrusions, flanged before cauda and curving inward to elytral suture; elytral humera obliquely truncated; elytral disc with numerous tuberculate protrusions or short, oblique or transverse ridges; discal costa strongly raised in basal third, reaching basal margin of elytra; sutural costa tuberculate and raised behind scutellum to marginal costa. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely punctate and setose; tarsi venter clothed with long golden setae; combined protarsal segments approximately two-thirds length of protibia, apical protibial spine thin and setose to tip; anterior protibial spur shorter than basitarsi. **Abdomen:** Densely punctate and setose.

**Diagnosis.** *P. lobatus* can be separated from the other members of the *Sicharbas* subgenus based on the following character combination: Pronotum angularly sinuate, dilated before middle and forming a triangular flange, posterior apicies projecting over elytra; tomentose sensilla on antennal segment 10 coalesced into a broad continuous band.

**Distribution.** MEXICO: Guerrero, Mexico D.F., and Morelos.

**Biology.** Unknown. The few specimens with elevational data were collected from 10,000 to 10,500 feet above sea level.

***Pelecyphorus* (*Sicharbas*) *oaxacensis* Smith, New Species**

**Type Material.** HOLOTYPE (male) labeled: a)"MEX: OAXACA / MICROO. LA CUMBRE / N 16° 27.277' / W 97° 00.262' / 29 vi 95 2130 m / D. Curoe, Hopkins"; b) on red paper, "HOLOTYPE / *Pelecyphorus* / (*Sicharbas*) / *oaxacensis* ♂/ Aaron D. Smith" (CASC). (EMEC).

**Description (see fig. 2.14).** Length 11.3mm, width 5.7. Integument darkly ferruginous, nearly black; setae short, orange-brown, acuminate or lanceolate scales unless otherwise noted; elytra wider than pronotum, nearly equal at base, and approximately 2.7X longer. **Head:** Confluently foveate with short erect setae emerging from sides fovea, margins of combined fovea forming short longitudinal ridges; frontoclypeal suture deeply impressed at sides, epistomal suture not indented at margin; medial depression on frons deeply broadly impressed; eye broadly oval. Mentum anterior margin with a shallow median emargination. Antenna sparsely clothed in erect golden setae; antennal segment 10 conical, widest at apicies, tomentose sensilla coalesced into a broad continuous band around apical half; antennal segment 11, nearly as large as, and deeply amplected into segment 10, exposing only the broad tomentose sensillum on apex. **Prothorax:** Pronotum margin costate and sinuate, dilated before middle and forming a rounded, slightly reflexed flange; anterior apicies slightly produced and rounded; posterior apicies acute, barely produced, slightly divergent, and not projecting over elytral humera; posterior margin vaguely convex. Pronotal disc densely shallowly foveate; anterior margins of fovea raised, forming rounded tubercles, each with a single seta on lateral face;

longitudinal medial depression distinct; two rounded paramedial fossae present.

**Pterothorax:** Elytra widening from base to apical third before sharply sloping and tapering caudad; with scattered fovea and moderately clothed in erect or decumbent setae arising from sides of rounded tubercles; marginal costa tuberculate, slightly reflexed, flanged before cauda and curving inward to meet elytral costa in apical third; elytral humera oblique; discal costa tuberculate and raised over entire length, reaching basal margin of elytra anteriorly, meeting marginal costa posteriorly; sutural costa tuberculate and slightly raised throughout; low tuberculate protrusions or short, oblique or transverse costa irregularly distributed across disc. **Legs:** Mesotrocantin small, exposed. Femora foveate, fovea denser distally, and shiny; tibia slightly flared at apicies, densely foveate and setose, setae stout and erect; tarsi venter with long golden setae and shorter stouter setae laterally; combined protarsal segments approximately two-thirds length of protibia, apical protibial spine short and setose to tip; anterior protibial spur shorter than basitarsi.

**Abdomen:** Densely punctate and setose.

**Diagnosis.** *P. oaxacensis* can be separated from the other members of the *Sicharbas* subgenus based on the following character combination: Pronotum sinuate, dilated before middle and forming a broadly rounded flange, posterior apicies not projecting over elytra; tomentose sensilla on antennal segment 10 coalesced into a broad continuous band.

**Distribution.** Known only from type specimen.

**Etymology.** The species is named for the Mexican state of Oaxaca, the only state where it is known to occur.

**Biology.** Unknown. The type specimen was collected at an elevation of nearly 7,000 feet.

## *Pelecyphorus* (*Sicharbas*) *debilis* (Champion), New Combination

*Astrotus debilis* Champion, 1884:66

*Pelecyphorus* (*Astrotus*) *debilis* (Champion). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (female) labeled: a) Orange bordered white circle reading "Type"; b) "Mexico. / Salle Coll."; c) handwritten det. "Astrotus / debilis Champ"; d) "Sp. figured."; e) "B.C.ACol.IV.1. / Astrotus /debilis"; f) d) on red paper, "LECTOTYPE / *Astrotus* / *debilis* / Champion, 1884 / det. Aaron D. Smith". (BMNH). PARALECTOTYPES, designated here, (5 specimens) [all bearing the label "PARALECTOTYPE / *Astrotus* / *debilis* / Champion, 1884 / Aaron D. Smith" on yellow paper] with the following locality data: 2 specimens (BMNH) same data as holotype; 3 specimens (BMNH) labeled "Tehuacan, / Mexico. / Hoege."

Additional Material Examined. (3 specimens). MEXICO: Puebla.

**Redescription (see fig. 2.15).** Length 7.0-9.6mm, width 3.2-4.6 (lectotype length: 9.4mm, width: 4.6mm). Integument black or ferruginous, often densely coated with debris; setae yellowish-white to light brown, acuminate scales unless otherwise noted; elytra wider than pronotum, approximately equal at base, and 2.5-3.5X longer. **Head:** Densely foveate, anterior margins of some fovea raised, forming rounded tubercles, each with a single seta; frontoclypeal suture slightly impressed, epistomal suture not indented at margin; medial depression on frons shallowly impressed; eye elongate oval. Mentum anterior margin straight or with a shallow median notch. Antenna moderately clothed in

erect acuminate setae; antennal segment 10 conical, widest at apicies, tomentose sensilla meeting or nearly meeting on one side, surrounding most of apex; antennal segment 11 amplected into segment 10, exposing most of segment. **Prothorax:** Pronotum margin costate and sinuate, widest near middle, costa crenulate, slightly or sharply reflexed; anterior apicies produced and acute; posterior apicies acute, not produced; posterior margin nearly straight, narrower than anterior margin. Pronotal disc densely foveate; anterior margins of fovea raised, forming rounded tubercles, each with an erect squamate setae; longitudinal medial depression distinct; two or four rounded paramedial fossae present. **Pterothorax:** Elytra clothed with dark erect squamate or lanceloate scales; margin nearly parallel sided, slightly widening caudad; marginal costa tuberculate; elytral humera oblique; defined costae absent on disc, a few low, oblique or sinuous elevations present and densely setose, forming several dark brown setal patches in posterior half. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely punctate and setose; tarsi venter clothed with long golden or reddish setae; combined protarsal segments approximately two-thirds length of protibia, apical protibial spine small and setose to tip; anterior protibial spur shorter than basitarsi. **Abdomen:** Densely punctate and setose, setae short and acuminate.

**Diagnosis.** *P. debilis* can be separated from the other members of the *Sicharbas* subgenus based on the following character combination: pronotum margin sinuate, widest near middle, marginal costa crenulate, slightly or sharply reflexed; tomentose sensilla on antennal segment 10 meeting or nearly meeting on one side not forming a broad continuous band; erect squamate setae on elytra coalesced into several distinct dark patches in posterior half.

**Distribution.** Only known from the vecinity of Tehuacan in the Mexican state of Puebla.

**Biology.** Unknown.

### *Pelecyphorus* (*Sicharbas*) *seticornis* (Champion), New Combination

*Astrotus seticornis* Champion, 1884:67

*Pelecyphorus* (*Astrotus*) *seticornis* (Champion). Smith, 2010

= *Astrotus seticornis humeralis* Champion 1884:67, **New Synonym**

**Type Material.** LECTOTYPE, designated here, (female) labeled: a) Orange bordered white circle reading "Type"; b) "Toluca"; c) "1745; d) "Mexico. / Salle Coll."; e) handwritten det. "Astrotus / seticornis, / Champ."; f) "Sp. figured."; g) "B.C.ACol.IV.1. / Astrotus / seticornis"; h) on red paper, "LECTOTYPE / *Astrotus* / seticornis / Champion, 1884 / det. Aaron D. Smith". (BMNH). PARALECTOTYPE, designated here, 1 specimen labeled a) "Mexico. / Salle Coll."; b) handwritten det. "Astrotus / seticornis, / Champ."; c) "B.C.ACol.IV.1. / Astrotus / seticornis"; d) on yellow paper "PARALECTOTYPE / *Astrotus* / *seticornis* / Champion, 1884 / Aaron D. Smith". (BMNH).

**Additional Material Examined.** (159 specimens). MEXICO: Hidalgo, Mexico, Mexico D.F., Michoacán, and Puebla.

**Redescription (see fig. 2.16).** Length 6.0-8.6mm, width 2.3-4.1 (lectotype length: 8.2mm, width: 3.9mm). Integument black or ferruginous, often densely encrusted with

debris; setae short, yellowish-white to brown, acuminate scales unless otherwise noted; elytra wider than pronotum and 2.9-3.2X longer. **Head:** Densely foveate, anterior margins of some fovea raised, forming rounded tubercles, each with a single seta; frontoclypeal suture impressed, clypeus elongate, epistomal suture indented at margin; medial depression on frons deeply broadly impressed; area around eye impressed, giving the eye a slightly stalked appearance, eye broadly oval. Mentum anterior margin straight or with a shallow median notch. Antenna moderately clothed in erect acuminate reddish-brown setae; antennal segment 10 conical, widest at apicies, tomentose sensilla coalesced into a broad continuous band around apical half; antennal segment 11 deeply amplected into segment 10, exposing only the broad tomentose sensillum on apex. **Prothorax:** Pronotum margin costate and sinuate, widest near middle, costa tuberculate and reflexed; anterior apicies slightly produced and rounded; posterior apicies acute, slightly produced, not projecting over elytra; posterior margin weakly convex, slightly emarginate on each side near apicies. Pronotal disc densely punctate; anterior margins of punctures raised, forming rounded tubercles, each with an erect, occassionally squamate, setae; longitudinal medial line tuberculate, rarely depressed or punctate; two large paramedial fossae present, two smaller fossae occasionally present posterad. **Pterothorax:** Elytra parallel sided or slightly wider behind middle, clothed with squamate or lanceloate scales arising from minute tubercles, denser along crests of costae; elytral humera oblique; marginal costa tuberculate, slightly reflexed, flanged before cauda and sinuately curved inward towards elytral suture in apical third; discal costa tuberculate, distinct in basal half; sutural costa tuberculate and slightly raised throughout; additional oblique or transverse costae present and irregularly distributed across disc, connecting all costae into

a confused network. **Legs:** Mesotrocantin small and concealed in most specimens. Femora and tibia minutely tuberculate and clothed in long acuminate setae, anterior margins of tibia also with stouter erect setae; tarsi venter clothed with long golden or reddish setae; combined protarsal segments approximately one-half length of protibia, apical protibial spine acute and glabrous; anterior protibial spur shorter than basitarsi. **Abdomen:** Densely minutely tuberculate, with short acuminate setae arising from tubercles.

**Diagnosis.** *P. seticornis* can be separated from the other members of the *Sicharbas* subgenus based on the following character combination: pronotum margin sinuate, widest near middle, marginal costa tuberculate and reflexed; pronotum not medially longitudinal depressed; tomentose sensilla on antennal segment 10 coalesced into a broad continuous band around apical half; antennal segment 11 deeply amplected into segment 10; apical protibial spine acute and glabrous.

**Distribution.** MEXICO: Hidalgo, Mexico, Mexico D.F., Michoacán, and Puebla.

**Discussion.** The subspecies *humeralis* was described based on a single specimen from the same locality as the nominal subspecies. The characters used to define the subspecies represent individual variation and are mutable within a larger series of specimens.

**Biology.** Unknown.

## *Pelecyphorus* (*Sicharbas*) *erosus* (Champion), New Combination

*Astrotus erosus* Champion, 1892:504

*Pelecyphorus* (*Astrotus*) *erosus* (Champion). Smith, 2010

= *Pelecyphorus* (*Astrotus*) *nosodermoides* (Champion, 1892:505), **New Synonym**

**Type Material.** HOLOTYPE, by monotypy, (female) labeled: a) Orange bordered white circle reading "Type"; b) "San Juan de / los Llanos / Mex. Flohr"; c) handwritten det. "Astrotus / erosus, Ch."; d) "B.C.ACol.IV.1. / Astrotus / erosus". (BMNH).

**Additional Material Examined.** (5 specimens). MEXICO: Hidalgo (Real del Monte, 4mi N Tepeapulco).

**Redescription (see fig. 2.17).** Length 7.5-9.6mm, width 3.1-4.5 (holotype length: 9.6mm, width: 4.5mm). Integument black or ferruginous, often densely encrusted with debris; setae yellowish-white to brown, acuminate or apically truncate scales unless otherwise noted; elytra wider than pronotum and 2.9-3.1X longer. **Head:** Densely foveate, anterior margins of some fovea raised, forming rounded tubercles, each with a single seta; frontoclypeal suture slightly laterally impressed, clypeus elongate, epistomal suture indented at margin; medial depression on frons vaguely impressed; eye broadly oval. Mentum anterior margin with a shallow median notch. Antenna sparsely clothed in erect acuminate golden setae; antennal segment 10 laterally flattened, widest at apicies, tomentose sensilla meeting or nearly meeting on one side, surrounding most of apex; antennal segment 11 amplected into segment 10, exposing most of segment. **Prothorax:**

Pronotum margin costate, arctuate or slightly sinuate, widest near middle, costa tuberculate and reflexed; anterior apicies produced and rounded; posterior apicies acute, not produced; posterior margin truncate or weakly convex. Pronotal disc densely punctate; anterior margins of punctures raised, forming rounded tubercles, each with a semi-erect setae; smooth longitudinal medial line not reaching base or apex; paramedial fossae faintly indicated. **Pterothorax:** Elytra parallel sided or slightly wider behind middle, clothed with squamate or lanceloate scales, most arising from minute tubercles, denser along crests of costae or low projections; elytral humera oblique; marginal costa tuberculate, posteriorly reduced to a row of short projecting points and ridges; discal costa tuberculate, distinct in basal half or throughout; sutural costa not raised; additional low, tuberculate and setose, oblique or transverse, costae and protrusions irregularly distributed across disc. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely foveate and setose, setae on tibia arising from tubercles or not; tarsi venter clothed with long golden setae; combined protarsal segments approximately two-thirds length of protibia, apical protibial spine acute and glabrous; anterior protibial spur shorter than basitarsi. **Abdomen:** Densely punctate and setose.

**Diagnosis.** *P. erosus* can be separated from the other members of the *Sicharbas* subgenus based on the following character combination: pronotum margin arctuate or slightly sinuate, widest near middle, marginal costa tuberculate and reflexed; pronotum medially longitudinally depressed, not reaching base or apex; tomentose sensilla on antennal segment 10 meeting or nearly meeting on one side not forming a broad continuous band;

apical protibial spine acute and glabrous; elytral marginal carina reduced to a series of small setose projections in apical third.

**Distribution.** Known from only six specimens. The exact type locality is unknown, as there are several regions in Mexico called San Juan de los Llanos. According to an examination of localities listed in the B.C.A (Selander and Vaurie 1962) it may refer to a district in Puebla between Tlaxcala and Veracruz or a village in Guanajuato (40km northeast of Leon). Two of the other two known specimens are from the Mexican state of Hidalgo (Real del Monte, 4mi N Tepeapulco), the others are labeled simple as Mexico.

**Discussion.** Both *P. erosus* and *P. nosodermoides* were described by Champion based on unique specimens. Upon examination, and with the addition of four other specimens, it was determined that the type specimen of *P. nosodermoides* is a male *P. erosus*, while the holotype of *P. erosus* is a female. The sexes vary only in elytral shape, more parallel sided in the male, and the length of the discal costa, longer in the male. Hence, *P. nosodermoides* is synonymized under *P. erosus*.

**Biology.** Unknown.

### *Pelecyphorus* (*Sicharbas*) *undatus* (Champion), New Combination

*Astrotus undatus* Champion, 1892:504

*Pelecyphorus* (*Astrotus*) *undatus* (Champion, 1892:504). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (female) labeled: a) Orange bordered white circle reading "Type"; b) ""Ventanas, / Durango. / Hoge.""; c) handwritten det.

"Astrotus / undatus, Ch."; d) "Sp. figured."; e) "B.C.ACol.IV.1. / Astrotus / undatus". (BMNH). PARALECTOTYPES, designated here, (7 specimens) [all bearing the label "PARALECTOTYPE / *Astrotus* / *undatus* / Champion, 1892 / Aaron D. Smith" on yellow paper] with the same locality data as lectotype (BMNH).

**Additional Material Examined.** (2 specimens). MEXICO: Durango.

**Redescription (see fig. 2.18).** Length 8.8-12.6mm, width 4.2-6.3 (lectotype length: 11.6mm, width: 5.8mm). Integument ferruginous; setae yellowish-white lanceolate decumbent scales unless otherwise noted; elytra wider than pronotum and approximately 3X longer. **Head:** Densely foveate, each fovea subtended by a setae; frontoclypeal suture and medial depression on frons faintly impressed; epistomal suture obscured and not indented at margin; eye broadly oval. Mentum anterior margin with a shallow median emargination. Submentum narrower than buccal cavity, leaving at most a minute space laterally. Postgenal process produced and rounded. Antenna moderately clothed in erect acuminate reddish-brown setae; antennal segment 10 laterally flattened, widest at apicies, tomentose sensilla separate, surrounding most of apex; antennal segment 11 amplected into segment 10, exposing most of segment. **Prothorax:** Pronotum margin costate and sinuate, widest near middle, costa crenulate and reflexed; anterior apicies produced and acute; posterior apicies acute, not produced; posterior margin truncate or weakly convex. Pronotal disc densely foveate, each fovea subtended by a setae; smooth longitudinal medial line thin and faint; two or four paramedial fossae present. **Pterothorax:** Elytra nearly parallel sided, slightly wider behind middle, setose, some setae arising from minute tubercles and erect; elytral humera reflexed; marginal costa tuberculate; discal

costa absent or distinct in basal third and tuberculate; sutural costa not raised; additional low, tuberculate and setose, oblique or transverse, costae and protrusions irregularly distributed across disc. **Legs:** Mesotrocantin small, exposed. Femora and tibia densely foveate and setose, setae on tibia arising from tubercles or not; tarsi venter clothed with long golden setae and shorter spiniform setae laterally; combined protarsal segments approximately two-thirds length of protibia, apical protibial spine acute and glabrous; anterior protibial spur shorter than basitarsi. **Abdomen:** Densely finely punctate and setose.

**Diagnosis.** *P. undatus* can be separated from the other members of the *Sicharbas* subgenus based on the following character combination: pronotum margin sinuate, widest near middle, marginal costa tuberculate and reflexed; pronotum medially with a thin smooth longitudinal line, not depressed; pronotal disc not tuberculate; tomentose sensilla on antennal segment 10 separate; apical protibial spine acute and glabrous; elytral discal carina absent or faintly raised in basal third; elytral humera reflexed.

**Distribution.** Known only from the Ventanas region in Durango, Mexico.

**Biology.** Unknown.

### subgenus *Pelecyphorus* Solier, 1836, sensu strictu

*Pelecyphorus* Solier 1836:467. Type species: *Pelecyphorus mexicanus* Solier, 1836:469, by subsequent designation, Casey 1912:105. Lectotype (MNHN).

**Redescription** [Modified from Brown 1971b]. Length: 12.9-17.3mm, width: 7.5-9.5mm; body obovate and setose, setae often modified, lanceolate or squamate, always with

*Pelecyphorus*-type stellate setae. **Head:** Mentum subtrapezoidal to transversely cordate; separated from postgenal processes by a small space, not reaching mandibles when closed; lateral slightly curved inward near apicies; anterior margin medially emarginate. Ligula sclerotized, small, approximately one-fourth mentum width; slightly curved and partially visible above anterior margin of mentum. Apical segment of maxillary palps enlarged, weakly scalene in both sexes, more expanded in males. Submentum projecting into buccal cavity; width approximately two-thirds that of buccal cavity, partially exposing maxillary cardos laterally. Postgenal processes produced, acute, and slightly swollen, extending beyond middle of mentum. Labral margin broadly emarginate; clypeal membrane concealed. Clypeal margin broadly emarginate. Eyes elongate, narrow, occassionaly weakly reniform. Antenna weakly clavate, segments compact; apical tomentose sensilla on antennal segment 10, separated into two patches at lateral apices; antennal segment 11 one-half size of segment 10, apical tomentose sensillum covering one-fourth of segment. **Prothorax:** Pronotal margin costate and arctuate; pronotal disc without a median costa or paramedial fossae. Prosternal process thin, raised and projecting behind procoxal cavities, longitutunally impressed or not, apex broadly rounded. **Pterothorax:** Elytral sculpturing variable, marginal costa present. Mesonotum with two deep transverse depressions, leaving a thin medial ridge between the scutellum and scutum. **Legs:** Mesocoxal cavities open; mesotrocantin small and exposed. **Abdomen:** Tomentose band of setae present along apical margins of ventrites 1-4.

