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Unifying systematics and taxonomy:
Nomenclatural changes to Nearctic tiger beetles
(Coleoptera: Carabidae: Cicindelinae)
based on phylogenetics, morphology and life history

Daniel P. Duran

Department of Environmental Science
Rowan University
201 Mullica Hill Rd
Glassboro, NJ 08028-1700, USA

Harlan M. Gough

Florida Museum of Natural History
Biology Department
University of Florida
3215 Hull Rd
Gainesville, FL 32611-2062, USA

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Daniel P. Duran and Harlan M. Gough

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Daniel P. Duran

Department of Environmental Science
Rowan University
201 Mullica Hill Rd
Glassboro, NJ 08028-1700, USA
duran@rowan.edu

Harlan M. Gough

Florida Museum of Natural History
Biology Department
University of Florida
3215 Hull Rd
Gainesville, FL 32611-2062, USA
goughh@ufl.edu

Abstract. The taxonomy of Nearctic tiger beetles (Coleoptera: Carabidae: Cicindelinae) is reviewed in light of modern systematics research. Despite decades of published molecular phylogenies, the taxonomic nomenclature has not been formally updated since the 1950s. We generated a maximum likelihood phylogenetic tree based on three mitochondrial gene fragments (*16S*, *COX3* and *CytB*) to address the placement of Nearctic taxa that were not included in recent studies; these species were historically contained within *Cylindera* Westwood, 1831, a polyphyletic genus. Here we describe *Parvindela* Duran and Gough, **new genus**, and propose 20 new combinations based on a plurality of data, including our topology, prior molecular phylogenetic studies, morphology and ecology: *Apterodela unipunctata* (Fabricius, 1775) new combination; *Brasiella praecisa* (Bates, 1890) new combination; *Brasiella viridisticta* (Bates, 1881) new combination; *Cicindela amargosae* (Dahl, 1939) new combination; *Cicindela senilis* (G. Horn, 1866) new combination; *Cicindela willistoni* (LeConte, 1879) new combination; *Eunota californica* (Menetries, 1883) new combination; *Eunota circumpicta* (LaFerte, 1841) new combination; *Eunota fulgoris* (Casey, 1913) new combination; *Eunota gabpii* (G. Horn, 1866) new combination; *Eunota pamphila* (LeConte, 1873) new combination; *Eunota praetextata* (LeConte, 1854) new combination; *Eunota severa* (LaFerte, 1841) new combination; *Eunota striga* (LeConte, 1875) new combination; *Parvindela debilis* (Bates, 1890) new combination; *Parvindela celeripes* (LeConte, 1848) new combination; *Parvindela cursitans* (LeConte, 1860) new combination; *Parvindela terricola* (Say, 1824) new combination; *Parvindela nephelota* (Bates, 1882) new combination; *Parvindela lunalonga* (Schaupp, 1884) new combination.

Key words. New genus, *Parvindela*, North America, molecular phylogeny

Introduction

Tiger beetles are one of the most popular and well-studied groups of insects (Knisley and Schultz 1997; Pearson and Vogler 2001), yet the taxonomy of the group is critically outdated and has not been updated to reflect the results of modern phylogenetic studies. The systematic relationships of tiger beetles have been studied extensively using both morphological characters (e.g. Horn 1915; Rivalier 1950; Ball et al. 2011) and molecular data (e.g. Galián et al. 2002; Pons et al. 2004; Sota et al. 2010; Gough et al. 2019). The most recent substantial taxonomic revision was by Rivalier (1950, 1954, 1957, 1961, 1963, 1969, 1970, 1971) where he revised the largest genus, *Cicindela* Linné, 1758, based on genitalic characters, erected 50 genera and subgenera, and divided Cicindelinae into four tribes (Cicindelini, Collyridini, Megacephalini and Manticorini).

The Nearctic tiger beetle fauna has been thoroughly studied with respect to species-level phylogenies (Vogler and Welsh 1997; Barraclough and Vogler 2002; Vogler et al. 2005; Gough et al. 2019). These studies have used well-sampled trees to address other research questions such as macroevolutionary patterns (Vogler and Welsh 1997), speciation rates (Barraclough and Vogler 2002), or substitution rates in

mtDNA genes (Vogler et al. 2005). Although topologies were not identical across studies, some consistent patterns have emerged that challenge the traditional taxonomy (e.g. placement of *Cicindelidia willistoni* (LeConte) in *Cicindela*). Still, the taxonomic implications of tiger beetle molecular phylogenetic studies have been conspicuously ignored (but see Morgan et al. 2000; Duran et al. 2019), and to date, little has been done to reconcile newer phylogenetic data with prior taxonomic nomenclature.

