

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

By

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A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Entomology
and Ecology, Evolutionary Biology and Behavior

2010

ABSTRACT

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

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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, *Pelecyporus* 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. doyeri*, *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.

ACKNOWLEDGMENTS

This work would not have been possible without the support and guidance of my major professor, Dr. Anthony Cognato. I would also like to thank my Ph.D. committee members Dr. Barbara Lundrigan, Dr. Alan Prather, and Dr. James Smith for their guidance and review. This research was also aided by the advice and assistance of Gary Parsons, collection manager at the A.J. Cook Arthropod Research Collection, and my fellow graduate students in the Holistic Insect Systematics Laboratory: Stephanie Dole, Jiri Hulcr, and Sarah Smith. I also give thanks to all of the tenebrionid taxonomists who kindly provided advice and specimens throughout this project: Rolf Aalbu, Kirby Brown, Kojun Kanda, Fran Keller, Paulina Cifuentes-Ruiz, Warren Steiner, and Charles Triplehorn. I am deeply indebted to all of the museum curators and staff who provided most of the specimens upon which this study is based, especially Max Barclay, Cheryl Barr, Ed Riley, Norman Penny, James Boone, and again Warren Steiner and Charles Triplehorn for providing me with space and equipment in their museums. In the MSU Department of Entomology I would like to thank our wonderful office staff, for helping me over many of the bureaucratic pitfalls which graduate students so often fall into. And finally, I would like to thank my parents H. Dennis Smith and Barbara A. Haenelt for equipping me with the motivation and skills to pursue my passion for entomology.

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PREVIEW

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 (= *Pelecyporus* Solier), *Parasida* Casey (= *Pelecyporus* Solier), *Poliorcetes* Champion (= *Pelecyporus* Solier), *Sicharbas* Champion (= *Pelecyporus* Solier), *Stenosides* Solier (= *Pelecyporus* Solier), *Ucalegon* Champion (= *Pelecyporus* Solier), *Zaleucus* Champion (= *Pelecyporus* 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*, *Pelecyporus*, *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 *Pelecyporus* 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 Lacordaire’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*, *Peleciphorus*, *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 amplexed into antennal segment 11; submentum not concealed; prementum narrower than mentum, mostly membranous with the ligula sclerotized, one-half or less mentum length, exposed or concealed beneath apical margin of mentum; mentum large, cordate to trapazoidal or hexagonal, width greater than 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 trochantin 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.