**Diagnosis.** The subgenus *Pelecyphorus* is distinguished from other *Pelecyphorus* subgenera by a unique combination of the following characters: Ligula small, one-fourth mentum width, partially visible above anterior margin of mentum. Mesonotum with two

deep transverse depressions. Dense tomentose fringe present on abdominal ventrites 1-4; *Pelecyphorus*-type stellate setae present.

**Distribution.** MEXICO: Puebla, Queretaro, Veracruz.

## Species Descriptions

### *Pelecyphorus* (*Pelecyphorus*) *mexicanus* Solier

*Pelecyphorus mexicanus* Solier, 1836:469

*Asida mexicana* Solier, 1836:469. Horn, 1870:282.

*Pelecyphorus mexicanus* Solier 1836:469. Casey, 1912:105.

**Type Material.** LECTOTYPE (male) labeled: a) "Mexica- / nus"; b) "Pelecyphor. / mexicanus / "[illegible script], Sol" / "[illegible]"; c) "Col. Marseul / Col. Solier"; d) "LECTOTYPE / Pelecyphorus / mexicanus Sol.♂ / Examined by / Kirby W. Brown / August 1968". (MNHN).

**Additional Material Examined.** (61 specimens). MEXICO: Puebla.

**Redescription (see fig. 2.19).** Length: 12.9-17.3mm, width: 7.5-9.5mm (lectotype length: 15.1mm, width: 8.0mm). integument black, often densely coated with debris; setae pale and yellowish-white unless otherwise noted; elytra wider than pronotum and 2.7-3X longer, width of pronotum at base slightly less than width of elytral base. **Head:** Densely punctate with decumbent lanceolate or serrate scales, becoming erect and acuminate on

clypeus, emerging from sides of punctures; frontoclypeal suture not or vaguely impressed, epistomal suture indented at margin; medial depression on frons absent or weakly impressed. Mentum anterior margin straight with a small median emargination at ligula insertion. Antenna densely clothed in erect acuminate setae, nearly clear in color on basal segments; antennal segment 10 subquadrate or slightly wider at apicies, tomentose sensilla separated, curved and wrapping around apex; antennal segment 11 weakly amplected into segment 10, exposing most of segment. **Prothorax:** Pronotum margin costate and arcuate, widest near middle, not reflexed; anterior apicies produced and acute; posterior apicies acute, not produced; posterior margin nearly straight, without a medial tooth. Pronotal disc densely foveate and slightly rugose; each fovea with a single lanceolate or lanceo-serrate scale emerging from anterior side; longitudinal medial depression and paramedial fossa absent. **Pterothorax:** Elytra broadly oval, widest behind middle; marginal costa present, not reflexed; elytral humera rectiform, slightly reflexed or not; disc coarsely reticulate or with elytral and sutural costae distinct; depressions between costa and/or reticulations densely clothed with *Pelecyphorus*-type stellate setae and lanceo-serrate scales, often thickly coated with debris. **Legs:** Femora shallowly foveate, with short acuminate setae, and rugose; tibia densely tuberculate, pale acuminate or darker spiniform setae emerging from tubercles; tarsi venter laterally with black spiniform setae; apical protibial spine large, acute, and glaberous; anterior protibial spur length subequal to basitarsi. **Abdomen:** Moderately punctate, punctures small, each with a short acuminate setae; dense tomentose band of yellowish-white setae present along apical margins of ventrites 1-4.

**Diagnosis.** *P. mexicanus* is the only known member of the nominate subgenus and can be reliably separated from all other Pelecyphorus species based on its subgeneric diagnosis.

**Distribution.** MEXICO: Puebla, Queretaro, Veracruz.

**Biology.** Unknown. Collected at lights, from underneath rocks and plant debris, from spider webs, or while walking.

## subgenus *Ucalegon* Champion 1884

*Ucalegon* Champion 1884:65. Type species: *Ucalegon pulchellus* Champion, 1884:65, by monotypy.

**Redescription.** Length: 11-15.9mm, width: 4.9-7.9mm; body obovate and setose, with lanceolate or squamate scales. **Head:** Mentum subtrapezoidal to transversely cordate; reaching postgenal processes or separated by a small space, not reaching mandibles when closed; laterally curved inward near apicies; anterior margin medially emarginate. Ligula sclerotized, small, approximately one-fourth mentum width, curved and partially visible above anterior margin of mentum. Apical segment of maxillary palps enlarged, isotriangular to weakly scalene in both sexes, more expanded in males. Submentum projecting into buccal cavity; width approximately four-fifths that of buccal cavity, partially exposing maxillary cardos laterally. Postgenal processes produced, acute, and slightly swollen, extending beyond middle of mentum. Labral margin broadly emarginate; clypeal membrane concealed. Clypeal margin broadly emarginate. Eyes elongate, narrow, occassionaly weakly reniform. Antenna weakly clavate, segments nearly moniliform; apical tomentose sensilla on antennal segment 10 separated into two

patches at lateral apices; antennal segment 11 two-thirds size of segment 10 and slightly amplected into it, apical tomentose sensillum covering approximately half of segment. **Prothorax:** Pronotal margin costate and strongly sinuate; pronotal disc with or without a shallow median fossa. Prosternal process thin, raised and projecting behind procoxal cavities, broadly longitudinally impressed, apex rounded or sagittate. **Pterothorax:** Elytra nearly planate, lacking transverse costae or protrusions; marginal costa present; elytral costa present and not divided; thickly clothed with multihued scales, forming a contrasting colored pattern. Mesonotum with two deep transverse depressions, leaving a thin medial ridge between the scutellum and scutum. **Legs:** Mesocoxal cavities open; mesotrocantin prominent and exposed.

**Diagnosis.** The subgenus *Ucalegon* is distinguished from other *Pelecyphorus* subgenera by a unique combination of the following characters: pronotum strongly sinuate; elytra nearly planate, lacking transverse costae or protuberances, with elytral costa raised and not divided; elytral disc thickly clothed with multihued scales, forming a distinct contrasting colored pattern.

**Distribution.** MEXICO: Oaxaca.

## Species Descriptions

### *Pelecyphorus* (*Ucalegon*) *pulchellus* Champion

*Ucalegon pulchellus* Champion, 1884:65

*Asida pulchellus* (Champion). Champion, 1892:491

*Ucalegon pulchellus* Champion, 1884:65. Wilke, 1922:275

*Pelecyphorus* (*Ucalegon*) *pulchellus* (Champion), Smith, 2010

**Type Material.** LECTOTYPE, designated here, (male) labeled: a) Orange bordered white circle reading "Type"; b) "Sp. figured."; c) "Mexico. / Salle Coll."; d) "Tehuantepec"; e) handwritten det. "Ucalegon / pulchellus, / Champ"; f) handwritten det. "Philolithus / sumichrasti Salle / apud Salle MS"; g) "B.C.A. Col.IV.1. / Ucalegon / pulchellus". (BMNH). PARALECTOTYPES, designated here, (2 specimens) [all bearing the label "PARALECTOTYPE / *Ucalegon* / *pulchellus* / Champion, 1884 / Aaron D. Smith" on yellow paper]: 1 (BMNH) with the same locality data as lectotype (BMNH), 1 (BMNH) labeled "Mexico".

**Additional Material Examined.** (72 specimens). MEXICO: Oaxaca.

**Redescription (see fig. 2.20).** Length: 11.0-15.9mm, width: 4.9-7.9mm (lectotype length: 15.1mm, width: 6.9mm). Integument black to ferruginous, rarely densely encrusted with debris; elytra wider than pronotum and 2.5-3.5X longer, width of pronotum at base nearly equal to width of elytral base. **Head:** Densely punctate with lanceolate or squamate scales, becoming erect and acuminate on clypeus, emerging from sides of punctures; frontoclypeal suture laterally impressed, impression occasionally extended longitudinally towards eye, epistomal suture indented at margin; medial depression on frons absent or weakly impressed. Mentum anterior margin straight with a shallow median emargination at ligula insertion. Antenna moderately clothed in golden erect acuminate setae; antennal segment 10 subquadrate or wider at apicies, tomentose sensilla separated, curved and wrapping around apex; antennal segment 11 weakly amplected into segment 10, exposing

most of segment. **Prothorax:** Pronotum margin strongly sinuate, widest near middle, not or slightly reflexed; anterior apicies produced and acute; posterior apicies acute, not produced; posterior margin nearly straight, a medial tooth rarely lacking. Pronotal disc densely tuberculate, tubercles rounded and shiny, each with a lanceolate scale, tubercles near margins often with an associated puncture; longitudinal medial depression broad and shallow or absent; paramedial fossa absent; surface densely clothed with pale and dark squamate scales, usually forming two dense, nearly black, paramedial longitudinal lines . **Pterothorax:** Elytra elongate oval, widest behind middle; marginal costa present, tuberculate, and not reflexed; elytral humera slightly obtuse, not reflexed; discal costa present from base to apical third, not divided, sinuate, and tuberculate, with widely spaced erect acuminate setae along crest; densely clothed with pale, orange, and dark brown squamate scales, forming several thick dark brown patches and lines, including a large triangular patch near middle between elytral suture and discal costa, often extending anteriorly next to elytral suture. **Legs:** Femora shallowly foveate, with short acuminate setae, and rugose; tibia densely tuberculate, pale acuminate setae emerging from tubercles; tarsi venter with long pale setae, stouter laterally; apical protibial spine large, acute, and glaberous; combined protarsal segments subequal to protibial length in male, approximately two-thirds length of protibia in female; anterior protibial spur length shorter than basitarsi. **Abdomen:** Setose and slightly rugose with minute punctures and tubercles.

**Diagnosis.** *P. pulchellus* is the only known member of the *Ucalegon* subgenus and can be reliably separated from all other *Pelecyphorus* species based on the subgeneric diagnosis and the presence of two dense black triangular setal patches halfway down elytral length.

**Distribution.** MEXICO: Oaxaca.

**Biology.** Unknown. Collected at lights, from underneath fallen cactus pads, and on fallen tree branches.

### subgenus *Zaleucus* Champion, 1892

*Zaleucus* Champion, 1892:491. Type species: *Zamolxis dilatatus* Champion, 1884, by monotypy.

= *Zamolxis* Champion 1884:70 (preoccupied).

=*Poliorcetes* Champion, 1884:70. Type species: *Poliorcetes platesthoides* Champion, 1884:70.

**Redescription.** Length: 11.6-18.4mm, width: 5.8-9.1mm. Integument shiny, black or rarely ferruginous, occasionally encrusted with debris; body obovate; dorsal setae inconspicuous, lanceolate or truncate elongate scales. **Head:** Mentum subtrapezoidal; reaching postgenal processes or separated by a small space, nearly reaching mandibles when closed; laterally curved inward near apicies; anterior margin medially notched. Ligula sclerotized, small, approximately one-fourth mentum width, curved and partially visible above anterior margin of mentum or concealed. Apical segment of maxillary palps enlarged, isotriangular to weakly scalene in both sexes, more expanded in males. Submentum projecting into buccal cavity; width approximately four-fifths that of buccal cavity, partially exposing maxillary cardos laterally. Postgenal processes produced, reaching middle of mentum to apex, acute, and slightly or strongly swollen. Labral margin emarginate; clypeal membrane concealed. Clypeal margin broadly emarginate.

Eyes elongate, oval or weakly reniform. Antenna weakly clavate, segments nearly moniliform; apical tomentose sensilla on antennal segment 10 separated into two patches at lateral apices; antennal segment 11 two-thirds or more size of segment 10 and slightly amplected into it, apical tomentose sensillum covering approximately half of segment (Fig.). **Prothorax:** Pronotal margin costate, arctuate or weakly sinuate; pronotal disc broadly convex, fossae absent or faintly impressed, medial ridge absent; posterior margin truncate or convex, without a median tooth. Prosternal process longitudinally impressed, raised and projecting behind procoxal cavities or deflexed; apex rounded or sagittate. **Pterothorax:** Elytra broadly convex, sculpturing variable, but marginal and discal costae always present. Mesonotum mostly exposed, with two shallow transverse depressions, leaving a thin low medial ridge between the scutellum and scutum. **Legs:** Mesocoxal cavities open; mesotrocantin prominent and exposed.

**Diagnosis.** The subgenus ***Zaleucus*** is distinguished from other *Pelecyphorus* subgenera by a unique combination of the following characters: mentum subtrapezoidal, reaching postgenal processes or separated by a small space; pronotum arctuate or weakly sinuate; dorsal setae absent or inconspicous; mesotrocantin prominent and exposed.

**Distribution.** MEXICO: Coahuila, Nuevo Leon, Oaxaca, Puebla, Zacatecas.

## Species Descriptions

### *Pelecyphorus* (*Zaleucus*) *dilatatus* (Champion)

*Zamolxis dilatatus* Champion, 1884:70

*Asida dilatatus* (Champion). Champion, 1892:491

*Zaleucus dilatatus* (Champion). Wilke, 1922:275

*Pelecyphorus* (*Zaleucus*) *dilatatus* (Champion), Smith, 2010

**Type Material.** LECTOTYPE, designated here, (female) labeled: a) Orange bordered white circle reading "Type"; b) "Puebla"; c) "1749"; d) "Mexico. / Salle Coll."; d) handwritten det. "Zaleucus / dilatatus Ch"; e) "Sp. figured."; f) "Zamolxis / (Zaleucus) / dilatatus, Ch."; g) "B.C.ACol.IV.1. / Zamolxis / dilatatus". (BMNH). PARALECTOTYPE, designated here, one specimen (BMNH) with same locality data as lectotype and bearing the label "PARALECTOTYPE / *Zamolxis* / *dilatatus* / Champion, 1884 / Aaron D. Smith" on yellow paper.

**Additional Material Examined.** (18 specimens). MEXICO: Oaxaca, Puebla.

**Redescription (see fig. 2.21).** Length: 14.5-18.4mm, width: 6.6-9.1mm (lectotype length: 15.8mm, width: 7.8mm). Integument shiny, black, rarely encrusted with debris; setae short, yellowish white, and simple unless otherwise noted; elytra barely wider than pronotum and 3.0-3.5X longer, width of pronotum at base nearly equal to width of elytral base. **Head:** Densely foveate with thin simple setae emerging from sides of fovea;

frontoclypeal suture faintly or laterally impressed, epistomal suture indented at margin; medial depression on frons absent or weakly impressed. Mentum anterior margin straight with a rounded median emargination at ligula insertion. Submentum transversely impressed before apex, apex truncate. Postgenal processes swollen, acute, and extending nearly to anterior margin of mentum. Antenna moderately clothed in golden erect acuminate setae; antennal segment 10 wider at apicies, tomentose sensilla separated, curved and wrapping around apex; antennal segment 11 weakly amplected into segment 10, exposing most of segment. **Prothorax:** Pronotum margin strongly arcuate, dilated near middle, slightly reflexed; anterior apicies barely produced, broadly rounded or acute; posterior apicies oblique, occasionally with an acute point, not produced; posterior margin slightly convex, never with a medial tooth; paramedial fossa absent or faintly impressed. Prosternal process longitudinally impressed, deflexed behind procoxa. Prosternum densely foveate. **Pterothorax:** Elytra elongate oval, widest near middle; marginal costa not divided, smooth or with scattered punctures, not reflexed, meeting discal costa near cauda; elytral humera obtuse, not reflexed; discal costa bifurcate near base, branches reuniting in apical third, inner branch not raised as high as outer, occasionally barely indicated, crests smooth and shiny; intercostal spaces smooth, with scattered fovea and decumbent simple setae. **Legs:** Femora shiny, shallowly punctate and rugose; tibia densely foveate and setose, setae long, pale, and acuminate mixed with stouter spiniform setae emerging from small tubercles; tarsi venter with long pale setae and darker spiniform setae laterally; apical protibial spine large, acute, and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior

protibial spur length shorter than basitarsi. **Abdomen:** Shiny with scattered setose fovea, setae simple and inconspicuous; intercoxal process truncate at apex.

**Diagnosis.** *P. dilatatus* can be separated from the other members of the *Zaleucus* subgenus based on the following character combination: postgenal processes strongly swollen and nearly reaching anterior margin of mentum; pronotal margin dilated and slightly reflex; marginal costa not divided.

**Distribution.** MEXICO: Oaxaca, Puebla.

**Biology.** Unknown. Collected at lights, from underneath plant debris, and ovipositing in sandy soil at night.

### ***Pelecyphorus (Zaleucus) platesthoides* (Champion)**

*Poliorcetes platesthoides* Champion, 1884:71

*Asida platesthoides* (Champion). Champion, 1892:491

*Poliorcetes platesthoides* (Champion). Wilke, 1922:275

*Pelecyphorus* (*Zaleucus*) *platesthoides* (Champion, 1884:71). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (sex undetermined) labeled: a) Orange bordered white circle reading "Type"; b) "Ticomavaca, / Mexico. / Hoege"; c) handwritten det. "Poliorcetes / platesthoides, / Ch."; d) "Sp. figured."; d) "B.C.A. Col.IV.1. / Poliorcetes / platesthoides. (BMNH). PARALECTOTYPES (60 specimens) [all bearing the label "PARALECTOTYPE / *Ucalegon* / *pulchellus* / Champion, 1884 / Aaron D. Smith" on yellow paper]: with the same locality data as lectotype (48-BMNH,

2-NMNH, 1-RLAC, 1-KWBC); labeled "Ticomavaca, / Oaxaca. / Hoge" (7-BMNH, 1-CASC).

**Additional Material Examined.** (2 specimens). MEXICO: Oaxaca.

**Redescription (see fig. 2.22).** Length: 12.8-16.9mm, width: 6.6-9.2mm (lectotype length: 14.3mm, width: 7.3mm). Integument shiny, black to ferruginous, rarely encrusted with debris; setae short, yellowish white, and simple unless otherwise noted; elytra wider than pronotum and 3.1-3.5X longer, width of pronotum at base nearly equal to width of elytral base. **Head:** moderately punctate with thin simple setae emerging from sides of punctures; frontoclypeal suture faintly impressed, epistomal suture indented at margin; medial depression on frons absent or weakly impressed. Mentum anterior margin straight with a median notch at ligula insertion. Submentum not impressed before apex, apex emarginate. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna moderately clothed in golden erect acuminate setae; antennal segment 10 wider at apicies, tomentose sensilla separated, curved and wrapping around apex; antennal segment 11 weakly amplected into segment 10, exposing most of segment. **Prothorax:** Pronotal margin slightly sinuate, widest near middle, not or faintly reflexed; anterior apicies produced and acute; posterior apicies acute, not produced; posterior margin nearly straight, never with a medial tooth; paramedial fossa absent. Prosternal process not longitudinally impressed, raised behind procoxa, apex rounded. Prosternum moderately foveate, anterior margin of some fovea raised and weakly tuberculate. **Pterothorax:** Elytra elongate oval, widest near middle. Marginal costa slightly crenulate, crenulations becoming larger posterad, meeting discal costa near cauda, and not reflexed;

inner branch present from slightly before middle to apical third, not connecting primary branch of marginal costa or discal costa; elytral humera obtuse, not reflexed. Discal costa carinate, raised near elytral base and extending to apical fourth before uniting with marginal costa; inner branch absent or very faintly indicated; crest smooth and shiny. Intercostal spaces smooth, with scattered punctures and decumbent simple setae. **Legs:** Femora shallowly punctate and rugose; tibia densely shallowly punctate and setose, setae short, pale, and acuminate mixed with stouter spiniform setae emerging from small tubercles; tarsi venter with stout spiniform setae on laterally margins, medially glaberous, distal tarsi with longer acuminate setae; apical protibial spine large, acute, and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Shiny and moderately punctate, punctures with or without simple inconspicuous setae; intercoxal process broadly rounded at apex.

**Diagnosis.** *P. platesthoides* can be separated from the other members of the *Zaluecus* subgenus based on the following character combination: postgenal processes slightly swollen and reaching middle of mentum, submentum apex emarginate; pronotal margin weakly sinuate and not or slightly reflex; pronotal disc punctate; marginal costae of elytra crenulate and divided, inner branch raised from slightly before middle to apical third, not connecting primary branch of marginal costa or discal costa.