Rivalier's (1954) taxonomic revision of the *faune Américaine* remains the most thorough treatment of the Nearctic and Neotropical taxa; many species of *Cicindela* were transferred to other existing genera or to newly described genera and subgenera. For decades, most American workers had not adopted Rivalier's genera, instead treating them as subgenera (e.g. Boyd 1982; Freitag 1999). Erwin and Pearson's Treatise on the Western Hemisphere Caraboidea (2008) was the first American publication to largely follow Rivalier's generic circumscriptions, recognizing *Cylindera* Westwood, 1831, *Dromochorus* Guérin-Méneville, 1845, *Ellipsoptera* Dokhtoureff, 1883, *Brasiella* Rivalier, 1954, *Eunota* Rivalier, 1954, *Habroscelimorpha* Dokhtoureff, 1883, and *Microthylax* Rivalier, 1954, as well as the nominate *Cicindela* (*sensu stricto*). However, Erwin and Pearson (2008) did not recognize *Cicindelidia* Rivalier, 1954 as a full genus, treating it as a subgenus of *Cicindela*, although no justification was given for this decision. Molecular phylogenies have validated much of Rivalier's work, although a minority of species have been recovered in clades that are inconsistent with his taxonomic framework.

Recently, a comprehensive molecular phylogeny of the global tiger beetle diversity (Gough et al. 2019) sampled 328 species, including 108 Nearctic species. The resulting topology was largely consistent with prior molecular studies (Vogler and Welsh 1997; Barraclough and Vogler 2002; Vogler et al. 2005), and was based in part on the same sequence data that were used to generate those topologies, although with greater sampling and gene coverage. The results of Gough et al. (2019) demonstrated the existence of a polyphyletic *Cylindera* and recovered a clade of endemic Nearctic species that are not monophyletic with the Palearctic species. In addition, other genera were found to be in need of rearrangement (e.g. *Habroscelimorpha*, *Eunota*), and the new groupings were further supported by morphology and life history.

As such, the current nomenclature is outdated and, at times, incongruous with published systematic studies. Here we propose needed taxonomic changes to the Nearctic tiger beetle fauna based on molecular phylogenetics, congruent with morphological and ecological evidence.

Materials and Methods

Taxon selection

We generated a phylogeny to address the placement of key Nearctic taxa that were critically missing from Gough et al. (2019), all of which were classified in the genus *Cylindera* in Rivalier's (1954) revision; these were *C. unipunctata* (Fabricius, 1775), *C. lemniscata* (LeConte, 1854), *C. viridisticta* (Bates, 1881) and *C. praecisa* (Bates, 1890). For each of these taxa, sequences for three genes, 16S rRNA (mt-rnr2), cytochrome b (cytb), and cytochrome c oxidase subunit III (cox3), were available on NCBI GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and were included in our analysis. We sampled only taxa that had available sequences for these three genes, including *Cylindera germanica* (Linné, 1758) (Westwood's type for the genus). For *C. lemniscata*, we sequenced four freshly collected specimens, due to the conflicting results in prior studies which placed this taxon in different clades (Vogler and Welsh 1997; Barraclough and Vogler 2002; Vogler et al. 2005), indicating the possibility of error in one or more of the available sequences.

Due to the small size of this species, the whole body of each specimen was homogenized in order to guarantee sufficient yield of DNA. Additional specimens of *C. lemniscata* with identical collection data have been deposited in the molecular collection of the McGuire Center for Lepidoptera and Biodiversity, Gainesville, Florida (MGCL). The *C. lemniscata* collection data and the GenBank accession numbers for all sequences used in this study are provided in Appendices 1–2.

Model selection and phylogenetic reconstruction

We inferred phylogenetic relationships with IQ-TREE v. 1.6.9 (Nguyen et al. 2015). Partitioning and model selection was preformed using ModelFinder in IQ-TREE by specifying the command -MFP+merge

with the best model chosen using BIC (Kalyaanamoorthy 2017). The tree with the best maximum likelihood score was selected from 200 independent searches. For each of the 200 runs, we estimated nodal support using 1000 ultrafast bootstraps (UFBoot) (Hoang et al. 2018) and 1000 SH-aLRT tests. We used the `-bnni` command to avoid severe model violation resulting in overestimation of nodal support when performing ultrafast bootstraps. All analyses were performed on the HiPerGator 2.0 cluster at the University of Florida. The aligned molecular dataset, partitioning scheme, and IQ-TREE output file used to make Fig. 1 are all available to download from an Open Science Framework repository (<https://osf.io/d94tr/>).

