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Preliminary phylogenomic analyses reveal multiple reversions to nocturnal behavior and morphology within the primarily diurnal tribe Adesmiini (Coleoptera: Tenebrionidae)

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The darkling beetle tribe Adesmiini (Tenebrionidae: Pimeliinae) is a prominent part of African and western Palearctic desert faunas, with most species being day-active fast-running detritivores. Taxonomic diversity within the tribe is highest in the southern Afrotropical realm (where all genera are present); only 1 genus, the species-rich *Adesmia*, occurs north of the Sahara. Despite notable species, such as the fog-basking beetle *Onymacris unguicularis* (a focal taxon in desert ecological research), Adesmiini has undergone few modern taxonomic or phylogenetic studies. Hence, generic concepts and pronounced diurnal activity, rare in the primarily nocturnal family Tenebrionidae, remain poorly explored. To investigate evolutionary relationships and diurnal origins within the tribe, we generated a genomic dataset of 529 protein-coding genes across 43 species spanning 10 of 11 Adesmiini genera. Our resulting phylogeny for the tribe rejects the monophyly of 5 currently recognized Adesmiini genera (i.e., *Adesmia*, *Metriopus*, *Onymacris*, *Physadesmia*, and *Stenocara*). Ancestral state reconstruction of diurnal activity using eye shape as a proxy supports the hypothesis that Adesmiini were primitively diurnal, followed by at least 4 shifts to nocturnal or crepuscular activity.

Key words: phylogeny, darkling beetle, Pimeliinae, Africa, diurnal activity

Darkling beetles (Coleoptera: Tenebrionidae) are well-known for their ability to thrive in dry, desert environments (Koch 1962, Kamiński and Raś 2012, Wang et al. 2014, Kamiński 2016, Bouchard et al. 2021, Cheli et al. 2022, Johnston et al. 2022, Pinto et al. 2022, Purchart et al. 2022, Silvestro et al. 2022, Ragionieri et al. 2023). To adjust to these harsh environments, the group employs a wide variety of adaptive techniques, such as fog-basking, excretion of waxy pruinescence, modifications to respiratory activity, the longevity of imaginal forms, burrowing behaviors, and parental care (Schulze 1975, Hamilton and Seely 1976, Nicolson 1980, Nicolson 1990, Rasa 1990, Rasa and Endrödy-Younga 1997, Iwan 2000, Duncan 2021, Raś et al. 2022). In this context, the most common strategy in Tenebrionidae involves a shift to nocturnal or crepuscular activity to avoid overheating or predation (Cloudsley-Thompson 1963, Wharton 1980, Maeno et al. 2014). Contrastingly, diurnal behavior of xerophilous darkling beetles has been reported for some lineages, such as Adesmiini Lacordaire, 1859, Trachynotina Koch, 1955 (of Sepidiini Eschscholtz, 1829), and Zophosini Solier, 1834 — all representatives of Pimeliinae. When compared to their nocturnal "contribers", these groups share many adaptations (Koch 1955, Penrith 1979, 1984), e.g., modified eyes, elongated legs, white coloration of elytra, and expression patterns in heat shock proteins. However, the scarcity of phylogenetic data on the whole subfamily Pimeliinae, including the above-mentioned tribes, inhibits detailed evolutionary studies on shifts from nocturnal to diurnal activity among darkling beetles.

In the context of global studies on arid adaptations, Adesmiini is probably the most widely recognized group of darkling beetles (e.g., Holm and Edney 1973, Hamilton and Seely 1976, Penrith 1986, Lamb and Bond 2013, Mitchell et al. 2020). The species of this tribe inhabit the arid and semi-arid regions of Africa and the Palearctic (Koch 1944). However, only the genus *Adesmia* Fischer, 1822 occurs outside sub-Saharan Africa (Iwan et al. 2020). Fog-basking behavior is the most iconic and intensively investigated adaptation of adesmiine beetles and has been reported for 2 species of *Onymacris* Allard 1885 (Holm and Edney 1973, Hamilton and Seely 1976, Hauffe et al. 1988, Nørgaard and Dacke 2010, Lamb and Bond 2013, Mitchell et al. 2020). Another characteristic of Adesmiini which has received attention from previous authors is the seemingly high specificity in substrate selection within some diurnal, xerophilous members (Penrith 1979, 1986, Lamb and Bond 2013). Despite interest in adesmiine ecology and behavior, the tribe's generic classification has been poorly resolved within a phylogenetic context (Penrith 1986, Lamb and Bond 2013) inhibiting more detailed evolutionary studies.

The main aim of this paper is to provide a robust phylogenetic framework and a diverse molecular database for Adesmiini by using hybrid capture-based next-generation sequencing. In the long-term perspective, this data is meant to stimulate research revolving around this iconic group of darkling beetles, while in the present paper is used to test the relevance of the current classification and set directions for future analyses. Additionally, a preliminary investigation of the origins of diurnality among the tribe was conducted.