**Distribution.** MEXICO: Oaxaca.

**Biology.** Unknown.

## *Pelecyphorus* (*Zaleucus*) *foveolatus* Solier

*Pelecyphorus foveolatus* Solier, 1836:472

*Asida foveolata* (Solier). Horn, 1870:282. Wilke, 1922:270

*Parasida foveolata* (Solier). Wilke, 1922:275

*Pelecyphorus* (*Zaleucus*) *foveolatus* Solier, 1836:472. Smith, 2010

**Type Material.** LECTOTYPE, designated here, (male) labeled: a) "Mexico"; b) "Pelecyphorus / foveolatus / [illegible script] / [illegible script]) / [illegible, looks like ??61]"; c) "Col. Marseul / Col. Solier"; d) "LECTOTYPE / Pelecyphorus / foveolatus Sol. ♂ / Examined by / Kirby W. Brown / August 1968". (MNHN)

**Additional Material Examined.** (122 specimens). MEXICO: Oaxaca.

**Redescription (see fig. 2.23).** Length: 11.6-18.0mm, width: 5.8-8.7mm (lectotype length: 12.1mm, width: 6.0mm). Integument shiny, black, rarely encrusted with debris; setae short, yellowish white, and simple unless otherwise noted; elytra wider than pronotum and 2.6-3.4X longer, width of pronotum at base less than width of elytral base. **Head:** moderately foveate with thin simple setae emerging from sides of punctures; frontoclypeal suture faintly laterally impressed, epistomal suture indented at margin; medial depression on frons weakly impressed. Mentum anterior margin straight with a shallow median emargination at ligula insertion. Submentum not impressed before apex, apex broadly emarginate. Postgenal processes swollen, acute, and extending nearly to anterior margin of mentum. Antenna moderately clothed in golden erect acuminate setae;

antennal segment 10 wider at apicies, tomentose sensilla separated, curved and wrapping around apex; antennal segment 11 weakly amplected into segment 10, exposing most of segment. **Prothorax:** Pronotal margin slightly sinuate, widest near middle, not reflexed; anterior apicies produced and acute; posterior apicies acute, produced, slightly projecting over elytral humera or not; posterior margin concave, never with a medial tooth. Pronotal disc moderately foveate, each fovea with a decumbent acuminate setae arising from anterior face; paramedial fossa absent. Prosternal process not longitudinally impressed, strongly raised behind procoxae, apex sagittate. Prosternum moderately foveate, anterior margin of some fovea raised and weakly tuberculate. **Pterothorax:** Elytra elongate oval, widest behind middle. Marginal costa smooth, meeting discal costa near cauda, and not reflexed; inner branch absent or low, reticulate, and present from slightly before middle to apical third, not connecting primary branch of marginal costa or discal costa; elytral humera obtuse, not reflexed. Discal costa slightly reticulate and smooth; weakly raised near elytral base and bifurcate, branches reuniting in apical fourth before uniting with marginal costa near cauda; inner branch weak or barely indicated. Sutural costa weakly raised or not. Intercostal spaces rugose, with weakly raised irregular transverse costae; punctures widely scattered along bases of costae; short sparse nearly lanceolate scales present and inconspicuous. **Legs:** Femora shallowly punctate and rugose; tibia densely shallowly punctate and setose, setae short, pale, and acuminate mixed with stouter spiniform setae emerging from small tubercles; tarsi venter with long acuminate setae and stout spiniform setae on laterally margins, medially glaberous on tarsal segment 2-4; apical protibial spine large, acute, and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than

basitarsi. **Abdomen:** Shiny and sparsely punctate, punctures with or without simple inconspicuous setae; intercoxal process broadly rounded at apex.

**Diagnosis.** *P. foveolatus* can be separated from the other members of the *Zaluecus* subgenus based on the following character combination: postgenal processes swollen and nearly reaching anterior margin of mentum, submentum apex emarginate; pronotal margin weakly sinuate and not or slightly reflex; pronotal disc foveate; marginal costae of elytra smooth and divided, inner branch weak; intercostal spaces of elytra rugose.

**Distribution.** MEXICO: Oaxaca.

**Biology.** Unknown. Collected from dead cactus and walking on surface during day.

### ***Pelecyphorus (Zaleucus) doyeni* Smith, n. sp.**

**Type Material.** HOLOTYPE (female) labeled: a) "MEXICO. NUEVO / LEON: Hwy 58, 13 km / E of junction with Hwy / 57, 2000 m, / 5 JUN 1993."; b) on red paper, "HOLOTYPE / *Pelecyphorus* / (*Zaleucus*) / *doyeni* ♀ / Aaron D. Smith" (CASC). PARATYPES (31 specimens) [all bearing the label "PARATYPE / *Pelecyphorus* / (*Zaleucus*) / *doyeni* / Aaron D. Smith" on yellow paper]: 16 paratypes (CASC) with same locality data as holotype. 5 paratypes (CASC) labeled a) "MEXICO: Coahuila / 20 mi N of Conception / del Oro 5800' / 10 August 1993 / Collector unknown / Cal. Acad. Sci. Collection"; b) "California Academy / of Sciences / collection". 6 paratypes (CASC) labeled a) "MEXICO: Zacatecas 45 miles / NW of Matehuala 6000' / del Oro 5800' / 10 August 1993 / Collector unknown / Cal. Acad. Sci. Collection"; b) "California Academy /

of Sciences / collection". 4 paratypes (3-EMEC, 1-KWBC) labeled a) "MEX: 40 mi. / SE Zacatecas. / Zac. VIII-25-69"; b) "J.T. Doyen / collector".

**Redescription (see fig. 2.24).** Length: 13.9-17.8mm, width: 6.6-8.8mm (holotype length: 15.9mm, width: 7.5mm). Integument shiny, black, rarely encrusted with debris; setae short, yellowish white, and simple unless otherwise noted; elytra wider than pronotum and 2.7-3.3X longer, width of pronotum at base subequal to width of elytral base. **Head:** moderately foveate with thin simple setae emerging from sides of punctures; frontoclypeal suture not or faintly impressed, epistomal suture not indented at margin; medial depression on frons absent or weakly impressed. Mentum anterior margin straight with a median notch at ligula insertion. Submentum not impressed before apex, apex broadly emarginate. Postgenal processes slightly swollen, acute, and extending past middle of mentum, not reaching anterior margin of mentum. Antenna moderately clothed in golden erect acuminate setae; antennal segment 10 wider at apicies, tomentose sensilla separated, oval, not wrapping around apex; antennal segment 11 weakly amplected into segment 10, exposing most of segment. **Prothorax:** Pronotal margin arctuate, widest near middle, not significantly dilated, and weakly reflexed; anterior apicies produced and acute; posterior apicies obtuse; posterior margin concave, never with a medial tooth. Pronotal disc moderately foveate, each fovea with a minute simple setae arising from anterior side; paramedial fossa absent. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum moderately foveate, anterior margins of fovea not raised or tuberculate. **Pterothorax:** Elytra elongate oval, widest near middle. Marginal costa lightly punctate, meeting discal costa near cauda, and not reflexed; inner branch

absent or faintly indicated; elytral humera obtuse, not reflexed. Discal costa weakly raised near elytral base and bifurcate, branches reuniting in apical fourth before uniting with marginal costa near cauda, crests lightly punctate and shiny. Sutural costa not raised. Intercostal spaces rugose, with weakly raised irregular transverse or oblique costae; moderately and irregularly punctate with short inconspicuous simple setae. **Legs:** Femora shallowly punctate and rugose; tibia rugose and setose, setae short, pale, and acuminate mixed with stouter spiniform setae emerging from small tubercles; tarsi venter with long acuminate setae and stout spiniform setae on laterally margins, medially setose; apical protibial spine large, acute, and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi.

**Abdomen:** Shiny and sparsely punctate, punctures with or without simple inconspicuous setae; intercoxal process broadly rounded at apex.

**Diagnosis.** *P. doyeni* can be separated from the other members of the *Zaluecus* subgenus based on the following character combination: postgenal processes swollen, extending past middle of mentum, not reaching anterior margin; submentum apex emarginate; pronotal margin arctuate, widest near middle, not dilated, and slightly reflex; pronotal disc moderately foveate, posterior apicies obtuse; marginal costae of elytra lightly punctate and rarely divided, inner branch absent or weakly indicated; intercostal spaces of elytra rugose.

**Distribution.** MEXICO: Coahuila, Nuevo Leon, and Zacatecas.

**Etymology.** The species is named in honor of John T. Doyen, the only known collector of specimens in the type series.

**Biology.** Unknown.

**subgenus *Variodorsus* Smith, New Subgenus**

Type species: *Asida guanajuatensis* Champion, 1884:56.

**Description.** Length: 9.5-15.1mm, width: 4.8-8.4mm. Integument black; densely setose, with modified lanceolate and squamate scales dorsally, lacking stellate setae. **Head:** Mentum subtrapezoidal; contacting postgenal processes, nearly reaching mandibles when closed; lateral straight of slightly curved inward near apicies; anterior margin medially emarginate. Ligula sclerotized, small, approximately one-sixth mentum width; slightly curved, concealed or partially visible above anterior margin of mentum. Apical segment of maxillary palps enlarged, isotriangular to weakly scalene in female, scalene in male with interior-distal angle acute. Submentum medially depressed; apex deeply emarginate; projecting into buccal cavity; width four-fifths that of buccal cavity, partially exposing maxillary cardos laterally. Postgenal processes produced, acute, and slightly swollen, extending at least to middle of mentum. Labral margin broadly emarginate; clypeal membrane concealed. Clypeal margin emarginate. Eyes elongate, thin and weakly reniform. Antenna weakly clavate, segments 3-8 moniliform, length equal to width; apical tomentose sensilla on antennal segment 10 separated into two curved patches around apex; antennal segment 11 approximately one-fourth size of segment 10, apical tomentose sensillum covering one-half or less of segment, distinctly amplected into segment 10. **Prothorax:** Pronotal margin costate, sinuate, consticted near basal third, and not reflexed; pronotal disc variable, two or four paramedial fossae present. Prosternal process wide, raised and projecting behind procoxal cavities, apex broadly rounded. **Pterothorax:** Elytral sculpturing variable, marginal and distal costae. Mesonotum with

two shallow or deep transverse tomentose depressions, leaving a thin medial ridge between the scutellum and scutum. **Legs:** Mesocoxal cavities open; mesotrocantin small, exposed or rarely concealed. **Abdomen:** Foveate and setose, never with a tomentose band of setae along margins of ventrites. Intercoxal process broad, apex truncate or broadly rounded.

**Diagnosis.** The subgenus *Variodorsus* is distinguished from other *Pelecyphorus* subgenera by a unique combination of the following characters: mentum contacting postgenal processes, nearly reaching mandibles, anterior margin medially emarginate; submentum deeply emarginate, partially exposing maxillary cardos laterally; antennal segment 11 one-fourth or less size of segment 10, tomentose sensilla separate; dorsal setae lanceolate or squamate, stellate setae absent; mesotrocantin small, exposed or concealed.

**Distribution.** MEXICO: Aguascalientes, Guanajuato, Hidalgo, Morelos, Puebla.

## Species Descriptions

### *Pelecyphorus* (*Variodorsus*) *guanajuatensis* (Champion), New Combination

*Asida guanajuatensis* Champion, 1884:56

*Astrotus guanajuatensis* (Champion). Wilke, 1922:267

*Pelecyphorus* (*Astrotus*) *guanajuatensis* (Champion). Smith, 2010

= *Stenomorpha* (*Bothrasida*) *mucorea* (Wilke 1922:270), **new synonym**

**Type Material.** LECTOTYPE, designated here, (sex undetermined) labeled: a) Orange bordered white circle reading "Type"; b) "Guanajuato"; c) " Mexico. / Salle Coll."; d) "Ologlyptus, / guanajuatensis, / apud Salle Duges."; e) "a guanajuatensis, / Champ."; f) "B.C.ACol.IV.1. / Asida / guanajuatensis". (BMNH). PARALECTOTYPES (4 specimens) [all bearing the label "PARALECTOTYPE / *Asida* / *guanajuatensis* / Champion, 1884 / det. Aaron D. Smith" on yellow paper]: 3 paralectotypes (BMNH) with same locality data as holotype. 1 paratype (CASC) labeled a) "MEX".

**Additional Specimens Examined.** (15 specimens). MEXICO: Aguascalientes, Guanajuato, and Hidalgo.

**Redescription (see fig. 2.25).** Length: 9.5-14.1mm, width: 4.8-7.2mm (lectotype length: 11.6mm, width: 5.8mm). Integument black to ferruginous, rarely encrusted with debris; elytra wider than pronotum and 2.7-3.2X longer, width of pronotum at base less than width of elytral base. **Head:** Densely foveate with decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture not or faintly impressed, epistomal suture not indented at margin; medial depression on frons deeply impressed. Mentum anterior margin straight with a median emargination at ligula insertion; basal half of mentum with two paramedial longitudinal impressions. Submentum medially depressed, apex strongly emarginate. Postgenal processes slightly swollen, acute, and extending past middle of mentum, not reaching anterior margin of mentum. Antenna densely clothed in brown erect acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated, oval, not wrapping around apex. **Prothorax:** Pronotal margin sinuate, widest before middle; anterior apicies produced and acute; posterior apicies produced and acute,

slightly projecting over elytral humera; posterior margin nearly straight, weakly emarginate before apicies, lacking a medial tooth. Pronotal disc nearly confluently foveate, each fovea with an acuminate, lanceolate, or squamate seta arising from anterior side; four paramedial fossa present, anterior pair occasionally faintly indicated; medial ridge absent. Prosternal process longitudinally impressed, weakly raised and projecting behind procoxae. Prosternum densely foveate with long acuminate setae, anterior margins of some fovea raised and forming rounded tubercules. **Pterothorax:** Elytra elongate oval, widest behind middle; crests of all costae glaberous and shiny. Marginal costa reticulate, meeting discal costa near cauda, with low transverse costae branching ventrally along pseudoepiplura and dorsally onto elytra, not reflexed; elytral humera distinct, straight or weakly reflexed. Discal costa raised at elytral base reticulate, confused with a connected network of transverse and oblique costae over most of length, united with marginal costa caudally. Sutural costa raised. Intercostal spaces smooth, nearly impunctate, and moderately clothed in squamate scales, mixed with erect lanceolate scales near margins of costae. **Legs:** Femora and tibia confluently foveate, rugose in appearance, and clothed in short acuminate setae, mixed with stouter spiniform setae emerging from small tubercles on tibia; tarsi venter with dark brown stout spiniform setae on laterally margins, medially glabrous; apical protibial spine large, acute, and glaberous; combined protarsal segments approximately three-fifths length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately foveate, fovea with short acuminate setae; intercoxal process broadly rounded at apex.

**Diagnosis.** *P. guanajuatensis* can be separated from the other members of the *Variodorsus* subgenus based on the following character combination: Pronotum without a

raised medial ridge; elytral with a confused network of costae, crests of costae glabrous, intercostal regions smooth and clothed in short squamate setae.

**Distribution.** MEXICO: Aguascalientes, Guanajuato, and Hidalgo.

**Biology.** Unknown. Collected from underneath rocks and feeding on dry manure.

**Discussion.** Wilke (1922) described *Bothrasida mucorea* from a single specimen of *P. guanajuatensis* labeled "Chi." (presumably for Chihuahua). It is unknown whether Wilke had ever seen a specimen of *P. guanajuatensis*, but his description indicates that he placed his new species in *Bothrasida* based on the elytral sculpturing.

### *Pelecyphorus* (*Variodorsus*) *fasciculatus* (Champion), New Combination

*Asida fasciculatus* Champion, 1892:495

*Astrotus fasciculatus* (Champion). Wilke, 1922:267

*Pelecyphorus* (*Astrotus*) *fasciculatus* (Champion). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (male) labeled: a) Orange bordered white circle reading "Type"; b) "Flohr / Cuernavaca, / Morelos.."; c) handwritten det. "Asida / fasciculata. / Ch"; d) "Sp. figured."; e) "B.C.ACol.IV.1. / Asida / fasciculata". (BMNH).

**Additional Specimens Examined.** (24 specimens). MEXICO: Guerrero, Hidalgo, Mexico, Morelos, Puebla.

**Redescription (see fig. 2.26).** Length: 10.6-15.1mm, width: 5.8-8.4mm (lectotype length: 11.7mm, width: 6.6mm). Integument black to ferruginous, often lightly encrusted with debris; elytra wider than pronotum and approximately 2.5X longer, width of pronotum at base less than width of elytral base. **Head:** Densely foveate with decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture deeply impressed, epistomal suture indented at margin; medial depression on frons deeply impressed. Mentum anterior margin straight with a median emargination at ligula insertion; basal half of mentum with two paramedial longitudinal impressions. Submentum medially depressed, apex emarginate. Postgenal processes slightly swollen, acute, and extending past middle of mentum, not reaching anterior margin of mentum. Antenna densely clothed in brown erect acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated, curved, wrapping around apex. **Prothorax:** Pronotal margin sinuate, widest before middle, constricted in basal third before apicies; anterior apicies produced and rounded; posterior apicies produced and acute, slightly projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, with a medial tooth. Pronotal disc nearly confluently foveate, each fovea with a semi-erect, lanceolate, seta arising from anterior side; four paramedial fossa present, posterior pair occasionally faintly indicated; longitudinal medial ridge strongly raised throughout. Prosternal process longitudinally impressed, weakly raised and projecting behind procoxae. Prosternum densely foveate with long acuminate setae, anterior margins of fovea not raised or forming rounded tubercules. **Pterothorax:** Elytra elongate oval, widest behind middle; crests of costae lightly setose, mostly obscured by longer setae emerging from sides of costae. Marginal costa not reflexed, not meeting discal costa near cauda, with short transverse costa

branching dorsally onto elytra; elytral humera distinct, slightly obtuse or weakly reflexed. Discal costa raised at elytral base and bifurcate, inner branch visible in basal third then eroded and faintly indicated, weakly reticulate. Sutural costa weakly raised at base or not. Intercostal spaces smooth, moderately foveate, and setose. Costae and intercostal regions clothed in pale and dark brown squamate and lanceolate erect scales, dark squamate scales forming irregular points and lines across surface. **Legs:** Femora and tibia confluently foveate, rugose in appearance, and clothed in short acuminate setae, mixed with stouter spiniform setae emerging from small tubercles on tibia; tarsi venter with short acuminate setae and dark brown stout spiniform setae on laterally margins; apical protibial spine large, acute, and glaberous; combined protarsal segments approximately three-fifths length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately foveate, fovea with short acuminate setae; intercoxal process broadly rounded or truncate at apex.

**Diagnosis.** *P. fasciculatus* can be separated from the other members of the *Variodorsus* subgenus based on the following character combination: Pronotumwith a raised medial ridge; elytra with discal costae present and bifurcate, inner branch eroded after basal third, densely clothed in multicolored erect squamate and lanceolate scales, forming irregular darker points and lines across surface.

**Distribution.** MEXICO: Guerrero, Hidalgo, Mexico, Morelos, Puebla.

**Biology.** Unknown. Collected in pitfall traps.

**subgenus *Plesiasida* Smith, 2010, *Nomen Novum* (=*Parasida* Casey, 1912)**

Type species: *Euschides liratus* LeConte 1854:223

=*Parasida* Casey, 1912:126. (Junior homynym).Type species: Type species: *Parasida laciniata* Casey, 1912, (= *Pelecyphorus liratus* (LeConte)), by original designation.

**Redescription.** Length: 9.2-22.0mm, width: 4.1-11.5mm. Integument ferruginous to black; setose, with modified lanceolate or squamate scales dorsally, lacking stellate setae. **Head:** Mentum subtrapezoidal to transversely cordate; separated from postgenal processes, not reaching mandibles when closed; lateral straight of slightly curved inward near apicies; anterior margin medially emarginate. Ligula sclerotized, small, approximately one-fourth mentum width; slightly to strongly curved and partially visible above anterior margin of mentum. Apical segment of maxillary palps enlarged, isotriangular to strongly scalene, more expanded in males. Submentum medially depressed; apex broadly emarginate; projecting into buccal cavity; width two-thirds to four-fifths that of buccal cavity, partially exposing maxillary cardos laterally. Postgenal processes produced, acute, and slightly swollen, extending at least to middle of mentum. Labral margin broadly emarginate or truncate; clypeal membrane concealed or rarely exposed. Clypeal margin variable. Eyes elongate, oval or weakly reniform. Antenna weakly clavate, segments 3-8 moniliform, longer than wide; apical tomentose sensilla on antennal segment 10 meeting on one side or separated into two curved patches around apex; antennal segment 11 one-half or more size of segment 10, apical tomentose sensillum covering one-half to two-thirds of segment. **Prothorax:** Pronotal margin costate, arctuate or sinuate, reflexed or not; pronotal disc variable. Prosternal process

wide, raised and projecting or deflexed behind procoxal cavities, longitutunally impressed or not. **Pterothorax:** Elytral sculpturing variable, marginal costa present or rarely absent. Mesonotum with two shallow or deep transverse tomentose depressions, leaving a thin medial ridge between the scutellum and scutum. **Legs:** Mesocoxal cavities open; mesotrocantin prominate and exposed. **Abdomen:** Setation and punctation variable, never with a tomentose band of setae along margind of ventrites. Intercoxal process broad, apex rounded or truncate.

**Diagnosis.** The subgenus *Plesiasida* is distinguished from other *Pelecyphorus* subgenera by a unique combination of the following characters: mentum not reaching postgenal processes or mandibles, anterior margin medially emarginate; antennal segment 11 one-half or more size of segment 10, tomentose sensilla meeting on one side or not, never forming a continous band around apex; dorsal setae lanceolate or squamate, stellate setae absent; mesotrocantin prominent and exposed.

**Distribution.** MEXICO: Aguascalientes, Baja California Sur, Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Jalisco, Mexico, Mexico D. F., Puebla, Queretaro, Zacatecas. USA: Arizona.

## Species Descriptions

### *Pelecyphorus* (*Plesiasida*) *liratus* (LeConte)

*Euschides liratus* LeConte, 1854: 223

*Asida lirata* (LeConte). Horn, 1870:283

*Parasida lirata* (LeConte). Casey, 1912:130

*Pelecyphorus* (*Plesisida*) *liratus* (LeConte). Smith, 2010

=*Pelecyphorus* (*Plesiasida*) *laciniatus* (Casey, 1912:128), **New Synonym**

=*Pelecyphorus* (*Plesiasida*) *cristatus* (Pallister, 1954:24), **New Synonym**

**Type Material.** HOLOTYPE, by monotypy, (female) labeled: a) silver LeConte locality disc = Arizona; Valley of Gila; b) "A. lirata / LeC"; c) red MCZ type label reading "Type 4525". (MCZ).