Results

The root of the tree was placed between *C. germanica* and the rest of the tree based on results from Gough et al. (2019). The topology was consistent with that previous study, even with the inclusion of these additional taxa (Fig. 1). *Cylindera unipunctata* was strongly supported (UFBoot = 97.9, SH-aLRT = 100) as sister to *C. (Apterodela) ovipennis*, a species from the Oriental biogeographic realm. *Cylindera viridisticta* and *C. praecisa* were recovered as sister taxa and nested within a larger strongly supported *Brasiella* clade (UFBoot = 97.5, SH-aLRT = 96). The four *C. lemniscata* individuals included in our analysis represent sequences from five specimens we sequenced for this study and sequences pulled from

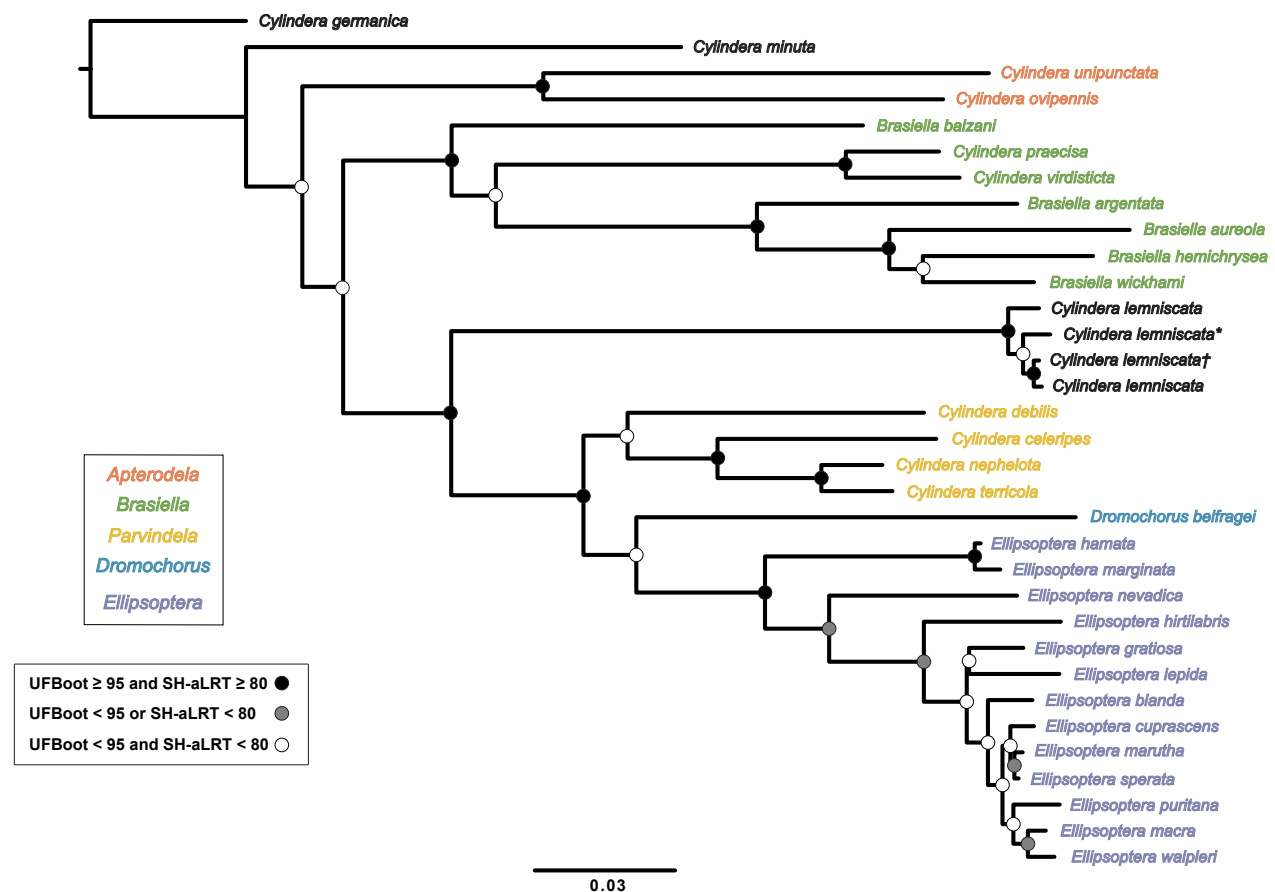


Figure 1. Maximum-likelihood phylogenetic hypothesis for North American lineages *Ellipsoptera*, *Dromochorus*, *Brasiella*, and *Cylindera*. Maximum-likelihood phylogeny inferred in IQ-TREE based on three mitochondrial fragments (*16S*, *COX3* and *CytB*). Taxon naming follows previous naming conventions with different colors highlighting new generic groupings we propose. * denotes the *C. lemniscata* specimen from GenBank and † denotes the chimera specimen.