**Additional Specimens Examined.** (92 specimens). MEXICO: Chihuahua; USA: Arizona (Cochise, Pima, and Santa Cruz Counties), New Mexico (Grant Co.).

**Redescription (see fig. 2.27).** Length: 10.2-15.9mm, width: 5.0-7.9mm. Integument black to ferruginous, often lightly encrusted with debris; setae pale yellowish-white lanceolate scales unless otherwise noted; elytra wider than pronotum and approximately 3.5X longer, width of pronotum at base less than width of elytral base. **Head:** Densely foveate with decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture impressed, epistomal suture indented at margin; medial depression on frons

impressed; labral margin broadly emarginate; clypeal membrane concealed or exposed. Mentum anterior margin straight with a median notch at ligula insertion; basal half of mentum with two paramedial longitudinal impressions. Apical segment of maxillary palps expanded, weakly scalene in female, strongly scalene in male. Postgenal processes slightly swollen, acute, and extending past middle of mentum, not reaching anterior margin of mentum. Antenna densely clothed in brown erect acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex. **Prothorax:** Pronotum broadly arctuate, narrow at anterior apicies, gradually widening to near middle, slightly sinate before posterior apicies; marginal costa reflexed; anterior apicies produced and broadly rounded; posterior apicies produced and acute, projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, fringed with golden tomentose setae and with a medial tooth. Pronotal disc nearly confluently foveate, each fovea with decumbent lanceolate scale; four paramedial fossa present, occasionally faintly indicated; longitudinal medial ridge thin, smooth, and weakly raised throughout. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum densely shallowly foveate with acuminate setae, anterior margins of some fovea near lateral margins raised and forming rounded tubercules. **Pterothorax:** Scutellum almost entirely concealed beneath elytra, deep transverse tomentose depressions present on mesonotum, separated by a narrow triangular ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base depressed before costa and tomentose; costae carinate, crests glabrous. Marginal costa divided in basal third, branches united near base or not, inner branch continuing to apical third, not uniting with marginal or discal costa; elytral humera prominent and reflexed. Discal costa

raised and divided near elytral base; branches not united near base, parallel, and united in apical third or not. Sutural costa raised from base to cauda. Intercostal spaces smooth, with irregular lines of fovea and decumbent lanceolate setae, emerging from minute tubercles or not. **Legs:** Femora and tibia confluently foveate, rugose in appearance, and clothed in short acuminate setae, mixed with stouter spiniform setae emerging from small tubercles on tibia; tarsi venter with short acuminate setae and dark brown stout spiniform setae on laterally margins; apical protibial spine small and glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately punctate, punctures minute with short acuminate setae.

**Diagnosis.** *P. **liratus*** can be separated from the other members of the ***Plesiasida*** subgenus based on the following character combination: Pronotumwith a thin medial ridge; elytra with three distinct longitudinal carinae on each elytron, lacking transverse carinae; elytral base depressed and tomentose; abdominal puntures minute and setose.

**Distribution.** MEXICO: Chihuahua; USA: Arizona (Cochise, Pima, and Santa Cruz Counties), New Mexico (Grant Co.).

**Discussion.** Casey (1912) differentiated his new species *Parasida laciniata* from *P. lirata* based on its description and an image in Horn (1870), both of which lacked two distinctive characters (elytral base tomentose, intercostal spaces with a row of fovea) noted by Casey. However, examination of the *P. lirata* type specimen showed that these features are present. Likewise, Pallister's *P. cristatus* was also separated from *P. lirata* by the lack of these features. The type specimens of both *P. cristatus* and *laciniata* are unremarkable specimens of *P. lirata*.

**Biology.** Unknown. Collected along sandy trails at dusk feeding on fallen grass seeds.

### *Pelecyphorus* (*Plesiasida*) *dispar* (Champion)

*Asida dissimilis* Champion, 1884:59, Junior Homynym

*Asida dispar* Champion, 1892:496, *Nomen Novum*

*Parasida dissimilis* (Champion). Casey, 1912:131

*Pelecyphorus* (*Plesisida*) *liratus* (LeConte). Smith, 2010

= *Pelecyphorus* (*Plesisida*) *trisinuata* (Pallister, 1954:22), **New Synonym**

= *Pelecyphorus* (*Stenosides*) *kulzeri* (Pallister, 1954:12), **New Synonym**

= *Pelecyphorus* (*Stenosides*) *bisinuatus* (Pallister, 1954:13), **New Synonym**

**Type Material.** LECTOTYPE, designated here, (male) labeled: a) Orange bordered white circle reading "Type" ; b) "1747" ; c) "Mexico / Salle Coll" ; d) handwritten det. "Asida / dissimilis, / Champ" ; e) "Sp. figured." ; f) "B.C.ACol.IV.1. / Asida / dispar / dissimilis.".

**Additional Specimens Examined.** (41 specimens). MEXICO: Aguascalientes, Chihuahua, Durango, Zacatecas.

**Redescription (see fig. 2.28).** Length: 9.2-14.2mm, width: 4.1-7.1mm (lectotype length: 10.0mm, width: 4.4mm). Integument black to ferruginous, often lightly encrusted with debris; setae pale yellowish-white lanceolate scales unless otherwise noted; elytra wider than pronotum and 2.8-3.0X longer, width of pronotum at base less than width of elytral

base. **Head:** Densely foveate with decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture impressed, epistomal suture indented at margin; medial depression on frons impressed; labral margin broadly emarginate; clypeal membrane concealed or exposed. Mentum anterior margin straight, medial notch absent or minute; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, weakly scalene in female, strongly scalene in male. Postgenal processes slightly swollen, acute, and extending past middle of mentum, not reaching anterior margin of mentum. Antenna densely clothed in brown erect acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex or barely meeting on one side. **Prothorax:** Pronotum broadly arctuate or slightly sinate before posterior apicies, widest near middle; marginal costa weakly reflexed; anterior apicies produced and broadly rounded; posterior apicies produced and acute, projecting over elytral humera; posterior margin nearly straight, emarginate and fringed with golden tomentose setae before apicies, medial tooth absent. Pronotal disc nearly confluently foveate, each fovea with decumbent lanceolate scale; four paramedial fossa present, occasionally faintly indicated; longitudinal medial ridge thin, smooth, and weakly raised throughout. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum densely shallowly foveate with acuminate setae, anterior margins of some fovea raised and forming rounded tubercules. **Pterothorax:** Scutellum almost entirely concealed beneath elytra, deep transverse tomentose depressions present on mesonotum, separated by a narrow triangular ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base depressed before costa and tomentose; costae carinate, crests often setose. Marginal costa tuberculate and meeting discal costa in

apical fourth, divided in basal third, branches united near base or not, inner branch continuing to apical third, not uniting with marginal or discal costa; elytral humera prominent and reflexed. Discal costa raised and divided in basal third; branches frequently united near base and in apical third, inner branch often eroded. Sutural costa weakly raised or not. Intercostal spaces smooth, with scattered fovea and decumbent lanceolate setae, emerging from minute tubercles or not. **Legs:** Femora and tibia confluently foveate, rugose in appearance, and clothed in short acuminate setae, mixed with stouter spiniform setae emerging from small tubercles on tibia; tarsi venter with short acuminate setae and dark brown stout spiniform setae on laterally margins; apical protibial spine small and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately coarsely punctate with short acuminate setae.

**Diagnosis.** *P. dispar* can be separated from the other members of the ***Plesiasida*** subgenus based on the following character combination: pronotum with a thin medial ridge; elytra with marginal costa divided and tuberculate, discal costa bifurcate, united near base and apex, lacking transverse carinae; elytral base depressed and tomentose; abdomen coarsely punctate with short acuminate setae.

**Distribution.** MEXICO: Aguascalientes, Chihuahua, Durango, Zacatecas.

**Discussion.** The three species described by Pallister (1954) and synonymized under *P. dispar* were all based on specimens collected during the Rockefeller Mexican expedition of 1947. Representative specimens were sent to Hans Kulzer, a German tenebrionid worker, who made suggestions on the generic placement and status of the material. All three fall well within the range of variation seen within *P. dispar* populations.

in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in brown erect acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex or barely meeting on one side. **Prothorax:** Pronotum broadly arctuate, narrow at anterior apicies and gradually widening to middle, nearly parallel sided from middle to base; marginal costa weakly reflexed; anterior apicies produced and broadly rounded; posterior apicies produced and acute, projecting over elytral humera; posterior margin nearly straight, fringed with golden tomentose setae and emarginate before apicies, medial tooth present. Pronotal disc nearly confluently foveate, each fovea with minute decumbent scale; four paramedial fossa present, posterior pair faintly indicated; longitudinal medial ridge thin, smooth, and weakly raised throughout. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum densely shallowly punctate with acuminate setae, anterior margins of fovea raised and forming rounded tubercules. **Pterothorax:** Scutellum almost entirely concealed beneath elytra, deep transverse tomentose depressions present on mesonotum, separated by a narrow triangular ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base depressed before costa and tomentose. Marginal costa rounded and glabrous, raised to cauda and not meeting discal costa; divided in basal third, branches not united basally, inner branch continuing to apical third, not uniting with marginal or discal costa; elytral humera prominent and reflexed. Discal costa raised and divided in basal third; branches rarely united near base or in apical third, crests rounded and shiny. Sutural costa raised, crest rounded and shiny. Intercostal spaces smooth and opaque, with sparse minute punctures and decumbent lanceolate setae, appearing nearly glabrous. **Legs:** Femora and tibia confluently shallowly foveate, rugose

in appearance, and clothed in short pale acuminate setae, mixed with stouter black spiniform setae emerging from small tubercles on tibia; tarsi venter with stout black spiniform setae on laterally margins; apical protibial spine small and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Densely minutely punctate with short acuminate setae, faintly rugose.

**Diagnosis.** *P. bibasalis* can be separated from the other members of the ***Plesiasida*** subgenus based on the following character combination: pronotum with a thin medial ridge; elytra with crests of all costae rounded and shiny, marginal costa divided, branches completely separate, discal costa divided, branches rarely united near base or apex, lacking transverse carinae; elytral intercostal spaces nearly glabrous and opaque; elytral base depressed and tomentose; abdomen minutely punctate with short acuminate setae.

**Distribution.** Known only from the Promotorio region in the Mexican state of Durango.

**Biology.** Unknown.

### ***Pelecyphorus* (*Plesiasida*) *sexcostatus* LeConte**

*Pelecyphorus sexcostatus* LeConte, 1861:337

*Asida sexcostata* (LeConte). Horn, 1870:283

*Parasida sexcostata* (LeConte). Casey, 1912:130

*Pelecyphorus* (*Plesiasida*) *sexcostatus* LeConte. Smith, 2010

**Type Material.** HOLOTYPE, by monotypy, (sex undetermined) labeled: a) "Type 4536"; b) "P. 6-costatus / S. Lucas LeC"; c) on red paper "HOLOTYPE / *Pelecyphorus* / *sexcostatus* / LeConte, 1861 / det. Aaron D. Smith".

**Additional Specimens Examined.** (31 specimens). MEXICO: Baja California Sur.

**Redescription (see fig. 2.30).** Length: 10.9-14.0mm, width: 5.6-7.0mm. Integument black to ferruginous; setae pale yellowish-white lanceolate scales unless otherwise noted; elytra wider than pronotum and 2.9-3.4X longer, width of pronotum at base less than width of elytral base. **Head:** Densely foveate with decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture impressed, epistomal suture indented at margin; medial depression on frons weakly impressed; labral margin broadly emarginate; clypeal membrane concealed or exposed. Mentum anterior margin straight, weakly emarginate medially; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, isotriangular in female, scalene in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in brown erect acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex. **Prothorax:** Pronotum arctuate or slightly sinuate before posterior apicies, widest near middle; marginal costa weakly reflexed or nearly straight; anterior apicies produced and acute; posterior apicies slightly produced and acute, barely projecting over elytral humera; posterior margin nearly straight, not fringed with golden tomentose setae and weakly emarginate before apicies, medial tooth absent. Pronotal disc densely foveate, each fovea with a long decumbent lanceolate scale; paramedial fossa absent; longitudinal medial ridge absent, faintly

indicated by thin smooth line. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum moderately punctate with acuminate setae, anterior margins of fovea raised and forming rounded tubercules. **Pterothorax:** Scutellum exposed, shallow transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose. Marginal costa tuberculate with short erect setae, raised to cauda and not meeting discal costa; divided in basal third, branches not united basally, inner branch continuing to apical third, not uniting with marginal or discal costa; elytral humera slightly obtuse, weakly reflexed or not. Discal costa raised, tuberculate with erect acuminate setae along crest, inner branch absent or faintly indicated. Sutural costa not raised. Intercostal spaces moderately foveate and clothed in decumbent lanceolate scales. **Legs:** Femora and tibia confluently shallowly foveate, rugose in appearance, and clothed in pale lanceolate scales, mixed with stouter darker spiniform setae emerging from small tubercles on tibia; tarsi venter with long acuminate setae and stout spiniform setae on laterally margins; apical protibial spine small and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately foveate with long acuminate setae.

**Diagnosis.** *P. sexcostatus* can be separated from the other members of the ***Plesiasida*** subgenus based on the following character combination: pronotum without a medial ridge; elytra with crests of costae tuberculate, marginal costa divided, branches completely separate, discal costa not apparently divided, lacking transverse carinae;

elytral intercostal spaces foveate with decumbent lanceolate scales; elytral base neither depressed nor tomentose.

**Distribution.** Known only from the Mexican state of Baja California Sur, from sea level to approximately 1000 feet in elevation.

**Biology.** Unknown. Collected in pitfall traps and from underneath rocks.

### *Pelecyphorus* (*Plesiasida*) *cifuentesi* Smith, New Species

**Type Material.** HOLOTYPE (male) labeled: a) "MEXICO: Baja Cal. Sur / Sier. de la Laguna trail / el 1495m, N23°32.78' / W110°00.99',BCS#41 / 28.VII.2009, ADSmith"; b) on red paper, "HOLOTYPE / *Pelecyphorus* / (*Plesiasida*) / *cifuentesi* ♂/ Aaron D. Smith" (CNIN). PARATYPES (5 specimens) [all bearing the label "PARATYPE / *Pelecyphorus* / (*Plesiasida*) / *cifuentesi* / Aaron D. Smith" on yellow paper] with the following locality data: 1 paratype (MSUC) labeled same as holotype. 3 paratypes (ADSC) labeled a) "MEXICO: Baja Cal. Sur / Sier. de la Laguna trail / el 1573m, N23°32.78' / W110°00.83',BCS#43 / 28.VII.2009, ADSmith". 1 paratype (CASC) labeled a) "Sierra Laguna / Lower Cal. / VIII-15-1919"; b) "Coll. by / J.R. Slevin".

**Description (see fig. 2.31).** Length: 11.2-12.6mm, width: 4.8-6.0mm (lectotype length: 11.2mm, width: 5.3mm). Integument black and glossy; setae pale yellowish-white lanceolate scales unless otherwise noted; elytra wider than pronotum and 3.3-3.7X longer. **Head:** Densely foveate with long decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture weakly impressed, epistomal suture indented at margin;

**Biology.** Unknown.

### *Pelecyphorus* (*Plesiasida*) *bibasalis* (Casey)

*Parasida bibasalis* Casey, 1912: 128

*Pelecyphorus* (*Plesiasida*) *bibasalis* (Casey). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (male) labeled: a) "Promontorio Durango."; b) on red paper "LECTOTYPE / *Parasida* / *bibasalis* / Casey, 1912 / det. Aaron D. Smith". PARALECTOTYPES, three specimens (NMNH): with same locality information as lectotype and bearing the label "PARALECTOTYPE / *Parasida* / *bibasalis* / Casey, 1912 / det. Aaron D. Smith".

**Additional Specimens Examined.** (24 specimens). MEXICO: Durango, Promontorio.

**Redescription (see fig. 2.29).** Length: 14.4-19.4mm, width: 7.0-9.7mm. Integument black to ferruginous; setae pale yellowish-white lanceolate scales unless otherwise noted; elytra wider than pronotum and approximately 3.5X longer, width of pronotum at base less than width of elytral base. **Head:** Densely foveate with decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture impressed, epistomal suture indented at margin; medial depression on frons impressed; labral margin broadly emarginate; clypeal membrane concealed or exposed. Mentum anterior margin straight, weakly emarginate medially; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, weakly scalene in female, strongly scalene

medial depression on frons weakly impressed; labral margin broadly emarginate; clypeal membrane concealed. Mentum anterior margin straight, weakly emarginate medially; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, isotriangular in female, scalene in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in dark brown erect acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex. **Prothorax:** Pronotum weakly arctuate, widest at middle, to nearly parallel sided; marginal costa strongly reflexed; anterior apicies produced and acute; posterior apicies acute, not or slightly produced, not projecting over elytral humera; posterior margin nearly straight, not fringed with golden tomentose setae and weakly emarginate before apicies, medial tooth absent. Pronotal disc densely foveate, each fovea with a long decumbent lanceolate scale; paramedial fossa absent; longitudinal medial ridge absent. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum densely foveate with acuminate setae, anterior margins of fovea weakly raised or not. **Pterothorax:** Scutellum exposed, shallow transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum. Elytra elongate oval, widest near middle; elytron base not depressed or tomentose. Marginal, sutural, and elytral costae absent or faintly indicated; elytral humera obtuse, weakly reflexed or not. Elytral disc moderately punctate and clothed in decumbent lanceolate scales, elytral margins with short erect acuminate setae raised on minute tubercles. **Legs:** Femora and tibia confluently shallowly foveate, rugose in appearance, and clothed in dark brown acuminate setae, mixed with stouter darker spiniform setae emerging from small tubercles on tibia; tarsi venter with dark

brown acuminate setae and stout spiniform setae on laterally margins; apical protibial spine small and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately punctate with long acuminate setae.

**Diagnosis.** *P. cifuentesi* can be separated from the other members of the ***Plesiasida*** subgenus based on the following character combination: pronotum without a medial ridge; pronotal margin strongly reflexed; prosternal process deflexed behind procoxa; elytra costa absent or faintly indicated; elytral base neither depressed nor tomentose.

**Distribution.** Known only from Sierra de la Laguna in Mexican state of Baja California Sur, above 4500 feet in elevation.

**Biology.** Unknown. Collected walking at night along trails.

### ***Pelecyphorus* (*Plesiasida*) *longipennis* (Champion)**

*Asida longipennis* Champion, 1884:56

*Parasida longipennis* (Champion). Wilke, 1922:270

*Pelecyphorus* (*Plesiasida*) *longipennis* (Champion). Smith, 2010

=*P.* (*Plesiasida*) *mixtecae* (Wilke, 1922:271), **New Synonym**

=*P.* (*Plesiasida*) *esperanzae* (Wilke, 1922:271), **New Synonym**

**Type Material.** LECTOTYPE, designated here, (male) labeled: a) Orange bordered white circle reading "Type"; b) "1759"; c) "San Antonio / de Ariba / Mexico / Salle Coll"; d) handwritten det. "Pelecyphorus / longipennis, Ch. / apund Salle"; e) handwritten

det. "Asida / longipennis, Champ."; f) "Sp. figured."; g) "B.C.ACol.IV.1. / Asida / longipennis.". (BMNH). PARATYPE, 1 specimen (BMNH) labeled "San Andres"

**Additional Specimens Examined.** (16 specimens). MEXICO: Puebla.

**Redescription (see fig. 2.32).** Length: 10.9-14.7mm, width: 5.2-6.1mm (lectotype length: 12.6mm, width: 5.6mm). Integument black to ferruginous; setae yellowish-white to golden unless otherwise noted; elytra wider than pronotum and 2.7-3.2X longer, width of pronotum at base nearly equal to width of elytral base. **Head:** Densely foveate with decumbent lanceolate setae emerging from inside fovea; frontoclypeal suture impressed, epistomal suture not indented at margin; medial depression on frons weakly impressed; labral margin truncate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, isotriangular in both sexes. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect golden acuminate setae; antennal segment 10 widest at apicies, tomentose sensilla separated and curved around apex or meeting on one side. **Prothorax:** Pronotum arctuate or slightly sinuate before posterior apicies, widest near middle; marginal costa not reflexed; anterior apicies weakly produced and rounded; posterior apicies acute, not produced; posterior margin nearly straight, not fringed with golden tomentose setae, medial tooth absent. Pronotal disc nearly confluently foveate, each fovea with a thin golden setae; four paramedial fossa present or faintly indicated; longitudinal medial ridge absent. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum densely foveate with golden acuminate setae, anterior margins of

fovea rarely raised and forming rounded tubercules. **Pterothorax:** Scutellum exposed, shallow transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose. Marginal costa punctate and meeting discal costa near cauda, divided in basal third, inner branch curved towards suture and meeting discal costa in apical third; elytral humera slightly oblique and not reflexed. Discal costa weakly or strongly raised and divided at base, outer branch meeting inner branch of marginal costa in apical third or not. Sutural costa weakly raised or not. Costal crests punctate with scattered setae; intercostal spaces densely foveate and punctate with decumbent lanceolate or acuminate setae.**Legs:** Femora deeply foveate, tibia confluently shallowly foveate, rugose in appearance, and clothed in pale lanceolate setae; tarsi venter with long pale setae; apical protibial spine large acute and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Densely foveate with long golden setae.