GenBank. Due to incomplete sequencing success across all specimens for all genes, we created chimeras by pooling sequences from two of the specimens when necessary (Appendix 1). *Cylindera lemniscata* was recovered as monophyletic with strong support (UFBoot =100, SH-aLRT =100) and recovered as sister to a larger Nearctic endemic clade that consists of “*Cylindera*” (to be named below) + (*Dromochorus* + *Ellipsoptera*) with moderate support (UFBoot = 94.8, SH-aLRT = 89).

Taxonomy

Parvindela Duran and Gough, new genus

(Fig. 2)

Etymology. The generic name is derived from *Parv-* (Latin root meaning “small”) and *Cicindela* (the type genus of the tribe Cicindelini); gender is feminine. *Parvindela* adults are small (7–12 mm), and the genus includes some of the smallest tiger beetles in the Nearctic region.

Type species. *Cicindela debilis* Bates, 1890; by present designation

Parvindela debilis (Bates, 1890), new combination

Parvindela celeripes (LeConte, 1848), new combination

Parvindela cursitans (LeConte, 1860), new combination

Parvindela terricola (Say, 1824), new combination

Parvindela nephelota (Bates, 1882), new combination

Parvindela lunalonga (Schaupp, 1884), new combination

Description. Small size, 7–12mm. Body shape variable, with humeral region narrow and ant-like (e.g., *P. celeripes*) to more robust (e.g., *P. terricola*). Head with fine rugosity present in supraorbital region. Frons glabrous except for supraorbital setae. Proepisternum glabrous or with only a few scattered setae near margins. Marginal line, if present, typically not fully touching outer edge of each elytron. No single morphological synapomorphy has been identified that unites *Parvindela*, but this new genus is strongly supported by recent phylogenetic studies (Gough et al. 2019; this study), previously recognized as a subgroup of *Cylindera*.

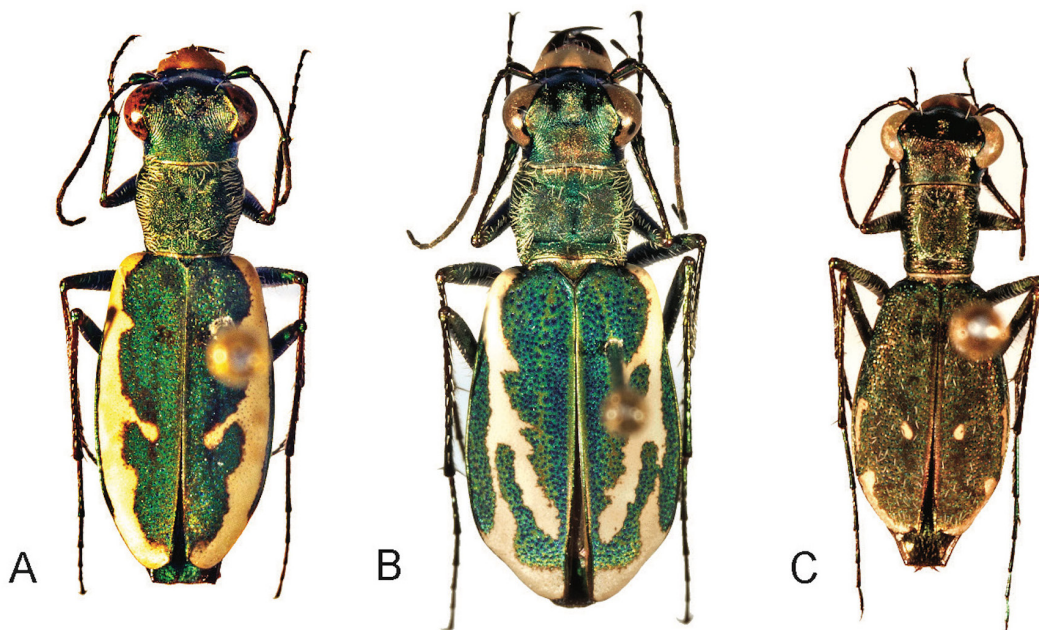


Figure 2. Representative dorsal habitus of *Parvindela* new genus. A) *Parvindela debilis* (type species). B) *Parvindela terricola*. C) *Parvindela celeripes*.

The genus *Cylindera* initially included only Palearctic species, but in Rivalier's (1954) revision of *Cicindela* (*s.l.*) the genus was amended to include American species that possessed aedeagi with similarly wound flagella. He noted that there were a number of inconsistencies and "aberrant" species but did not believe it was necessary to name a genus for the American species. The phylogeny of Gough et al. (2019) recovered a polyphyletic *Cylindera*, with each clade found in a particular biogeographic realm. A monophyletic clade of Nearctic species was part of a larger Nearctic endemic clade that also included *Ellipsoptera* and *Dromochorus*. This previously unnamed lineage that is now designated as *Parvindela*, new genus.

Distribution. Nearctic region (Canada, USA, Mexico). To date, all known species are found within this biogeographic realm. All of the above listed species were included in Gough et al. (2019) and/or this study.

***Apterodela unipunctata* (Fabricius, 1775), new combination**

Rivalier (1950) described *Apterodela* as a subgenus of *Cylindera* and designated *C. ovipennis* Bates, 1883 as the type. Given the polyphyly of *Cylindera* (Gough et al. 2019; this study) and a monophyletic and morphologically distinct *Apterodela* (Sota et al. 2011), we recognize the clade as a full genus.

The Nearctic species, *A. unipunctata*, is strongly supported (Bootstrap = 98) as sister to *A. ovipennis* in our phylogeny (Fig. 1) and is remarkably similar in morphology to species of *Apterodela* from Asia. Like the other members of the genus, it is large (14–18 mm), with a coarsely striated concave frons, flattened ovate elytra with reduced maculations, dark infuscations and prominent subsutural foveae.

Ecologically, *A. unipunctata* is unlike any other species of Nearctic Cicindelini. Adult beetles are typically found when they cross forest trails and openings, but they also frequent darker closed-canopy forested areas where they may hunt in or on the leaf litter. The first author has collected beetles in dense late-succession oak forest in areas that were over 100m from a trail or opening. It is quite likely that most casual observations of this species are biased towards edges, as it is more likely to be seen when crossing trails and light gaps. Asian *Apterodela* species share similar forest-dwelling natural history and affinity for leaf litter (Fig. 3).



Figure 3. In situ photographs of *Apterodela* spp. **A)** *Apterodela ovipennis* (Asia). **B)** *Apterodela unipunctata* (North America).

Brasiella viridisticta* (Bates, 1884), new combination**Brasiella praecisa* (Bates, 1890), new combination**

The above species were both classified as *Cylindera* by Rivalier (1954), despite his caveats that many of the American species fit poorly within that genus. Gough et al. (2019) did not include these taxa in their analysis, but they were sampled in the present study. Both *B. viridisticta* and *B. praecisa* were recovered in a strongly supported *Brasiella* clade and are sister taxa (Fig. 1). Both species lack setae on the middle trochanters, a trait shared with other *Brasiella*.

Cicindela willistoni* (LeConte, 1879), new combination**Cicindela senilis* (G. Horn, 1866), new combination*****Cicindela amargosae* (Dahl, 1939), new combination**

These three closely related taxa were placed in the genus *Cicindelidia* by Rivalier (1954) based on characteristics of the male genitalia. At the time of publication, *C. willistoni* and *C. senilis* were treated as full species and *C. amargosae* was considered a subspecies or form of *C. willistoni*. In his revision, Rivalier recognized that *C. willistoni* did not fit well within his newly erected genus and stated this explicitly, indicating that he believed that species formed a “bridge from *Cicindela* to *Cicindelidia*”.

The three taxa possess white setae on the frons (in addition to the supraorbital setae), a character shared with *Cicindela* that is not present in any other *Cicindelidia*. Some populations possess dense white setae throughout the frons, whereas other populations may have a greatly reduced number of setae.

Life history/phenology patterns for the group are complex and may be incompletely known in some geographic areas, but most populations of these species appear to have bimodal adult activity periods, a trait that is typical for *Cicindela* and nonexistent in *Cicindelidia*. Some populations are apparently exclusively active in the spring (e.g., southern populations of *C. amargosae*), and others may have adopted a summer activity period (e.g., southeastern Arizona *C. willistoni* “*sulfontis*”).