**Diagnosis.** *P. longipennis* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum without a medial ridge, posterior apicies acute and not produced; elytra with crests of costae punctate; elytral intercostal spaces foveate and punctate with decumbent lanceolate scales; elytral base neither depressed nor tomentose; tarsi venter with long golden setae only.

**Distribution.** MEXICO: Puebla.

**Biology.** Unknown. Collected from underneath dead cactus.

## *Pelecyphorus* (*Plesiasida*) *indutus* (Champion)

*Asida induta* Champion, 1884:56

*Parasida induta* (Champion). Wilke, 1922:270

*Pelecyphorus* (*Plesiasida*) *indutus* (Champion). Smith, 2010

= *P.* (*Stenosides*) *bicarinatus* (Champion, 1884:69), **New Synonym**

**Type Material.** HOLOTYPE, by monotypy, (male) labeled: a) Orange bordered white circle reading "Type"; b) "MEX / ICO"; c) handwritten "Characters of Pel: / :cyphorus but / hind angles of / prothorax not produced"; d) handwritten det. "Asida / induta, Champ"; e) "Sp. figured."; f) "B.C.ACol.IV.1. / Asida / induta.". (BMNH).

**Additional Specimens Examined.** (1 specimen). HOLOTYPE, by monotypy, of *Ologlyptus bicarinatus* Champion, 1884:69, (female) labeled a) Orange bordered white circle reading "Type"; b) "Oaxaca, / Mexico. / Hoge."; c) "Ologlyptus / bicarinatus, Champ."; d) "Sp. figured."; e) "Belongs to / Asida"; f) "B.C.ACol.IV.1. / Ologlyptus / bicarinatus."

**Redescription (see fig. 2.33).** Length: 12.0-14.2mm, width: 5.9-8.7mm (holotype length: 12.0mm, width: 5.9mm). Integument black to ferruginous; setae yellowish-white to golden unless otherwise noted; elytra wider than pronotum and approximately 3.2X longer, width of pronotum at base less than width of elytral base. **Head:** Moderately punctate with decumbent acuminate setae emerging from inside punctures; frontoclypeal suture faintly impressed, epistomal suture indented at margin; medial depression on frons

weakly impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, isotriangular in female, scalene in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect golden acuminate setae; antennal segment 10 widest at apicies, tomentose sensilla separated and curved around apex. **Prothorax:** Pronotum arctuate or slightly sinuate before posterior apicies, widest near middle; marginal costa slightly reflexed; anterior apicies weakly produced and rounded; posterior apicies acute, not produced; posterior margin nearly straight, not fringed with golden tomentose setae, medial tooth absent. Pronotal disc densely punctate, each puncture with a thin golden setae; four paramedial fossa absent or faintly indicated; longitudinal medial ridge absent. Prosternal process longitudinally impressed, deflexed behind procoxae. Prosternum densely foveate with golden acuminate setae, anterior margins of some fovea raised and forming rounded tubercules. **Pterothorax:** Scutellum exposed, shallow transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose. Marginal costa meeting discal costa near cauda or not, divided in basal third, inner branch not connected to other costae; elytral humera oblique and weakly reflexed. Discal costa, raised, and divided at base, outer branch meeting inner branch of marginal costa in apical third or not, inner branch weak or barely indicated. Costal crests tuberculate with erect acuminate setae; intercostal spaces with scattered punctures and acuminate erect and decumbent setae. **Legs:** Femora deeply foveate, rugose in appearance; tibia confluently shallowly foveate, clothed in pale

acuminate setae and darker stout spiniform setae emerging from tubercles; tarsi venter with pale acuminate setae and stout spiniform setae on laterally margins; apical protibial spine large acute and glaberous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately punctate with short acuminate setae.

**Diagnosis.** *P. indutus* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum without a medial ridge, posterior apicies acute and not produced; elytra with crests of costae tuberculate and setose, marginal costa divided, branches completely separate, discal costa divided, lacking transverse carinae; elytral intercostal spaces punctate with erect acuminate setae; elytral base neither depressed nor tomentose.

**Distribution.** MEXICO: Oaxaca.

**Biology.** Unknown.

### ***Pelecyphorus* (*Plesiasida*) *tristis* (Champion)**

*Asida tristis* Champion, 1884:55

*Parasida tristis* (Champion). Wilke, 1922:270

*Pelecyphorus* (*Plesiasida*) *tristis* (Champion). Smith, 2010

= *P.* (*Plesiasida*) *purpusi* (Wilke, 1922:271), **New Synonym**

**Type Material.** LECTOTYPE, designated here, (male) labeled: a) Orange bordered white circle reading "Type"; b) "1758"; c) "San Antonio / de Ariba / Mexico / Salle Coll"; d) handwritten det. "Pelecyphorus / tristis, Chev. / apund Salle". (BMNH).

**Additional Specimens Examined.** (56 specimens). MEXICO: Veracruz, Puebla.

**Redescription (see fig. 2.34).** Length: 12.0-13.7mm, width: 5.3-7.5mm (lectotype length: 12.1mm, width: 5.8mm). Integument black, usually with a glossy sheen, legs ferruginous; setae dark brown to black unless otherwise noted; elytra wider than pronotum and approximately 2.8X longer, width of pronotum at base less than width of elytral base. **Head:** Moderately foveate with decumbent acuminate setae emerging from inside fovea; frontoclypeal suture faintly impressed, epistomal suture indented at margin; medial depression on frons weakly impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, isotriangular in female, scalene in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect dark brown acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex. **Prothorax:** Pronotum arctuate, widest near middle; marginal costa slightly reflexed; anterior apicies weakly produced and rounded; posterior apicies acute, slightly produced, not projecting over elytral humera; posterior margin nearly straight, weakly emarginate before apicies, not fringed with golden tomentose setae, medial tooth absent. Pronotal disc densely foveate, each fovea with a minute setae; four paramedial fossa absent or faintly indicated; longitudinal medial ridge absent. Prosternal process

longitudinally impressed, deflexed behind procoxae. Prosternum rugose, moderately foveate with dark acuminate setae, anterior margins of some fovea raised and forming rounded tubercules. **Pterothorax:** Scutellum exposed, deep transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose. Marginal costa meeting discal costa near cauda or not, divided in basal third, inner branch not connected to other costae; elytral humera oblique and weakly reflexed. Discal costa, raised, and divided at base, outer branch meeting inner branch of marginal costa in apical fourth or not, inner branch reuniting with outer branch in apical third. Costal crests rounded and glabrous; intercostal spaces with scattered punctures and inconspicuous decumbent lanceolate setae. **Legs:** Femora rugose; tibia tuberculate, stout black spiniform setae emerging from tubercles; tarsi venter with black stout spiniform setae on laterally margins, medially glabrous; apical protibial spine large acute and glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately punctate with inconspicuous black acuminate setae.

**Diagnosis.** *P. tristis* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotumwithout a medial ridge; posterior apicies acute, slightly produced, not projecting over elytral humera; elytra with crests of costae rounded and glabrous, marginal costa divided, branches completely separate; integument black and glossy, legs ferruginous; elytral base neither depressed nor tomentose.

**Distribution.** MEXICO: Oaxaca, Puebla.

**Biology.** Unknown.

### *Pelecyphorus* (*Plesiasida*) *asidoides* Solier

*Pelecyphorus asidoides* Solier, 1836:471

*Asida asidoides* (Solier). Horn, 1870: 283

*Parasida asidoides* (Solier). Wilke, 1922:270

=*Parasida zacualpanicola* Wilke, 1921:272, **New Synonym**

*Pelecyphorus* (*Plesiasida*) *asidoides* (Champion). Smith, 2010

**Type Material.** HOLOTYPE, (male) labeled: a) "Asida / asidoides / [illegible script] / [illegible, looks like ??61]"; b) "Col. Marseul / Col. Solier"; c) "asidoides. Sol 471, 2 Chili"; d) on red paper "HOLOTYPE / Pelecyphorus / asidoides Sol. ♂ / Examined by / Kirby W. Brown / August 1968". (MNHN).

**Additional Specimens Examined.** (17 specimen). MEXICO: Hidalgo, Mexico, Queretaro.

**Redescription (see fig. 2.35).** Length: 12.5-17.9mm, width: 6.7-9.8mm (holotype length: 14.6mm, width: 8.5mm). Integument black, opaque; setae yellowish-brown unless otherwise noted; elytra wider than pronotum and approximately 2.9X longer, width of pronotum at base less than width of elytral base. **Head:** Densely foveate with short acuminate setae emerging from inside fovea; frontoclypeal suture not or faintly impressed, epistomal suture indented at margin; medial depression on frons weakly

impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, scalene in both sexes, distal angle more elongate in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect dark brown acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex. **Prothorax:** Pronotum sinuate, widest near middle; marginal costa straight; anterior apicies produced and acute; posterior apicies acute, produced and projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, fringed with golden tomentose setae, medial tooth present. Pronotal disc densely punctate, each puncture with a minute setae; four paramedial fossa absent or faintly indicated; longitudinal medial ridge absent or thin and not raised. Prosternal process thickened and projecting behind procoxa, gradually deflexed. Prosternum moderately foveate with pale acuminate setae, anterior margins of some fovea raised and forming rounded tubercules. **Pterothorax:** Scutellum partially exposed, deep transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose; costae weakly raised or indicated by glabrous reticulate lines. Marginal costa meeting discal costa near cauda or not, divided in basal third, inner branch not connected to other costae; elytral humera prominent and weakly reflexed. Discal costa divided at base, outer branch meeting inner branch of marginal costa in apical fourth or not, inner branch reuniting with outer branch in apical third. Costal crests rounded and glabrous; intercostal spaces rugose, with low transverse or oblique ridges.

**Legs:** Femora rugose; tibia tuberculate, stout spiniform setae emerging from tubercles; tarsi venter with stout spiniform setae on laterally margins, medially glabrous; apical protibial spine large acute and glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi.

**Abdomen:** Rugose, minutely punctate with inconspicuous acuminate setae.

**Diagnosis.** *P. asidoides* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum with a tomentose fringe and median tooth on posterior margin, without a medial ridge, posterior apicies acute, produced, projecting over elytral humera; elytral costa low, reticulate, connected by low transverse costa; integument black and opaque; elytral base neither depressed nor tomentose.

**Distribution.** MEXICO: MEXICO: Hidalgo, Mexico, Queretaro.

**Biology.** Unknown.

### ***Pelecyphorus (Plesiasida) fallax* Champion**

*Asida fallax* Champion, 1884:57

*Parasida fallax* (Champion). Casey, 1912:131

*Pelecyphorus (Plesiasida) fallax* (Champion). Smith, 2010

=*Pelecyphorus (Plesiasida) favosus* (Champion, 1884:58), **New Synonym**

=*Pelecyphorus (Plesiasida) similatus* (Champion, 1884:58), **New Synonym**

**Type Material.** LECTOTYPE, designated here, (sex undetermined) labeled: a) Orange bordered white circle reading "Type"; b) "Guanajuato"; c) "1761"; d) "Mexico / Salle Coll"; e) handwritten det. "Asida / fallax, / Champ."; f) "Sp. figured."; g) "B.C.ACol.IV.1. / Asida / fallax / favosa / similata.". (BMNH).

**Additional Specimens Examined.** (89 specimens). MEXICO: Guanajuato, Hidalgo, Jalisco, Mexico, Mexico D. F., Zacatecas.

**Redescription (see fig. 2.36).** Length: 12.6-16.9mm, width: 5.9-8.4mm (lectotype length: 14.3mm, width: 6.9mm). Integument black to ferruginous; elytra wider than pronotum and approximately 3X longer, width of pronotum at base subequal to width of elytral base. **Head:** Densely foveate with lanceolate scales emerging from fovea; frontoclypeal suture deeply or faintly impressed, epistomal suture indented at margin; medial depression on frons weakly impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, scalene in both sexes, distal angle more elongate in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect dark brown acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex or meeting on one side. **Prothorax:** Pronotum sinuate, widest before middle; marginal costa straight; anterior apicies produced and broadly rounded; posterior apicies acute, produced and projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, fringed with golden tomentose setae, medial tooth present. Pronotal disc confluently foveate, each fovea with a brown

lanceolate scale; four paramedial fossa absent or faintly indicated; longitudinal medial ridge thin, usually raised throughout. Prosternal process thickened and projecting behind procoxa, gradually deflexed. Prosternum moderately foveate with short dark acuminate setae, anterior margins of fovea not raised and forming rounded tubercules. **Pterothorax:** Deep transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum; scutellum mostly concealed, apparently carinate. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose. Costae thin and sharply raised, crests glabrous; marginal costa meeting discal costa near cauda, divided in basal third, inner branch reunited with outer and discal costa near cauda; elytral humera prominent, straight or weakly reflexed; discal costa divided at base, reunited in apical third; sutural costa raised throughout; transverse costae variably present or absent between marginal and discal branches. Intercostal spaces medially tuberculate, tubercles with semi-erect dark squamate scales, laterally with pale squamate scales not set on tubercles, overall producing a pattern of light and dark setal lines. **Legs:** Femora rugose punctate; tibia shallowly foveolate and tuberculate, with pale acuminate setae and stout spiniform setae emerging from tubercles; tarsi venter with stout spiniform setae on laterally margins, medially glabrous; apical protibial spine large acute and glabrous; combined protarsal segments approximately two-thirds length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Sparsely punctate with inconspicuous acuminate setae.

**Diagnosis.** *P. fallax* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum with a tomentose fringe and median tooth on posterior margin, medial ridge present on disc, posterior apicies acute,

produced, projecting over elytral humera; elytral costa sharply raised, crest glabrous; transverse costae usually present; intercostal regions with alternating rows of light and dark scales; elytral base neither depressed nor tomentose.

MEXICO: Guanajuato, Hidalgo, Jalisco, Mexico, Mexico D. F., Zacatecas.

**Biology.** Unknown.

### *Pelecyphorus* (*Plesiasida*) *intricatus* Champion, New Combination

*Asida intricata* Champion, 1892:493

*Notiasida intricata* (Champion). Wilke, 1922:270

*Pelecyphorus* (*Plesiasida*) *intricatus* (Champion). Smith, 2010

**Type Material.** HOLOTYPE, by monotypy, (female) labeled: a) Orange bordered white circle reading "Type"; b) "State of Jalisco, / Mexico. / Richardson."; c) handwritten det. "Asida / intricata / Ch."; d) "Sp. figured."; g) "B.C.ACol.IV.1. / Asida / intricata.". (BMNH).

**Redescription (see fig. 2.37).** Length: 17.7mm, width: 9.7mm. Integument ferruginous; elytra wider than pronotum and approximately 3.2X longer, width of pronotum at base less than width of elytral base. **Head:** Densely foveate with decumbent lanceolate scales emerging from fovea; frontoclypeal suture impressed, epistomal suture not indented at margin; medial depression on frons impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half

of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, scalene in female, unknown in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect dark brown acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex. **Prothorax:** Pronotum arctuate, widest near middle; marginal costa straight; anterior apicies produced and broadly rounded; posterior apicies acute, produced and projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, fringed with golden tomentose setae, medial tooth present. Pronotal disc nearly confluently foveate, each fovea with a pale ducumbent lanceolate scale; paramedial fossa absent; longitudinal medial ridge thin and raised. Prosternal process thickened and projecting behind procoxa, gradually deflexed. Prosternum moderately foveate with pale acuminate setae, anterior margins of some fovea raised and forming rounded tubercules. **Pterothorax:** Scutellum partially exposed, deep transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose; marginal costa not divided, nearly reaching cauda; elytral humera prominent and slightly reflexed; elytral disc with a dense confused network of low reticulated costae, crests glabrous; intercostal regions densely clothed in yellowish-white decumbent lanceolate scales, emerging from minute tubercles or not. **Legs:** Femora rugose; tibia tuberculate, stout spiniform setae emerging from tubercles; tarsi venter with stout spiniform setae on laterally margins, medially glabrous; apical protibial spine large acute and glabrous; combined protarsal segments subequal to length of protibia; anterior

protibial spur length shorter than basitarsi. **Abdomen:** Rugose, minutely punctate with inconspicuous acuminate setae.

**Diagnosis.** *P. intricatus* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum with a tomentose fringe and median tooth on posterior margin, medial ridge present on disc, posterior apicies acute, produced, projecting over elytral humera; elytral disc with a dense confused network of low reticulated costae, crests glabrous; intercostal regions densely clothed in yellowish-white decumbent lanceolate scales, emerging from minute tubercles or not; elytral base neither depressed nor tomentose.

**Distribution.** Only known from the type specimen, collected in the Mexican state of Jalisco.

**Biology.** Unknown.

### *Pelecyphorus* (*Plesiasida*) *laticollis* Champion

*Asida laticollis* Champion, 1884:58

*Parasida laticollis* (Champion). Casey, 1912:131

*Pelecyphorus* (*Plesiasida*) *laticollis* (Champion). Smith, 2010

=*Pelecyphorus* (*Plesiasida*) *planatulus* (Casey, 1912:129), **New Synonym**

**Type Material.** LECTOTYPE, designated here, (female) labeled: a) Orange bordered white circle reading "Type"; b) "Guanajuato / Mexico. / Salle Coll"; c) handwritten det. "Asida / laticollis, / Champ."; f) "Sp. figured."; g) "B.C.ACol.IV.1. / Asida / laticollis.".

(BMNH). PARALECTOTYPES, 3 specimens (BMNH) labeled: a) "MEX / ICO"; b) "F. Bates. / 81-19."; c) on yellow paper "PARATYPE / *Asida* / *laticollis* / Champion, 1884 / det. Aaron D. Smith"

**Additional Specimens Examined.** (43 specimens). MEXICO: Durango, Guanajuato.

**Redescription (see fig. 2.38).** Length: 15.1-18.4mm, width: 6.6-9.2mm (lectotype length: 18.3mm, width: 8.5mm). Integument black to ferruginous; elytra wider than pronotum and approximately 3X longer, width of pronotum at base subequal to width of elytral base. **Head:** Densely foveate with short white lanceolate scales emerging from fovea; frontoclypeal suture faintly impressed, epistomal suture indented at margin; medial depression on frons weakly impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, scalene in both sexes, distal angle more elongate in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect dark brown acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex or meeting on one side. **Prothorax:** Pronotum arctuate, narrowest at apex, widening to middle, nearly parallel sided to base; marginal costa straight; anterior apicies produced and broadly rounded; posterior apicies rounded, produced and projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, fringed with golden tomentose setae, medial tooth present. Pronotal disc nearly confluently foveate, each fovea with short pale squamate scale; paramedial fossae absent or faintly indicated; longitudinal medial ridge absent or thin and partially raised.

Prosternal process thickened and projecting behind procoxa, gradually deflexed. Prosternum lightly punctate with short pale acuminate setae, anterior margins of punctures not raised. **Pterothorax:** Deep transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum; scutellum mostly concealed, apparently carinate. Elytra elongate oval, widest behind middle, nearly planate; elytron base not depressed or tomentose. Costae thin and weakly raised, tubercles and scales covering sides and occasionally crests; marginal costa extending to cauda, meeting discal costa in apical fourth or not, divided in basal third, inner branch not connected to outer branch or discal costa; elytral humera prominent, straight or weakly reflexed; discal costa divided at base, reunited in apical third; sutural costa weakly raised throughout; transverse costae variably present or absent between marginal and discal branches. Intercostal spaces medially tuberculate, tubercles with semi-erect dark squamate scales, laterally with pale squamate scales not set on tubercles, overall producing a pattern of light and dark setal lines. **Legs:** Femora rugose punctate; tibia shallowly foveolate and tuberculate, with pale acuminate setae and stout spiniform setae emerging from tubercles; tarsi venter with stout spiniform setae on laterally margins, medially glabrous; apical protibial spine large acute and glabrous; combined protarsal segments approximately three-fourths length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Sparsely minutely punctate with inconspicuous acuminate setae.

**Diagnosis.** *P. laticollis* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum with a tomentose fringe and median tooth on posterior margin, medial ridge absent or incomplete on disc,

posterior apicies rounded, produced, projecting over elytral humera; elytral costa weakly raised, crest setose; transverse costae rarely present; intercostal regions with alternating rows of light and dark scales; elytral base neither depressed nor tomentose.

**Distribution.** MEXICO: Aquascalientes, Durango, Guanajuato.

**Biology.** Unknown.

### ***Pelecyphorus* (*Plesiasida*) *obliviosus* Wilke**

*Parasida obliviosa* Wilke, 1922:270

*Pelecyphorus* (*Plesiasida*) *obliviosus* (Wilke). Smith, 2010

**Type Material.** LECTOTYPE, designated here, (female) labeled: a) "Promontorio / Durango"; b) "obliviosa / det. S. Wilke"; c) "SYNTYPUS / Parasida / obliviosa Wilke, 1921 / labeled by MNHUB 2008"; d) "Museum für Naturkunde / Humboldt-Univ. Berlin / (MNHUB)"; e) "LECTOTYPE / Parasida obliviosa / Wilke, 1921 / ADSmith 2009". (ZMHB).

**Additional Specimens Examined.** (31 specimens). MEXICO: Durango.

**Redescription (see fig. 2.39).** Length: 18.0-20.3mm, width: 8.0-10.7mm (lectotype length: 18.0mm, width: 8.0mm). Integument black to ferruginous; elytra wider than pronotum and approximately 3X longer, width of pronotum at base subequal to width of elytral base. **Head:** Densely foveate with short white lanceolate scales emerging from fovea; frontoclypeal suture faintly impressed, epistomal suture not indented at margin;

medial depression on frons weakly impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, scalene in both sexes, distal angle more elongate in male. Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect dark brown acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex or meeting on one side. **Prothorax:** Pronotum arctuate, narrowest at apex, widening to middle, nearly parallel sided to base; marginal costa straight; anterior apicies produced and broadly rounded; posterior apicies rounded, produced and projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, fringed with golden tomentose setae, medial tooth present. Pronotal disc nearly confluently foveate, each fovea with short pale lanceolate scale; paramedial fossae absent or faintly indicated; longitudinal medial ridge absent or faintly indicated but not raised. Prosternal process thickened and projecting behind procoxa, gradually deflexed. Prosternum minutely punctate with short pale acuminate setae, anterior margins of punctures not raised. **Pterothorax:** Deep transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum; scutellum mostly concealed, apparently carinate. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose. Costae thick and strongly rounded crests impunctate and glabrous; marginal costa extending down cauda, meeting discal costa at apex, bifurcate in basal third, inner branch not connected to outer branch or discal costa at apex; elytral humera prominent, straight or weakly reflexed; discal costa divided at base, reunited in apical third; sutural costa raised throughout; transverse costae

rarely present and only between branches of marginal costa. Intercostal spaces medially tuberculate, tubercles with semi-erect yellowish-white squamate scales, laterally with white squamate scales not set on tubercles, overall producing a faint pattern of lighter and darker setal lines. **Legs:** Femora rugose punctate; tibia shallowly foveolate and tuberculate, with pale acuminate setae and stout spiniform setae emerging from tubercles; tarsi venter with stout spiniform setae on laterally margins, medially glabrous; apical protibial spine large acute and glabrous; combined protarsal segments approximately three-fourths length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Nearly impunctate, sparse minute punctures with inconspicuous paleacuminate setae.

**Diagnosis.** *P. obliviosus* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum with a tomentose fringe and median tooth on posterior margin, medial ridge absent or faintly indicated on disc, posterior apicies rounded, produced, projecting over elytral humera; elytral costa raised, broadly rounded, crests impunctate and glaberous; transverse costae rarely present; intercostal regions with faint alternating rows of lighter and darker scales; elytral base neither depressed nor tomentose; prosternum minutely punctate.

**Distribution.** MEXICO: Chihuahua, Durango.

**Biology.** Unknown.

### *Pelecyphorus* (*Plesiasida*) *scutellaris* (Champion)

*Asida scutellaris* Champion, 1884:57

*Parasida scutellaris* (Champion). Casey, 1912:131

*Pelecyphorus* (*Plesiasida*) *scutellaris* (Champion). Smith, 2010

=*Pelecyphorus* (*Plesiasida*) *tolucanus* Casey, 1912:130), **New Synonym**

**Type Material.** LECTOTYPE, designated here, (sex undetermined) labeled: a) Orange bordered white circle reading "Type"; b) "Jalapa / Mexico. / Hoge."; c) handwritten det. "Asida / scutellaris, / Champ."; d) "Sp. figured."; g) "B.C.ACol.IV.1. / Asida / scutellaris.". (BMNH).

**Additional Specimens Examined.** (99 specimens). MEXICO: Durango, Guanajuato, Hidalgo, Mexico, Mexico D. F., Puebla, Oaxaca, Veracruz.

**Redescription (see fig. 2.40).** Length: 12.8-18.0mm, width: 5.7-9.4mm (lectotype length: 15.2mm, width: 7.3mm). Integument black to ferruginous; elytra wider than pronotum and approximately 3X longer, width of pronotum at base subequal to width of elytral base. **Head:** Densely foveate with decumbent acuminate brown setae emerging from fovea; frontoclypeal suture faintly impressed, epistomal suture not indented at margin; medial depression on frons weakly impressed; labral margin emarginate; clypeal membrane concealed. Mentum anterior margin straight, medially emarginate; basal half of mentum with two faint paramedial longitudinal impressions. Apical segment of maxillary palps expanded, scalene in both sexes, distal angle more elongate in male.

Postgenal processes slightly swollen, acute, and extending to middle of mentum. Antenna densely clothed in erect dark brown acuminate setae; antennal segment 10 subquadrate, tomentose sensilla separated and curved around apex or meeting on one side. **Prothorax:** Pronotum weakly sinuate, widest near middle; marginal costa straight; anterior apicies produced and broadly rounded; posterior apicies rounded, produced and projecting over elytral humera; posterior margin nearly straight, emarginate before apicies, fringed with golden tomentose setae, medial tooth present. Pronotal disc nearly confluently foveate, each fovea with short pale squamate scale; paramedial fossae absent or faintly indicated; longitudinal medial ridge absent or faintly indicated but not raised. Prosternal process thickened and projecting behind procoxa, gradually deflexed. Prosternum densely foveate with short brown acuminate setae, anterior margins of punctures not raised. **Pterothorax:** Deep transverse tomentose depressions present on mesonotum, separated by a smooth narrow ridge between scutum and scutellum; scutellum mostly concealed, apparently carinate. Elytra elongate oval, widest behind middle; elytron base not depressed or tomentose. Costae thick and strongly rounded crests impunctate and glabrous; marginal costa extending down cauda, meeting discal costa at apex, bifurcate in basal third, inner branch not connected to outer branch or discal costa at apex; elytral humera prominent, straight or weakly reflexed; discal costa divided at base, reunited in apical third; sutural costa raised throughout; transverse costae rarely present and only between branches of elytral costa. Intercostal spaces medially sparsely and weakly tuberculate, tubercles with semi-erect light brown squamate scales, laterally with yellowish-white squamate scales not set on tubercles, overall producing a faint pattern of lighter and darker longitudinal setal lines between costa. **Legs:** Femora rugose punctate; tibia shallowly foveolate and

tuberculate, with brown acuminate setae and stout black spiniform setae emerging from tubercles; tarsi venter with stout black spiniform setae on laterally margins, medially glabrous; apical protibial spine large acute and glabrous; combined protarsal segments approximately three-fourths length of protibia; anterior protibial spur length shorter than basitarsi. **Abdomen:** Moderately foveate with short dark acuminate setae.

**Diagnosis.** *P. scutellaris* can be separated from the other members of the *Plesiasida* subgenus based on the following character combination: pronotum with a tomentose fringe and median tooth on posterior margin, medial ridge absent or faintly indicated on disc, posterior apicies rounded, produced, projecting over elytral humera; elytral costa raised, broadly rounded, crests impunctate and glaberous; transverse costae rarely present; intercostal regions with faint alternating rows of lighter and darker scales; elytral base neither depressed nor tomentose; prosternum densely foveate.

**Distribution.** MEXICO: Durango, Guanajuato, Hidalgo, Mexico, Mexico D. F., Puebla, Oaxaca, Veracruz.

**Biology.** Unknown.

## ***Pelecyphorus* Species Checklist**

**subgenus *Astrotus* LeConte**

***Pelecyphorus* (*Astrotus*) *alveolatus*** (Casey 1912:83)

***Pelecyphorus* (*Astrotus*) *contortus*** (LeConte, 1853:446)

***Pelecyphorus* (*Astrotus*) *regularis*** (Horn, 1870:290)

***Pelecyphorus* (*Astrotus*) *hebes*** (Champion, 1892:506)

***Pelecyphorus* (*Astrotus*) *crypticus* Smith, new species**

**subgenus *Stenosides* Solier**

***Pelecyphorus* (*Stenosides*) *anastomosis* (Say, 1824:256)**

=*P.* (*Stenosides*) *breviuscula* (Casey, 1912:87), **new synonym**

=*P.* (*Stenosides*) *exoleta* (Casey, 1912:87), **new synonym**

=*P.* (*Stenosides*) *luteotecta* (Casey, 1912:88), **new synonym**

=*P.* (*Stenosides*) *monticola* (Casey, 1912:88), **new synonym**

=*P.* (*Stenosides*) *obtecta* (Casey, 1912:89), **new synonym**

=*P.* (*Stenosides*) *sigillata* (Casey, 1912:89), **new synonym**

***Pelecyphorus* (*Stenosides*) *graciliformis* (Solier, 1836:486)**

=*P.* (*Stenosides*) *canus* (Champion, 1884:68), **new synonym**

=*P.* (*Stenosides*) *sinuaticollis* (Champion, 1884:69), **new synonym**

***Pelecyphorus* (*Stenosides*) *limosus*** (Champion, 1884:66)

***Pelecyphorus* (*Stenosides*) *cavatus* Smith, new species**

***Pelecyphorus* (*Stenosides*) *deaztlani* Smith, new species**

***Pelecyphorus* (*Stenosides*) *triplehorni* Smith, new species**

***Pelecyphorus* (*Stenosides*) *texanus*** (Wickham, 1903:72)

**subgenus *Sicharbas* Champion**

***Pelecyphorus* (*Sicharbas*) *lobatus*** (Champion, 1884:67)

***Pelecyphorus* (*Sicharbas*) *debilis*** (Champion 1884:66)

***Pelecyphorus* (*Sicharbas*) *erosus*** (Champion 1892:504)

=*Pelecyphorus* (*Astrotus*) *nosodermoides* (Champion, 1892:505), **new synonym**