Several molecular phylogenies have included at least one member of the group. *Cicindela willistoni* was included in molecular phylogenies based on mtDNA sequences (Vogler and Welsh 1997; Barraclough and Vogler 2002; Vogler et al. 2005) or combined mtDNA and nuclear genes (Pons et al. 2004; Gough et al. 2019); *C. amargosae* was included in mtDNA sequence-based phylogenies (Barraclough and Vogler 2002; Vogler et al. 2005); and *C. senilis* was included in a combined mtDNA and nuclear gene phylogeny (Gough et al. 2019). In all cases, these species were recovered within the genus *Cicindela*, not *Cicindelidia*.

Eunota californica* (Menetries, 1883), new combination**Eunota circumpicta* (LaFerte, 1841), new combination*****Eunota fulgoris* (Casey, 1913), new combination*****Eunota gabbii* (G. Horn, 1866), new combination*****Eunota pamphila* (LeConte, 1873), new combination*****Eunota praetextata* (LeConte, 1854), new combination*****Eunota severa* (LaFerte, 1841), new combination*****Eunota striga* (LeConte, 1875), new combination**

All of the above species were sampled in Vogler et al. (2005), and all but *E. striga* were sampled in Gough et al. (2019). In both studies, the species formed a monophyletic clade that also included *Eunota togata* LaFerte, 1841. *Habroscelimorpha dorsalis* Say, 1817 (the type species) and *H. curvata* Chevrolat 1834 were recovered as a monophyletic clade in a different part of the tree, never monophyletic with the above species.

In Rivalier’s (1954) revision of *Cicindela* (*sensu lato*), a number of American species were transferred to *Habroscelimorpha* based on structures of the aedeagus. He noted that there were two distinct groups: *H. dorsalis* + *H. curvata*, and the remaining species, which included the taxa listed above. The *dorsalis* species-group had prominent eyes, remarkably long hind femora, trapezoidal pronotum, and atypically formed white maculations. The other species had prominent eyes, a typical pronotum, and less exaggerated hind femora. These latter species also share an ecological synapomorphy, as all are halophiles. In contrast, *H. dorsalis* and *H. curvata* are found on sandy ocean beaches.

Rivalier (1954) created a monotypic genus for *Eunota togata* owing to peculiarities of the aedeagus, despite a strong similarity in maculations, setal characteristics and overall gestalt to the above species.

One Nearctic species currently classified in *Habroscelimorpha* was not included in any recent phylogeny: *H. rockefelleri* Cazier, 1954, from the Mexican state of Sonora, but it is nearly identical to *E. californica* except for its glabrous pronotum (Cazier 1954) and slightly smaller size. This species also occurs in saline muddy areas and is almost certainly a *Eunota* as well, but as it was never included in any modern phylogeny, we will not transfer it to that genus at the present.

Cylindera lemniscata (LeConte, 1854), *incertae sedis*

This taxon has been the most difficult to place in the Nearctic fauna. In Vogler and Welsh (1997), *C. lemniscata* was the sister taxon to the only other sampled *Cylindera* in their study: *C. celeripes*. In two other studies (Barracough and Vogler 2002; Vogler et al. 2005), *C. lemniscata* was recovered in a clade of *Microthylax* species, a surprising result. Given the incongruency of these results, we extracted DNA from fresh specimens and sequenced three gene fragments (*16S*, *COX3* and *CytB*), in addition to using the GenBank sequences. In our tree, *C. lemniscata* is contained within a large Nearctic endemic clade, positioned as sister to the *Parvindela* + (*Dromochorus* + *Ellipsoptera*) clade (Fig. 1), a third result that is inconsistent with prior studies.

Morphologically, *C. lemniscata* appears most similar to *Parvindela* based on its small size, shape of the thorax, and full-length marginal lines that do not meet the elytral edge. However, this species is atypical for that genus in other respects; it has a polished shining dorsal surface, whereas all *Parvindela* have a dull texture; it lacks setae on the middle trochanters, a trait that it shares with *Brasiella*, although it does not resemble that group in any other way. Behaviorally, *C. lemniscata* shares an affinity for flying to lights at night with *Ellipsoptera* and *Brasiella*. No *Parvindela* species exhibit this behavioral trait.

It is possible that additional genes will further resolve the placement of *C. lemniscata*. If the results of our tree are upheld with larger datasets, a new genus would have to be erected to accommodate this taxon.

Discussion

Adopting an integrative approach, we were able to use molecular phylogenetic data in conjunction with morphological synapomorphies and life histories to update the nomenclature of the Nearctic tiger beetle fauna, leading to the description of a new genus, and 20 new combinations (Table 1). In light of these changes, we recognize 13 genera of Cicindelinae in the Nearctic region (Table 2).

Our phylogeny, in conjunction with Gough et al. (2019) supports a polyphyletic *Cylindera* and indicates that none of the Nearctic or Neotropical taxa are monophyletic with *Cylindera* (*sensu stricto*). Given these results, additional genera may need to be erected to place Neotropical species, e.g., *Cylindera morio* (Klug, 1834), which are recovered in unnamed clades. The placement of problematic taxa, such as *C. lemniscata* may be aided by expanded gene sampling. This study highlights the need for integration of molecular phylogenetic data with life history and morphology to better inform tiger beetle taxonomy.

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Table 1. Proposed taxonomic changes to Nearctic tiger beetles (Coleoptera: Carabidae: Cicindelinae).

New name	Change	Previous name	Based on
<i>Apterodela unipunctata</i>	new combination	<i>Cylindera unipunctata</i>	phylogeny (this study); morphology; ecology
<i>Brasiella praecisa</i>	new combination	<i>Cylindera praecisa</i>	phylogeny (this study); morphology
<i>Brasiella viridisticta</i>	new combination	<i>Cylindera viridisticta</i>	phylogeny (this study); morphology
<i>Cicindela amargosae</i>	new combination	<i>Cicindelidia amargosae</i>	phylogeny (Barraclough and Vogler 2002; Vogler et al. 2005); morphology; ecology
<i>Cicindela senilis</i>	new combination	<i>Cicindelidia senilis</i>	phylogeny (Gough et al. 2019); morphology; ecology
<i>Cicindela willistoni</i>	new combination	<i>Cicindelidia willistoni</i>	phylogeny (Vogler and Welsh 1997; Barraclough and Vogler 2002; Vogler et al. 2005; Pons et al. 2004; Gough et al. 2019); morphology; ecology
<i>Eunota californica</i>	new combination	<i>Habroscelimorpha californica</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Eunota circumpicta</i>	new combination	<i>Habroscelimorpha circumpicta</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Eunota fulgoris</i>	new combination	<i>Habroscelimorpha fulgoris</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Eunota gabbii</i>	new combination	<i>Habroscelimorpha gabbii</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Eunota pamphila</i>	new combination	<i>Habroscelimorpha pamphila</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Eunota praetextata</i>	new combination	<i>Habroscelimorpha praetextata</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Eunota severa</i>	new combination	<i>Habroscelimorpha severa</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Eunota striga</i>	new combination	<i>Habroscelimorpha striga</i>	phylogeny (Vogler et al. 2005; Gough et al. 2019)
<i>Parvindela</i>	new genus	<i>Cylindera</i> (<i>in part</i>)	phylogeny (Gough et al. 2019; this study)
<i>Parvindela celeripes</i>	new combination	<i>Cylindera celeripes</i>	phylogeny (Gough et al. 2019; this study)
<i>Parvindela cursitans</i>	new combination	<i>Cylindera cursitans</i>	phylogeny (Gough et al. 2019; this study)
<i>Parvindela debilis</i>	new combination	<i>Cylindera debilis</i>	phylogeny (Gough et al. 2019; this study)
<i>Parvindela lunalonga</i>	new combination	<i>Cylindera lunalonga</i>	phylogeny (Gough et al. 2019; this study)
<i>Parvindela nephelota</i>	new combination	<i>Cylindera nephelota</i>	phylogeny (Gough et al. 2019; this study)
<i>Parvindela terricola</i>	new combination	<i>Cylindera terricola</i>	phylogeny (Gough et al. 2019; this study)

Table 2. Updated list of Nearctic genera of Cicindelinae.

Genus	Author	Year
<i>Cicindela</i>	Linné	1758
<i>Omus</i>	Eschscholtz	1829
<i>Amblycheila</i>	Say	1830
<i>Tetracha</i>	Hope	1838
<i>Dromochorus</i>	Guérin-Méneville	1845
<i>Ellipsoptera</i>	Dokhtouroff	1883
<i>Habroscelimorpha</i>	Dokhtouroff	1883
<i>Apterodela</i>	Rivalier	1950
<i>Brasiella</i>	Rivalier	1954
<i>Cicindelidia</i>	Rivalier	1954
<i>Eunota</i>	Rivalier	1954
<i>Microthylax</i>	Rivalier	1954
<i>Parvindela</i>	Duran and Gough	2019

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Appendix 1. Collection information for the *Cylindera lemniscata* specimens collected and sequenced for this study.