***Pelecyphorus* (*Sicharbas*) *seticornis*** (Champion, 1884:67)

***Pelecyphorus* (*Sicharbas*) *oaxacensis* Smith, n. sp.**

***Pelecyphorus* (*Sicharbas*) *undatus*** (Champion, 1892:504)

**subgenus *Pelecyphorus* Solier**

***Pelecyphorus* (*Pelecyphorus*) *mexicanus*** Solier, 1836:469

**subgenus *Ucalegon* Champion**

***Pelecyphorus* (*Ucalegon*) *pulchellus*** (Champion, 1884:65)

**subgenus *Zaleucus* Champion**

***Pelecyphorus* (*Zaleucus*) *dilatatus*** (Champion, 1884:70)

***Pelecyphorus* (*Zaleucus*) *platesthoides*** (Champion, 1884:71)

***Pelecyphorus* (*Zaleucus*) *foveolatus*** Solier, 1836:472

***Pelecyphorus* (*Zaleucus*) *doyeni* Smith, n. sp.**

**subgenus *Variodorsus* Smith, new subgenus**

***Pelecyphorus* (*Variodorsus*) *fasciculatus*** (Champion, 1892:495)

***Pelecyphorus* (*Variodorsus*) *guanajuatensis*** (Champion, 1884:56)

*Stenomorpha* (*Bothrasida*) *mucorea* (Wilke 1922:270), **new synonym**

**subgenus *Plesiasida* Smith, replacement name (=*Parasida* Casey)**

***Pelecyphorus* (*Plesiasida*) *bibasalis*** (Casey, 1912:128)

***Pelecyphorus* (*Plesiasida*) *dispar*** (Champion, 1892:496)

=*Pelecyphorus* (*Plesiasida*) *dissimilis* (Champion, 1884:59), junior homynym

=*P.* (*Stenosides*) *bisinuatus* (Pallister, 1954:13), **new synonym**

=*P.* (*Stenosides*) *kulzeri* (Pallister, 1954:12), **new synonym**

=*P.* (*Plesiasida*) *trisinuatus* (Pallister, 1954:22), **new synonym**

***Pelecyphorus* (*Plesiasida*) *liratus*** (LeConte, 1854:223)

=*Pelecyphorus* (*Plesiasida*) *laciniatus* (Casey, 1912:128), **new synonym**

=*Pelecyphorus* (*Plesiasida*) *cristatus* (Pallister 1954:24), **new synonym**

***Pelecyphorus* (*Plesiasida*) *asidoides*** Solier, 1836:471

=*P.* (*Plesiasida*) *zacualpanicolus* (Wilke, 1922:272), **new synonym**

***Pelecyphorus* (*Plesiasida*) *fallax*** (Champion, 1884:57)

=*Pelecyphorus* (*Plesiasida*) *favosus* (Champion, 1884:58), **new synonym**

=*Pelecyphorus* (*Plesiasida*) *similatus* (Champion, 1884:58), **new synonym**

***Pelecyphorus* (*Plesiasida*) *intricatus*** (Champion, 1892:493), **new combination**

*Notiasida intricata* (Champion) 1892:493

***Pelecyphorus* (*Plesiasida*) *laticollis*** (Champion, 1884:58)

=*Pelecyphorus* (*Plesiasida*) *planatulus* (Casey, 1912:129), **new synonym**

***Pelecyphorus* (*Plesiasida*) *obliviosus*** (Wilke, 1922:270)

***Pelecyphorus* (*Plesiasida*) *scutellaris*** (Champion, 1884:57)

=*Pelecyphorus* (*Plesiasida*) *tolucanus* Casey, 1912:130), **new synonym**

***Pelecyphorus* (*Plesiasida*) *longipennis*** (Champion, 1884:56)

=*P.* (*Plesiasida*) *mixtecae* (Wilke, 1922:271), **new synonym**

=*P.* (*Plesiasida*) *esperanzae* (Wilke, 1922:271), **new synonym**

***Pelecyphorus* (*Plesiasida*) *tristis*** (Champion, 1884:55)

=*Pelecyphorus* (*Plesiasida*) *purpusi* (Wilke, 1922:271), **new synonym**

***Pelecyphorus* (*Plesiasida*) *indutus*** (Champion, 1884:56)

=*P.* (*Stenosides*) *bicarinatus* (Champion, 1884:69), **new synonym**

***Pelecyphorus* (*Plesiasida*) *sexcostatus*** LeConte, 1861:337

***Pelecyphorus* (*Plesiasida*) *cifuentesi* Smith, n. sp.**

**Figure 2.1:** Dorsal habitus of *Pelecyphorus* (*Astrotus*) *alveolatus* (Casey), holotype, ♂ (L=11.5mm)

**Figure 2.2:** Dorsal habitus of *Pelecyphorus* (*Astrotus*) *contortus* (LeConte), ♂ (L=11.3mm)

**Figure 2.3:** Dorsal habitus of *Pelecyphorus* (*Astrotus*) *regularis* (Horn), ♀ (L=12.2mm)

**Figure 2.4:** Dorsal habitus of *Pelecyphorus* (*Astrotus*) *hebes* (Champion), ♂ (L=18.3mm)

**Figure 2.5:** Dorsal habitus of *Pelecyphorus* (*Astrotus*) *crypticus* Smith, **n. sp.**, ♂ (L=9.5mm)

**Figure 2.6:** Dorsal habitus of *Pelecyphorus* (*Stenosides*) *anastomosis* (**Say**), ♀ (L=11.9mm)

**Figure 2.7:** Dorsal habitus of *Pelecyphorus* (*Stenosides*) *cavatus* Smith, **n. sp.**, (L=12.5mm)

**Figure 2.8:** Dorsal habitus of *Pelecyphorus* (*Stenosides*) *deaztlani* Smith, **n.sp.,** ♀ (L=10.5mm)

**Figure 2.9:** Dorsal habitus of *Pelecyphorus* (*Stenosides*) *triplehorni* Smith, **n. sp.**, ♂ (L=10.8mm)

**Figure 2.10:** Dorsal habitus of *Pelecyphorus* (*Stenosides*) *limosus* (Champion), holotype (L=7.8mm)

**Figure 2.11:** Dorsal habitus of *Pelecyphorus* (*Stenosides*) ***graciliformis*** (Solier), (L=9.7mm)

**Figure 2.12:** Dorsal habitus of *Pelecyphorus* (*Stenosides*) *texanus* (Wickham), (L=7.7mm)

**Figure 2.13:** Dorsal habitus of *Pelecyphorus* (*Sicharbas*) *lobatus* (Champion), holotype ♂ (L=10.6mm)

**Figure 2.14:** Dorsal habitus of *Pelecyphorus* (*Sicharbas*) *oaxacensis* Smith, **n. sp.,** holotype ♂ (L=11.3mm)

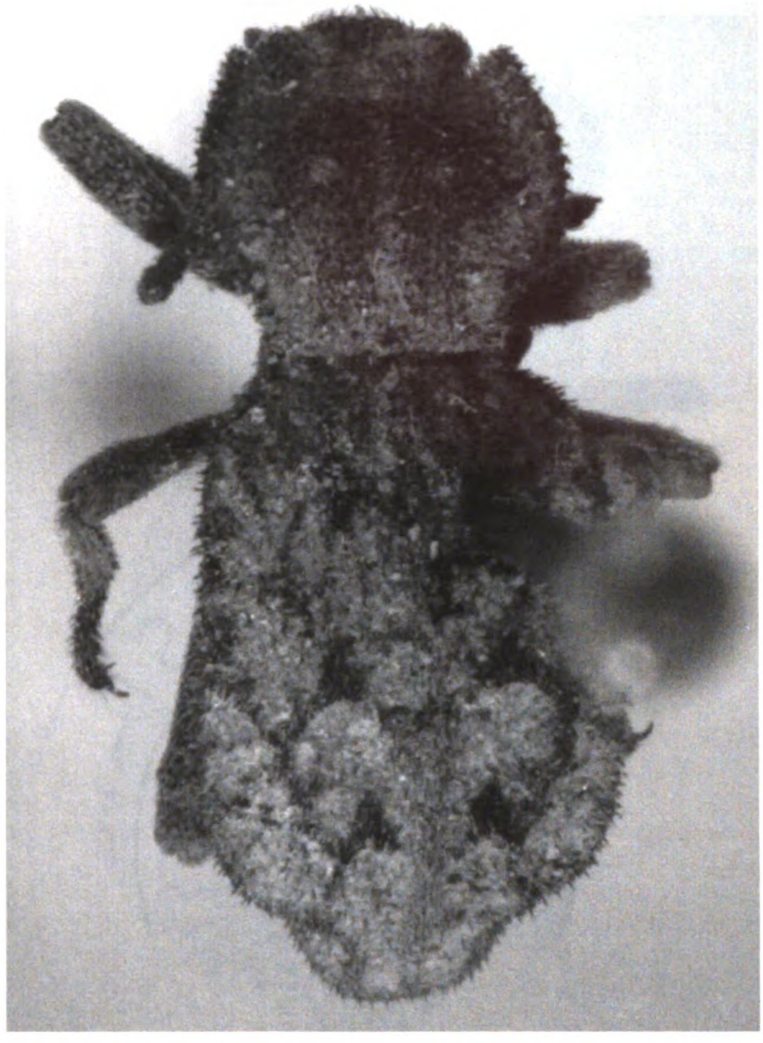

**Figure 2.15:** Dorsal habitus of *Pelecyphorus* (*Sicharbas*) *debilis* (Champion), ♂ (L=7.4mm)

**Figure 2.16:** Dorsal habitus of *Pelecyphorus* (*Sicharbas*) *seticornis* (Champion), ♂ (L=6.6mm)

**Figure 2.17:** Dorsal habitus of *Pelecyphorus* (*Sicharbas*) *erosus* (Champion), holotype ♀ (L=9.6mm)

**Figure 2.18:** Dorsal habitus of *Pelecyphorus* (*Sicharbas*) *undatus* (Champion), lectotype ♀ (L=11.6mm)

**Figure 2.19:** Dorsal habitus of *Pelecyphorus* (*Pelecyphorus*) *mexicanus* Solier, ♀ (L=13.9mm)

**Figure 2.20:** Dorsal habitus of *Pelecyphorus* (*Ucalegon*) *pulchellus* (Champion), ♀ (L=13.8mm)

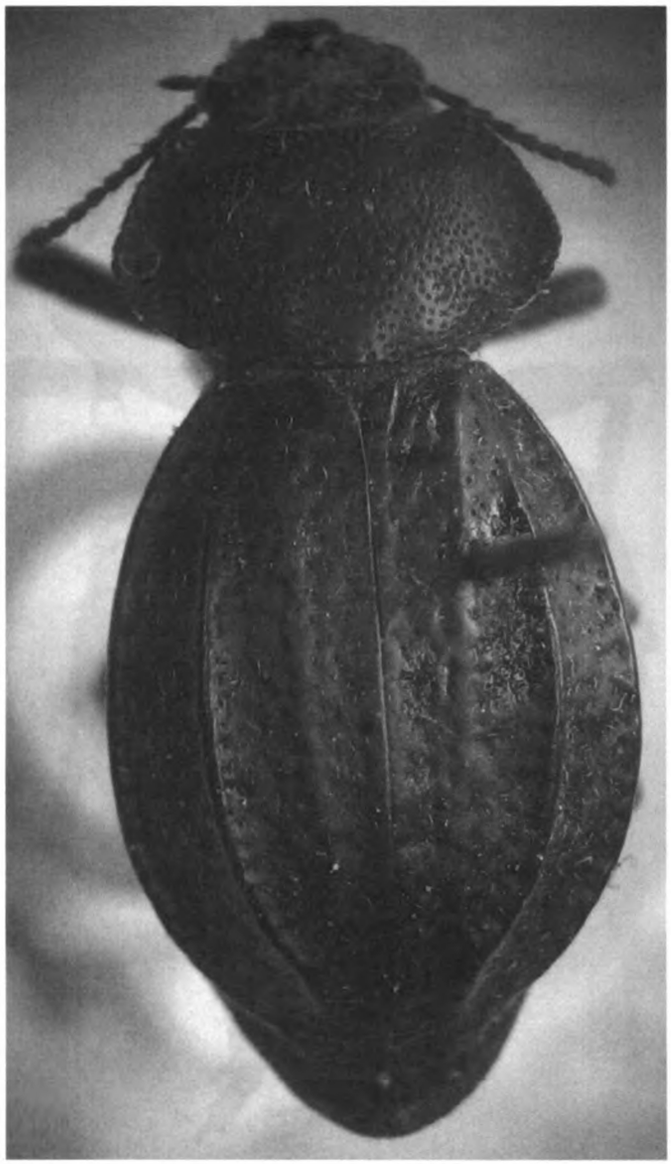

**Figure 2.21:** Dorsal habitus of *Pelecyphorus* (*Zaleucus*) *dilatatus* (Champion), lectotype ♀ (L=15.8mm)

**Figure 2.22:** Dorsal habitus of *Pelecyphorus* (*Zaleucus*) *platesthoides* (Champion), lectotype (L=14.3mm)

**Figure 2.23:** Dorsal habitus of *Pelecyphorus* (*Zaleucus*) *foveolatus* Solier, ♂ (L=13.5mm)

**Figure 2.24:** Dorsal habitus of *Pelecyphorus* (*Zaleucus*) *doyeni* Smith, **n. sp.**, ♂ (L=13.1mm)

**Figure 2.25:** Dorsal habitus of *Pelecyphorus* (*Variodorsus*) ***guanajuatensis*** (Champion), ♂ (L=11.3mm)

**Figure 2.26:** Dorsal habitus of *Pelecyphorus* (*Variodorsus*) *fasciculatus* (Champion), ♂ (L=11.7mm)

**Figure 2.27:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *liratus* (LeConte), ♂ (L=12.8mm)

**Figure 2.28:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *dispar* (Champion), ♂ (L=11.5mm)

**Figure 2.29:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *bibasalis* (Casey), (L=17.5mm)

**Figure 2.30:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *sexcostatus* LeConte, ♂ (L=11.2mm)

**Figure 2.31:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *cifuentesi* Smith, **n. sp.,** ♂ (L=11.1mm)

**Figure 2.32:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *longipennis* (Champion), ♂ (L=10.5mm)

**Figure 2.33:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *indutus* (Champion), holotype ♂ (L=12.0mm)

**Figure 2.34:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *tristis* (Champion), lectotype ♂ (L=12.1mm)

**Figure 2.35:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *asidoides* Solier, ♀ (L=13.3mm)

**Figure 2.36:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *fallax* (Champion) (L=15.0mm)

**Figure 2.37:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *intricatus* (Champion), **holotype** ♀ (L=17.7mm)

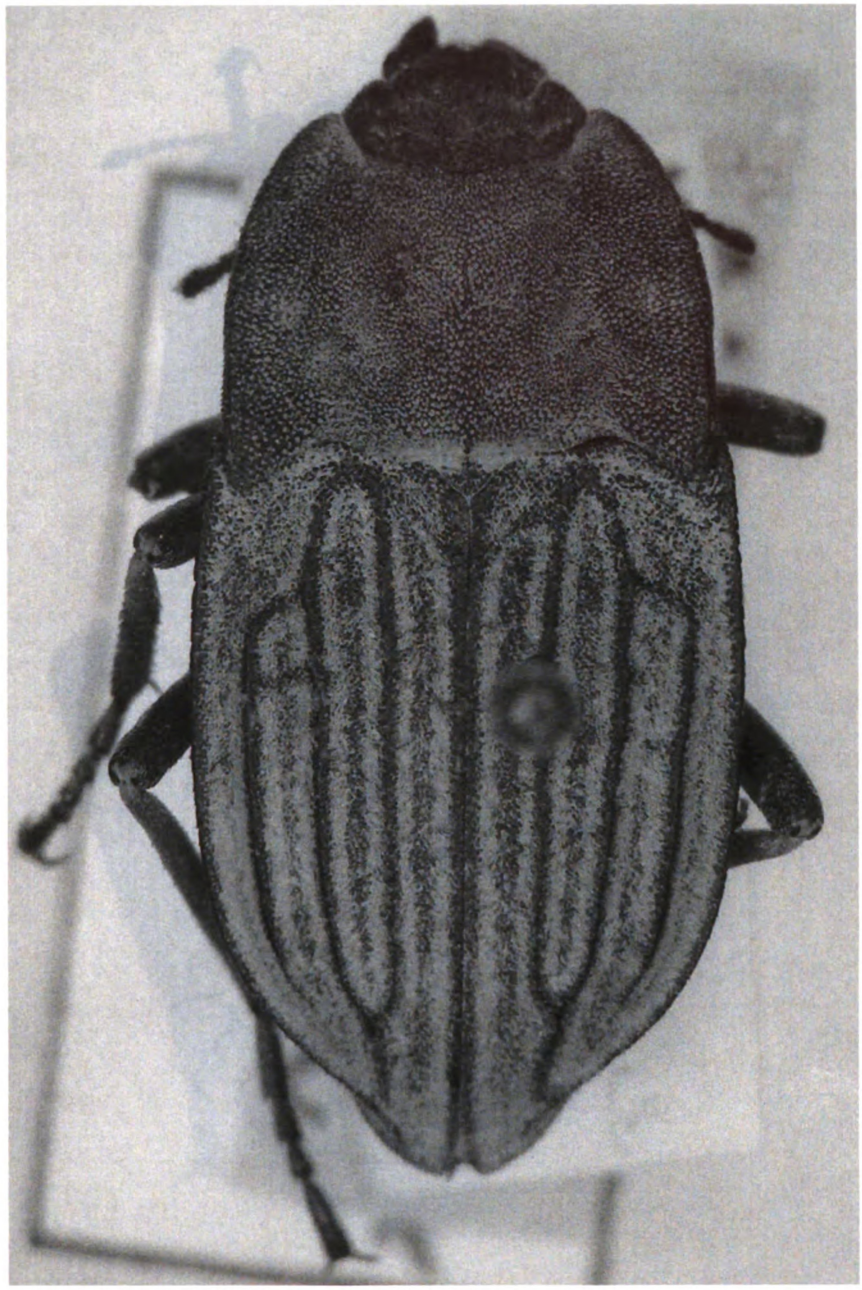

**Figure 2.38:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *laticollis* (Champion) (L=17.4mm)

**Figure 2.39:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *obliviosus* (Wilke), ♀ (L=20.3mm)

**Figure 2.40:** Dorsal habitus of *Pelecyphorus* (*Plesisida*) *scutellaris* (Champion) (L=15.2mm)

## CHAPTER THREE

The evolution of contrasting defensive strategies within the North American Asidini (Coleoptera: Tenebrionidae)

## ABSTRACT

The asidine darkling beetles (Coleoptera: Tenebrionidae: Asidini) are a morphologically diverse tribe of flightless tenebrionids found in many arid and sub-arid habitats around the world. The nearly 300 currently described North American species are contained in ten genera, all of which are restricted to the western half of the continent. The Asidini, like all members of the subfamily Pimeliinae, lack defensive glands. Instead, several morphological and behavioral traits are found within the tribe that may help limit predation. These include the contrasting defensive strategies of crypsis, either through background matching or pattern disruption, and Batesian mimicry of the chemically defended tenebrionid genus *Eleodes*. A phylogenetic analysis of the North American asidines is presented based on data from two genes, mitochondrial cytochrome c oxidase I (COI) and nuclear ribosomal 28S, and adult morphology; this tree supports multiple origins for Batesian mimicry within the tribe.

## INTRODUCTION

Many animals use multiple defensive mechanisms and strategies in order to avoid predation, and such is the case for the asidine darkling beetles (Coleoptera: Tenebrionidae: Asidini), a large tribe of flightless tenebrionids found in many arid and semi-arid regions around the world. Unlike most tenebrionids, the Asidini lack defensive glands. Instead, several traits occur within the tribe that presumably help to limit predation. These include subterranean larvae and, in adults, cryptic or mimetic morphologies and behaviors. The majority of asidine species are somewhat cryptic in coloration and sculpturing, but two distinct adaptive strategies have evolved within the North American Asidini that are so far unique or nearly unique within the tribe. One is a precise form of background matching, including the production of adhesive chemicals to coat themselves with soil or debris. The second is Batesian mimicry of other tenebrionids that do have defensive glands, specifically the widespread genus *Eleodes* (Brown 1971a).

The term crypsis covers a broad range of primary defensive mechanisms, *i.e.* traits that are used to avoid detection by predators when they are encountered (Edmunds 1974). These can include colorations or patterning that blend with the surrounding environment (background matching) and markings that obscure or distort the true outline or borders of the organism (pattern disruption). Cryptic coloration or morphology is also often associated with a behavioral trait known as thanatosis, or "playing dead", as many visually oriented predators track movement.

Crypsis appears to be widespread in many animal groups and has been widely cited in the literature; however reports on crypsis in insects is limited to a relatively small number of publications. Crypsis has been examined in several groups, including the

Hemiptera (Patra et al. 2008) and Plecoptera (Feltmate and Williams 1989), but the majority of crypsis studies involving insects have focused on the Lepidoptera (Poulton 1892, Endler 1988, Moss *et al.* 2006, Canfield *et al.* 2009), including the intensely studied case of industrial melanism (Kettlewell 1955) in the peppered moth, *Biston betularia*, which has recently been the subject of some debate (see Ruxton *et al.* 2004 for a review). Much research remains to quantify the effectiveness of crypsis versus its potential costs.

Most asidine species avoid predation as adults through some variation of cryptic coloration and sculpturing. The most widespread method is background matching based on the dry sandy substrates where they generally occur; hence many species are brown with light colored setae and are often dusted to some extend with sand or debris. A number of species in the genera *Craniotus, Heterasida*, *Pelecyphorus*, and *Stenomorpha* exhibit this general phenotype. All species in the *Pelecyphorus* subgenus *Astrotus* also display background matching; however they accomplish it by producing an adhesive compound upon emergence and coating themselves with a thick layer of soil (Fig 3.2). This allows for a precise color match to the regional substrate. In all of the *Astrotus* specimens reared thus far the adhesive has been produced as long thin filaments that become entangled in raised stellate setae (Fig. 3.3) that cover the integument, before hardening within approximately twenty-four hours (Smith, unpublished). Crypsis within both the subgenera *Astrotus* and *Sicharbas* is further enhanced by pronotal and elytral flanges and tubercles, which break up the overall outline of the body. A different camouflage strategy, disruptive coloration or pattern disruption, is exhibited within the subgenus *Plesiasida* (Fig. 2.39). Many *Plesiasida* species have three raised costae on

each elytron with dense longitudinal rows of white and brown squamose setae filling the space between them, making it difficult to discern their body shape by creating false edges and boundaries on the dorsal surface.

In addition to morphological crypsis, species in the subgenera *Astrotus*, *Stenosides*, and *Zaleucus* also play dead (thanatosize) when threatened. *Astrotus* species position their legs and antennae flush with the body and will hold them in this position for over thirty minutes under observation. *Stenosides* and *Zaleucus* bend their legs underneath the body and cross them in a scissor-like pose. The reason behind this posture is unclear, but it may either help them appear more like debris or inhibit swallowing by predators.

In contrast to inversigating crypsis, many studies have been devoted to examining secondary defensive mechanisms (reviewed in Edmunds 1974; Ruxton *et al.* 2004). The category of secondary defenses covers a wide range of traits and behaviors that deter predation after the prey species has been detected. These include physiological characters such as the production of toxins, mechanical defenses such as spines or armor, and behavioral defenses such as rapid escape and retaliation. Secondary defenses also generally involve signals from the prey species, which advertise their unprofitability to the predator, such as aposomatic colorations or warning displays.

One interesting variety of secondary defense is Batesian mimicry, which is when a palatable species mimics the warning signals of a less palatable, often chemically defended, model species and thereby gains some measure of protection from predation without incurring the energetic costs associated with producing defensive compounds. For example, Hetz and Slobodchikoff (1990) calculated that the energy required for an

*Eleodes obscurus* (Say) female to produce defensive secretions over the course of a year is approximately equal to 18% of the energy expended on egg production, so a co-occurring mimetic female could potentially receive the same protection from predation while also devoting more energy to reproduction.

The concept of Batesian mimicry dates back to Bate's (1862) seminal paper documenting mimicry between Amazonian butterfly species. Several components are generally thought to be necessary for Batesian mimicry to be an effective defensive strategy (Ruxton *et al.* 2004). 1) The model species is unpalatable and displays aposomatic signals that predators learn to avoid. 2) The mimic species exhibits signals similar enough to the model that predators avoid it. 3) The model co-occurs across the mimic's range. It is also expected that the model will occur in greater relative population densities and that individuals of the mimetic species will emerge at the same time or shortly after the peak emergence period of the model. Both hypothetically increase the chance of a naïve predator attacking a model specimen and learning to associate its aposomatic signals with unpalatability.

It follows that the more accurate the mimic's ability to imitate the defensive signals of the model the greater the protection it will receive. However many mimetic species have been shown to be inaccurate. Several theories have been put forth to account for imperfect signaling by mimics, including an evolutionary arms race between mimics and models (Ruxton *el al.* 2004), insufficient time for the mimic to converge on the model (Gilbert 2005), or that a signal which may appear imperfect is in fact accurate in relation to the cognitive abilities of target predators (Cuthill & Bennet 1993, Dittrich *et al.* 1993, Chittka & Osorio 2007). However, it is still generally assumed that even poor

mimics will gain a selective advantage when the model is very common (Ruxton *el al.* 2004, Harper & Pfennig 2007). Another possibility is that in areas where multiple similar models co-occur the optimal phenotype for a mimetic species may be intermediate between those of the available models (Edmunds 2000, Sherratt 2002).

Darkling beetles are well known for their production of distasteful defensive compounds, mostly a variety of quinones (Tschinkel 1975a), which are used to ward off predators. Defensive glands appear to have independently evolved four times within the family (Tschinkel & Doyen 1980). However, nearly half of all known tenebrionids, including those in the tribe Asidini, belong to the chemically undefended subfamily Pimeliinae. Doyen (1993) dissected specimens from all of the pimeliine tribes and confirmed the absence of defensive glands throughout the subfamily.

The endemic North American genus *Eleodes*, in the subfamily Tenebrioninae, is a remarkably successful genus of tenebrionids in terms of individual and species numbers. With approximately 235 species (Triplehorn *et al.* 2010), *Eleodes* have diversified throughout western North America and are a prominent portion of the desert insect fauna from southern Mexico to southern Canada. All *Eleodes* are flightless detritivores and secrete noxious defensive compounds. Nearly all *Eleodes* species are glabrous and black, with long hind legs. Doyen & Somerby (1974) argue that, in the case of darkling beetles, black is an aposomatic color as it makes them easily visible by increasing the contrast between the beetles and their substrate under low lighting conditions. The majority of *Eleodes* species are crepuscular, and individuals are often found on light colored sandy soils (Slobodchikoff 1978a, Thomas 1979, pers. obser.). Many *Eleodes*, including some of the most common species, also exhibit a behavior known as headstanding, which

involves lowering the beetle's head and raising the tip of the abdomen by 30-90 degrees from horizontal. This behavior is considered to be aposomatic and is often associated with the ability to forcefully eject defensive secretions as a spray (Tschinkel 1975b).

Evidence of mimetic relationships between members of two asidine genera and co-occurring species in the genus *Eleodes* have been documented in the literature. Brown (1971a) indicates that *Philolithus* (*Gonasida*) *elata* (LeConte) is likely to be an accurate mimic of *Eleodes obscurus* (Say) based on their overall phenetic similarity (Fig 3.4), the observation of headstanding behavior in all *P. elata* individuals studied, and changes in the dorsal patterning of the four *P. elata* subspecies, which match the dorsal variations seen in the three subspecies of *E. obscurus* with which they occur in different parts of both species' ranges.

A series of papers (Slobodchikoff *et al.* 1987, Hetz & Slobodchikoff 1988, 1990) examined the relationship between *Stenomorpha marginata* (LeConte), a large asidine species that superficially looks like an *Eleodes* and that headstands when threatened, and *E. obscurus*. They considered *S. marginata* to be an inaccurate mimic of *E. obscurus*, presumably based on their differing morphologies, but found that *S. marginata* gained some selective advantage from predation by mammalian predators in field studies, especially when alternative prey were available. An inaccurate mimetic relationship was also assumed to occur between *Stenomorpha* (*Megasida*) *obliterata* (Champion) and *Eleodes longicollis* (LeConte) due to their overlapping ranges and activity periods, somewhat similar phenotypes, and the presence of headstanding behavior within both species (Eisner 1966, Eisner & Meinwald 1966).

In this study I examine the evolution of both mimetic and cryptic traits within the North American asidines using a phylogeny based on data from two genes, mitochondrial cytochrome c oxidase I (COI) and nuclear ribosomal 28S, and adult morphology.

## MATERIALS AND METHODS

### *Taxon Sampling*

Most asidine species are rarely encountered and many species are known from only one or a handful of collecting events. Specimens sequenced for this study were either collected by the authors directly into 95% ethanol or donated by colleagues. Additional specimens of each species were also scored for morphology and used to examine potential intraspecific variability. Fifty North American asidine species were included in the analysis (Table 1.1) representing seven of the ten current genera. Outgroup taxa were selected from the South American Asidini (*Cardigenius laticollis* Solier) and the closely related tribes Coniontini (*Eusattus reticulatus* (Say)) and Branchini (*Branchus* n. sp.).

### *DNA Sequencing and Alignment*

Tissue was removed from either the head or a leg of each specimen and the DNA was extracted using DNeasy™ Tissue Kits (Qiagen). After extraction, DNA samples were stored a -20°C and specimens were either pinned or left in 95% ethanol at -80°C. All specimens were vouchered in the A.J. Cook Arthropod Research Collection at Michigan State University.

The purified DNA was used to amplify portions of the mitochondrial cytochrome c oxidase I (COI) and nuclear ribosomal 28S (D2 region) genes. PCR reactions for COI used the published primers (Herbert *et al.* 2003) LCO1490 (5'GGTCAACAA ATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCA AAAAATCA-3') and contained 15.75µl dd$H_2O$, 2.5 µl 5X *Taq*DNA polymerase buffer (Promega, Madison, WI), 2.0 µl 25 mM Promega $MgCl_2$, 0.5 µl 40 mM dNTPs (deoxynucleotide triphosphates), 0.25 µl Promega *Taq* DNA polymerase, 1 µl of 10 ρM/µl LCO1490 primer, 1 µl of 10 ρM/µl HCO2198 primer, and 2 µl of DNA template. PCR reactions for 28S used the primers 3665 (5'AGAGAGAGTTCAAGAGTACG TG-3') and 4068 (5'-TTGGTCCGTGTTTCAAGACGGG -3'). PCR reactions contained 15.75µl dd$H_2O$, 2.5 µl 10X *Taq*DNA polymerase buffer (Qiagen Inc., Santa Clara, CA), 2.0 µl 25 mM $MgCl_2$, 0.5 µl 40 mM dNTPs (deoxynucleotide triphosphates), 0.25 µl Qiagen Hotstar *Taq* DNA polymerase, 1 µl of 10 ρM/µl 3665 primer, 1 µl of 10 ρM/µl 4068 primer, and 2 µl of DNA template.

PCR amplifications for both genes were performed using a MJ thermal cycler (MJ Research, Waltham, MA) under the following conditions: activation (95°C, 5min.) for 1 cycle; denaturation (94°C, 30s), annealing (45-55°C, 45s), extension (72°C, 60s) for 35-40 cycles; final extension (72°C, 5min.). Negative controls were used to monitor for potential contamination and PCR products were examined using gel electrophoresis. PCR products were cleaned using ExoSAP-IT and the manufacturer's protocols (USB Corp., Cleveland, OH). The cleaned PCR products were sequenced in both directions, using the same primers as were used in amplification, with a BigDye® Terminator v1.1 cycle sequencing kit (Applied Biosystems, Foster City, CA) at the Research Support Facility at

Michigan State University. The resulting DNA sequences were examined and edited using Sequencer 4.5 (Genecodes, Ann Arbor, MI) and consensus sequences were created from the sense and antisense sequences.

The COI sequences showed no length variability and were aligned manually in Mega 4 (Tamura *et al.* 2007) since the alignments were unambiguous. 28S sequences were initially aligned using Clustal W (Thompson & Higgins 1994) in Mega 4 then manually adjusted in reference to a model of beetle 28S secondary structure (Gillespie *et al.* 2004) to correct misaligned conserved regions and to remove unalignable regions in the 28S dataset

### *Morphological Characters*

A total of 100 morphological characters (42 binary, 58 multistate) were included in the analyses. Characters include those previously used in asidine species and generic descriptions (Solier 1836; LeConte, 1853, 1858; Champion 1884, 1892; Casey 1912; Wilke 1822) and recent characters identified by one of the authors (Smith 2010, in prep.), including one behavioral character (defensive posture) and one character based on a species overall resemblance to known co-occurring *Eleodes* species (*Eleodes* mimic). Characters and their states are included in chapter 1 with a matrix of scored states for each species. Images of states and additional supplementary material are online at http://www.hisl.ent.msu.edu/research/asidini/ .

All measurements were taken using digital calipers or an optical micrometer attached to a Leica MZ125 microscope. Overall body length was measured along the midline from the anterior margin of the pronotum to the apex of the elytra. Width was measured across

the widest point of the elytra. Images of specimens or characters were taken with a Leica DFC320 camera mounted on a Leica MZ16 microscope. Montaged images were assembled with Helicon Focus 3.5 (HeliconSoft) software.

Dissection of specimens to examine internal structures followed established methods (Tschinkel & Doyen 1980, Flores 1997) for the subfamily and descriptive terminology followed Doyen (1966, 1993) and Harris (1979).

### *Phylogenetic Analysis*

Morphological and sequence data (100 morphological characters, 1152bp) for 55 North American asidine OTUs and 3 outgroup taxa were concatenated in Mesquite 2.5 (Maddison and Maddison, 2008) and exported in Nexus format for analyses in PAUP* 4.0b10 (Swofford, 2003). A heuristic maximum parsimony analysis was in performed in PAUP* using 10,000 random stepwise additions, TBR branch swapping, and with all characters given equal weight. Branch support was determined using the nonparametric bootstrap (Felsenstein 1985) with 1000 bootstrap replicates (200 random addition replicates each) in PAUP* and Bremer support indices in TreeRot.v3 (Sorenson & Franzosa 2007). Bremer support was assessed for the entire dataset and for three data partitions (COI, 28S, and morphology).

## RESULTS

The Asidini were recovered as monophyletic with the South American genus *Cardigenius* as sister to the North American asidines. The phylogenetic analysis yielded 4 most parsimonious trees (L=3615, CI=0.22, RI=0.47), of which one is show below (Fig

3.1). Branches in the tree are colored according to the dorsal habitus of the OTUs and their visual similarity to the genus *Eleodes*; red: mimetic, blue: potentially mimetic; green: precise background matching through encrusting; black: imprecise background matching, heavily setose, pattern disrupted, or without a potential model.

The phylogeny (Fig. 3.1) indicates that mimetic morphology has evolved multiple times within the North American asidines. *Philolithus* (*Gonasida*) *elata*, the only mimetic species that has strong biogeographical and morphological data linking it to a specific model (Brown 1971a), is far removed from the *Stenomorpha* species, which have also been implicated as mimetic.

The majority of potentially mimetic asidines occur within *Stenomorpha*. Six of the species within this genus have been observed exhibiting headstanding behavior, but data are not currently available for most of the species. Two species, *S.* (*Megasida*) *obliterata* and *S.* (*Stenomorpha*) *marginata*, have been cited (Slobodchikoff *et al.* 1987, Eisner 1966) as inaccurate mimics of specific *Eleodes* species. Relationships within *Stenomorpha* are poorly resolved in the current phylogeny; however the subgenera *Asidina*, *Asidopsis*, *Stenomorpha*, and *Trichiasida* are clearly not monophyletic. An expanded analysis using more molecular data may resolve these relationships and indicate a single origin for mimicry within the clade or provide support for multiple radiations of mimetic asidines.

The only species in the analysis that displays precise background matching though the chemical adhesion of soil, *P.* (*Astrotus*) *regularis*, was deeply embedded within the genus *Pelecyphorus*. It is not possible in the current analysis to ascertain whether there is a single or multiple origins for the trait, but the five species known from

the subgenus all display a unique set of morphological characters, including the presence of *Astrotus*-type stellate setae, and are in all likelihood monophyletic. Thus there is some evidence that this variation of background matching has evolved only once within the North American asidines.

## DISCUSSION

An examination of the current North American asidine phylogeny indicates that differing adult defensive strategies have evolved multiple times within the group. Many of the North American species display cryptic colorations and morphologies to avoid detection, as do most known asidine species in the rest of the world.

The evolution of precise background matching through the use of chemical adhesion may be unique to the *Pelecyphorus* subgenus *Astrotus*. Varying amounts of encrusting are seen in other asidine species, particularly members of the Mediterranean genus *Asida* and the southern African genera *Machla* and *Amachla*, though the mechanism behind their adhesion is still unclear and all lack the peculiar stellate setae associated with all *Astrotus* species.

No species of asidine outside of North America have been implicated as Batesian mimics of any chemically defended species, while fully half of the North American asidine species included in the analysis are at least potentially inaccurate mimics of the genus *Eleodes*, based on morphology, and seven species have been observed mimicking the *Eleodes* warning signal of headstanding. One possible explanation for this discrepancy is that asidines outside of North America lack potential models that inhabit approximately the same environmental niche as the potential mimics, occur in high

enough densities to be more commonly encountered by predators, and are sufficiently distasteful to induce an avoidance response in some subset of their potential predators.

The predominance of *Eleodes* species throughout much of Mexico and the western United States and the presumed effectiveness of their defensive secretions, in tandem with the ability of predators to recognize and avoid them based on their aposomatic morphology and the associated warning display of headstanding, may provide significant selective pressure for a species to evolve mimetic attributes based upon the *Eleodes* model even though *Eleodes* species are not immune to predation. Thomas (1979) studied the life history of *Eleodes armatus* LeConte, a large species that headstands and sprays its defensive secretions, and found that *Hadrurus arizonensis* Ewing, the desert hairy scorpion, easily feeds on *E. armatus*, although the scorpion's behavior is markedly different from its behavior when feeding on other arthropods (Bub & Bowerman 1979). This study, coupled with the frequency of *Eleodes* corpses found in spider webs (personal observation), may indicate that the defensive secretions and aposomatic signaling employed by *Eleodes* are less effective against other invertebrates.

*Eleodes* warning signals do appear to be reasonably effective against vertebrate predators that hunt by sight (Doyen & Somerby 1974), though some mammalian predators have devised strategies to overcome *Eleodes* defenses. For example, grasshopper mice, *Onychomys spp.*, grab *Eleodes* prey and push the beetle's abdomen into the ground before consuming them head first (Eisner 1966). Coatis, *Nasua* spp., (Weldon *et al.* 2006) and striped skunks, *Mephitis mephitis*, (Slobodchikoff 1978b) will roll chemically defended arthropods on the ground to wipe away the secretions before feeding. However, there is potentially an energetic cost associated with handling

defended prey and even predators that can neutralize *Eleodes* secretions seem to prefer undefended arthropods when given a choice (Doyen 1975, Hetz & Slobodchikoff 1988, Slobodchikoff *et al.* 1987).

Other factors that bear consideration are the potentially high opportunity costs associated with crypsis (Speed and Ruxton 2005). Foraging ranges may be restricted based on substrate or light levels, as might an organism's ability to search for a mate. Thus by removing the need for crypsis, mimics may gain a selective advantage even if the amount of predation on a species is only moderately diminished.

Of the species that exhibit mimetic morphologies and headstanding behavior, only *Philolithus* (*Gonasida*) *elata* can be reliably linked to a specific model (*E. obscurus*) as both are large (20-35mm) distinctive species and the dorsal patterning in subspecies of both match throughout much of their overlapping ranges. However, the mimetic or potentially mimetic *Stenomorpha* species are difficult to assign to specific models. Most are phenetically similar (Fig. 3.5) to *Eleodes* species in the nominate subgenus, which contains a majority of the *Eleodes* species. Most *Eleodes* are exceedingly difficult to identify at the species level and many are thought to form Müllerian rings (Doyen and Somerby 1974), so perhaps it is not surprising that *Stenomorpha* species are not easily tied to specific model species, though more research is needed to confirm this.

This study is the first to place the evolution of darkling beetle defense strategies in a phylogenetic context. However, much study is needed to quantify the relationships, benefits, and costs associated with the defensive strategies observed in the asidine, but given their diversity they will hopefully provide an excellent model system for further

research as we seek to unravel the complexities inherent in animal defensive mechanisms.

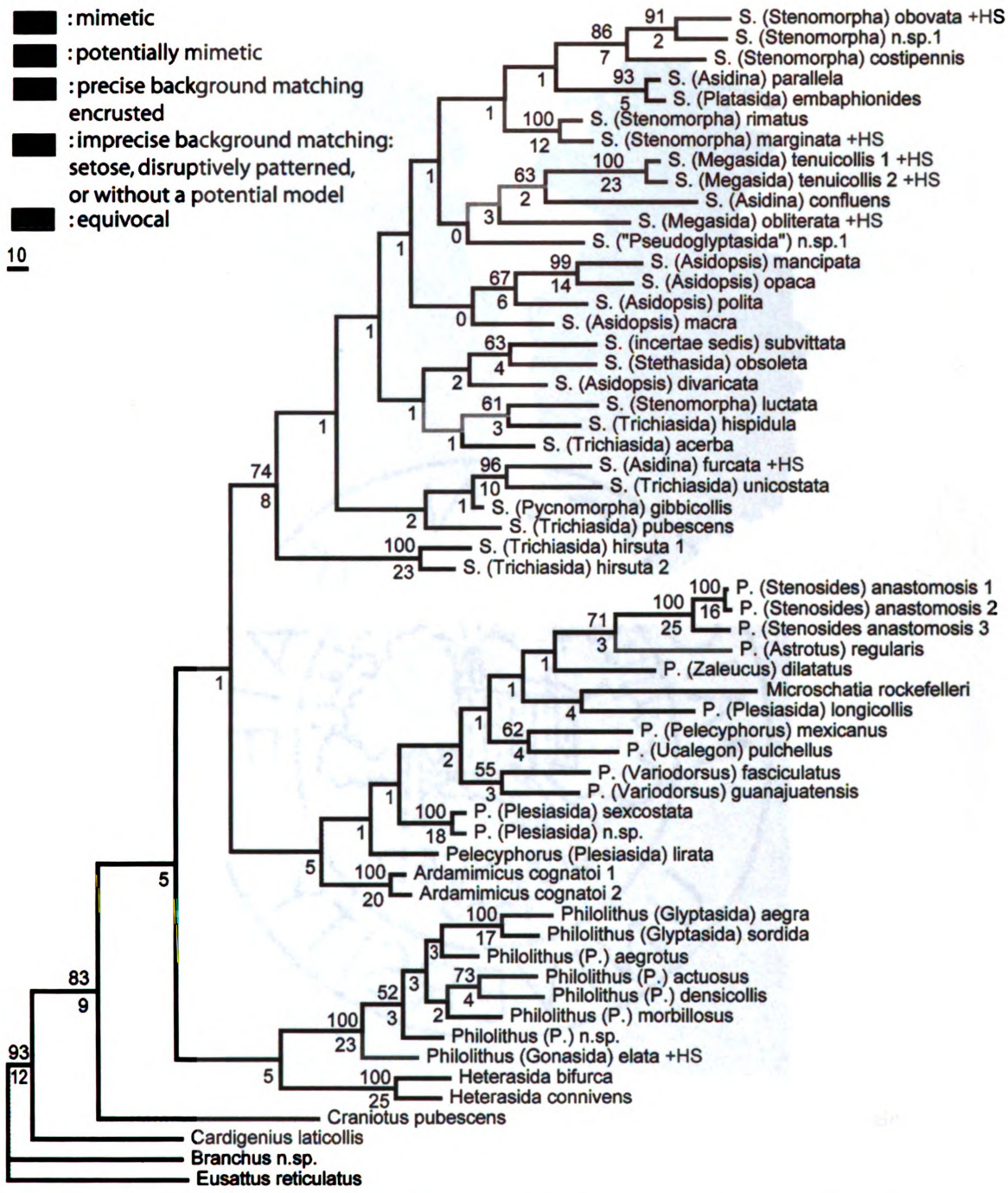


**Figure 3.1:** Phylogeny of the North American Asidini based on 28S, COI, and adult morphology (58 OTUs, 1252 characters). 1 of 4 most parsimonious trees (L=3615, CI=0.22, RI=0.47) is shown with Bootstrap values listed above the branches and Bremer support shown below the branches. Brown "+HS" indicates species known to exhibit headstanding.

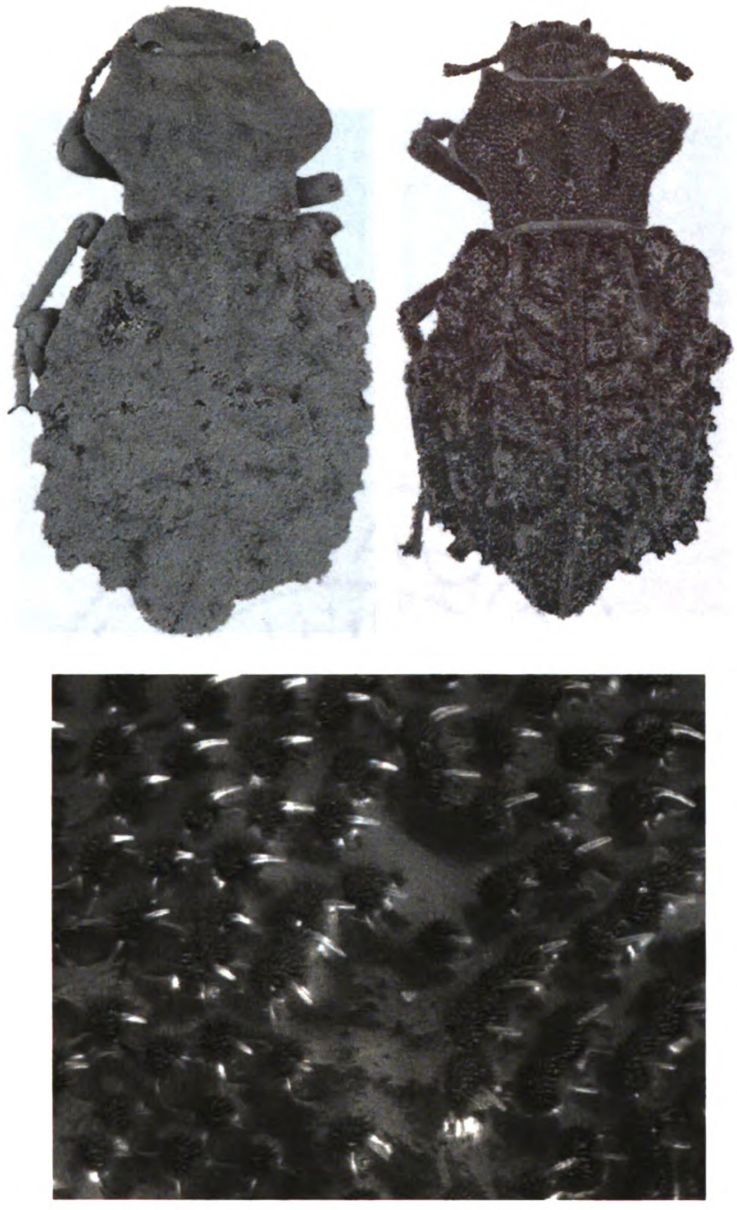

**Figure 3.2:** *Pelecyphorus* (*Astrotus) alveolatus* (Casey); top: encrusted ♀, left; cleaned ♀, right. bottom: Astrotus-type stellate setae.

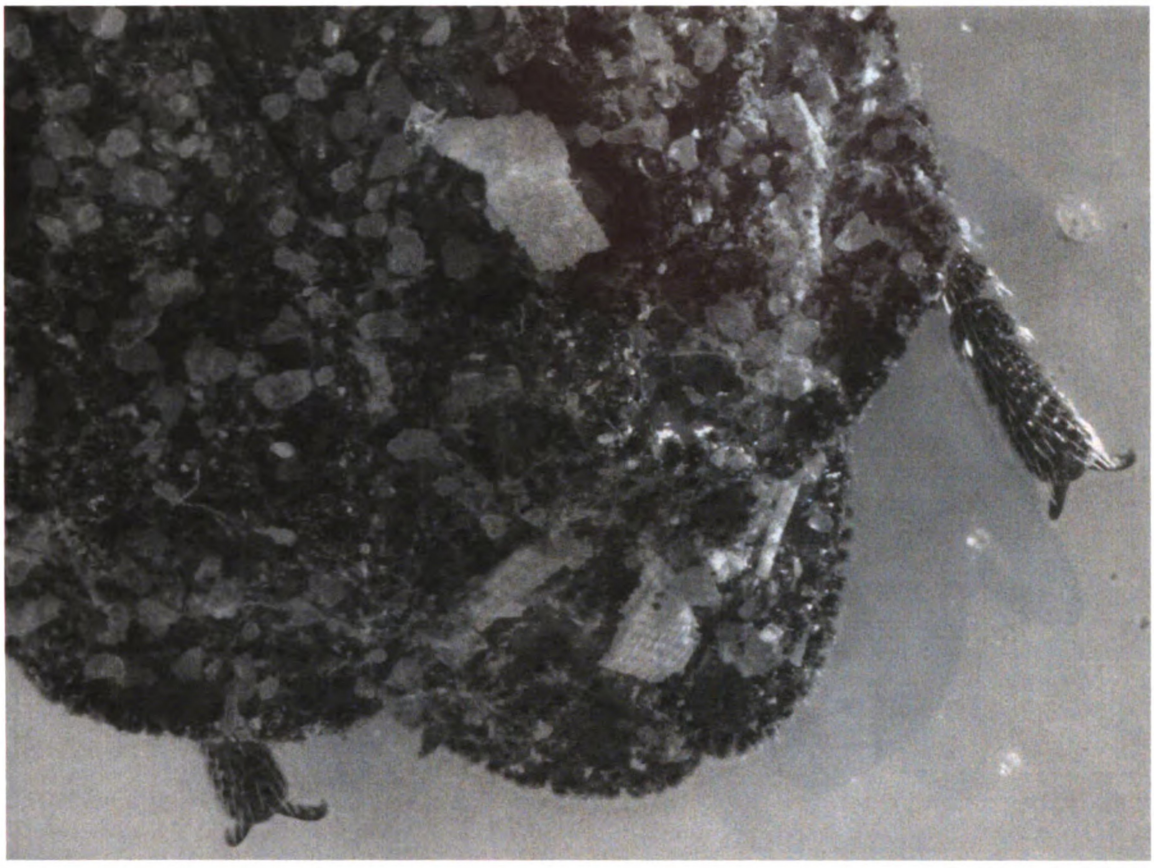

**Figure 3.3:** Webbing on *Pelecyphorus* (*Astrotus*) *regularis* (Horn) ♀, 1-8 hours after emergence.

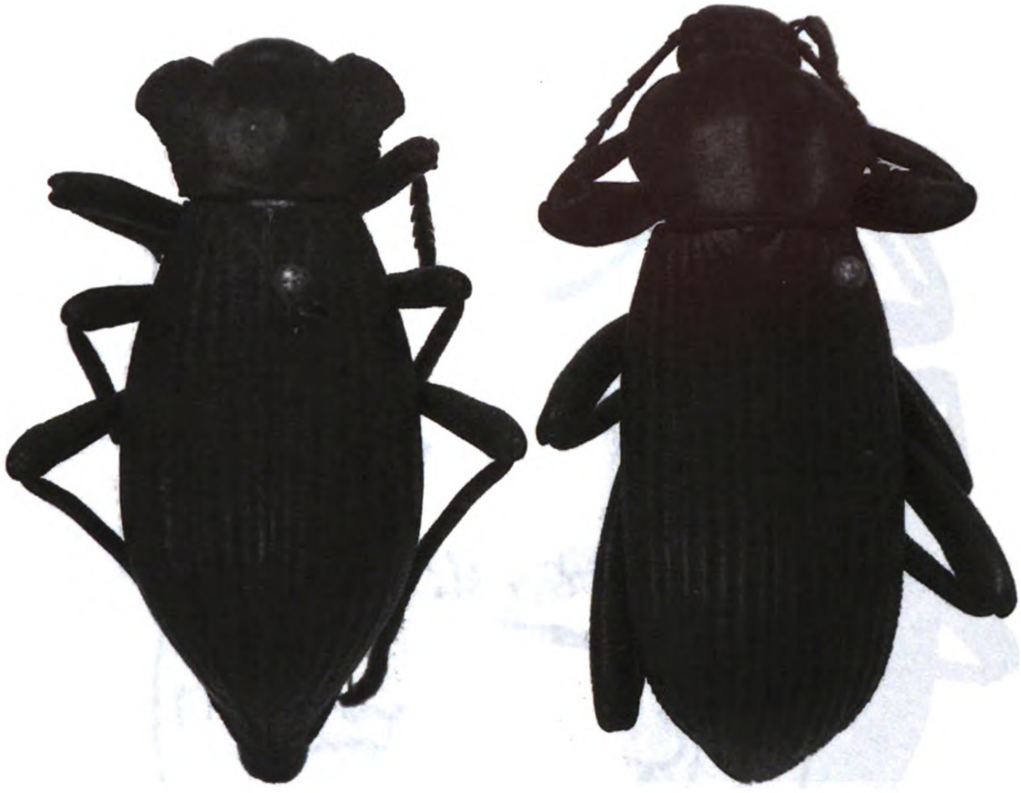

**Figure 3.4:** ***Philolithus*** **(*Gonasida elata difformis*** **(LeConte) ♂, left; *Eleodes obscurus sulcipennis*** **Mann. ♂, right.; both collected AZ: Cochise Co., August 22, 2006.**

**Figure 3.5:** *Stenomorpha convexicollis* (LeConte) ♀, left; *Eleodes longicollis* LeConte ♀, right; both collected NM: Luna Co., August 21, 2006.

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