GenBank accession	Isolate #	Gene	Date collected	Collection locality	Latitude, longitude
MN200446	LEM1	cytb	7/17/17	Green Valley, AZ	31.765650, -111.034902
MN200447	LEM2	cytb	7/17/17	Green Valley, AZ	31.765650, -111.034902
MN200453	LEM2	16s	7/17/17	Green Valley, AZ	31.765650, -111.034902
MN200449	LEM3	CO3	7/17/17	Green Valley, AZ	31.765650, -111.034902
MN200452	LEM3	16s	7/17/17	Green Valley, AZ	31.765650, -111.034902
MN200448	LEM4	cytb	7/17/17	Green Valley, AZ	31.765650, -111.034902
MN200451	LEM4	CO3	7/17/17	Green Valley, AZ	31.765650, -111.034902
MN200454	LEM4	16s	7/17/17	Green Valley, AZ	31.765650, -111.034902

Appendix 2. Accession numbers for the previously sequenced genes obtained from GenBank.

Previous name	New name	CytB	16S	COX3
<i>Brasiella argentata</i>		AF439142.1	AF439012.1	AF439073.1
<i>Brasiella aureola</i>		AF439144.1	AF439014.1	AF439075.1
<i>Brasiella balzani</i>		AF439141.1	AF439011.1	AF439072.1
<i>Brasiella hemichrysea</i>		AF439143.1	AF439013.1	AF439074.1
<i>Brasiella wickhami</i>		AF439145.1	AF439015.1	AF439076.1
<i>Cylindera celeripes</i>	<i>Parvindela celeripes</i>	AF133017.1	AF133001.1	AF133033.1
<i>Cylindera debilis</i>	<i>Parvindela debilis</i>	AF133018.1	AF133002.1	AF133034.1
<i>Cylindera germanica</i>		KC963633.1	KC963501.1	KC963633.1
<i>Cylindera lemniscata</i>		AF438948.1	AF438899.1	AF438924.1
<i>Cylindera minuta</i>		AJ515083.1	AJ515114.1	AJ515136.1
<i>Cylindera nephelota</i>	<i>Parvindela nephelota</i>	AF439150.1	AF439020.1	AF439081.1
<i>Cylindera ovipennis</i>	<i>Apterodela ovipennis</i>	KC963685.1	KC963555.1	N/A
<i>Cylindera praecisa</i>	<i>Brasiella praecisa</i>	AF438950.2	AF438901.1	AF438926.1
<i>Cylindera terricola</i>	<i>Parvindela terricola</i>	DQ923335.1	AF439017.1	AF438923.1
<i>Cylindera unipunctata</i>	<i>Apterodela unipunctata</i>	AF438949.1	AF438900.1	AF438925.1
<i>Cylindera viridisticta</i>	<i>Brasiella viridisticta</i>	AF439148.1	AF439018.1	AF439079.1
<i>Dromochorus belfragei</i>		AF133019.1	AF133003.1	AF133035.1
<i>Ellipsoptera blanda</i>		AF133010.1	AF132994.1	AF133026.1
<i>Ellipsoptera cuprascens</i>		AF133014.1	AF132998.1	AF133030.1
<i>Ellipsoptera gratiosa</i>		AF133008.1	AF132992.1	AF133024.1
<i>Ellipsoptera hamata</i>		AF133004.1	AF132988.1	AF133020.1
<i>Ellipsoptera hirtilabris</i>		AF133011.1	AF132995.1	AF133027.1
<i>Ellipsoptera lepida</i>		AF133007.1	AF132991.1	AF133023.1
<i>Ellipsoptera macra</i>		AF133015.1	AF132999.1	AF133031.1
<i>Ellipsoptera marginata</i>		AF133005.1	AF132989.1	AF133021.1
<i>Ellipsoptera marutha</i>		AF133016.1	AF133000.1	AF133032.1

Previous name	New name	CytB	16S	COX3
<i>Ellipsoptera nevadica</i>		AF133006.1	AF132990.1	AF133022.1
<i>Ellipsoptera puritana</i>		AF133013.1	AF132997.1	AF133029.1
<i>Ellipsoptera sperata</i>		AF133012.1	AF132998.1	AF133028.1
<i>Ellipsoptera waplery</i>		AF133009.1	AF132993.1	AF133025.1