Taxonomic History and Phylogeny

The tribe Adesmiini was originally described by Lacordaire (1859) for *Adesmia*, *Stenocara* Solier, 1835, and *Metriopus* Solier, 1835. The genera *Alogenius* Gebien, 1910, *Epiphysa* Blanchard, 1845, *Eustolopus* Gebien, 1938, *Onymacris*, and *Stenodesia* Reitter, 1916 were subsequently added by various authors over the next ~100 years. In 2 papers, Koch (1944, 1948) described 55 African species across 10 genera and erected *Renatiella* Koch, 1944 based on 3 species previously classified in *Adesmia*. The last major changes to tribal taxonomy were made when Penrith (1979, 1984, 1986) produced a series of publications focused on the southwestern African fauna.

Penrith's works involved critical examinations of morphology within the tribe, including the first reconstruction of relations among genera, as well as a review of habitat information and biogeography. Within Penrith's (1979) revision of the tribe, she moved subgenus *Orientacara* Koch, 1952 from *Stenodesia* to *Metriopus*. The genera *Ceradesmia* Gebien, 1920, and *Coeladesmia* Reitter, 1916, 2 *Stenodesia* species, and 1 *Stenocara* species were merged with *Metriopus*, the first 2 forming new subgenera. In 1986, Penrith elevated *Orientacara* from a subgenus in *Metriopus* to its own monotypic genus. She also reinterpreted the genera *Cauricara* Penrith, 1979, and *Arenacara* Penrith, 1979 as subgenera of the widely distributed genus *Stenocara*. *Physosterna* Solier, 1837 was reduced to a subgenus of *Adesmia*, making it the fourth *Adesmia* subgenus in southern Africa. Overall, Penrith (1979, 1986) recognized 88 species (107 subspecies) within 11 genera from sub-Saharan Africa, which are still considered valid today.

Penrith's (1986) cladistic analysis of generic relationships within Adesmiini is the most comprehensive phylogenetic treatment of the tribe prior to this paper and was based on 19 synapomorphic and apomorphic characters coded by genus. However, morphological traits were treated as catch-alls for genera despite species morphology discrepancies, and monophyly of some genera was assumed *a priori*. The presumption of generic monophyly is especially important for the present interpretation as the tribe's composition has changed over time and several genera (*Adesmia*, *Alogenius*, *Metriopus*, and *Stenocara*) have been further divided into subgenera. Furthermore, characteristics associated with diurnal activity, particularly eye shape, are potential sources of autocorrelated characters and features linked to convergent evolution that could significantly influence resulting phylogenies. Lastly, despite her extensive work on southern African adesmiines, Penrith did not examine the Palearctic or north-central African members of the genus *Adesmia*, a group that includes 121 species and subspecies and 8 subgenera not found in southern Africa (Iwan et al. 2020). Nevertheless, Penrith's (1986) study of generic relationships was ahead of its time and provided the framework for further research. Her analysis supported *Alogenius* and *Epiphysa* as the earliest diverging lineages within Adesmiini, with *Onymacris*, *Eustolopus*, and *Physadesmia* forming a clade sister to the remaining genera. The remaining genera formed a stepwise grouping of *Renatiella* + (*Adesmia* + (*Stenocara* + (*Metriopus* + (*Orientacara* + *Stenodesia*)))). Based on her results and the geographic distribution of genera, Penrith (1979) hypothesized that the center of origin for Adesmiini was in the western area of southern Africa.

Other phylogenetic contributions on Adesmiini have primarily focused on *Onymacris*. Penrith (1984) used 23 autapomorphic and synapomorphic traits to determine species relationships within the genus. *Onymacris* species with white versus black elytral coloration were separated into 2 clades, with the exception of the black species *O. unguicularis* Haag, 1875 being sister to the white *Onymacris* clade. *Onymacris* was a monophyletic genus closely related to *Eustolopus* and *Physadesmia*, in that order. Penrith also stated that *Onymacris* shares both enlarged and unequal tarsal claws and elongated tibial spurs with *Eustolopus*. Neither characteristic occurs in other adesmiine genera, hence Penrith (1979) had already hypothesized that they were closely related. Lamb and Bond (2013) later reconstructed a molecular phylogeny for *Onymacris* and compared it to Penrith's cladogram. Lamb and Bond used 6 genetic loci, 3 mitochondrial and 3 nuclear, to determine the relationships of 12 of the 14 *Onymacris* species, 2 *Physadesmia* species, and 1 representative each of *Eustolopus*, *Renatiella*, *Physosterna*, *Stenocara*, and *Epiphysa*. The Adelostomini genus *Stips* Koch, 1950 was used to root the phylogeny. They determined that although white and black *Onymacris* lineages are monophyletic, the genus itself is not (Lamb and Bond 2013). Both results contradict Penrith (1986). In the phylogeny of Lamb and Bond (2013), *Physadesmia* was sister to the white *Onymacris* clade, with *Eustolopus* sister to *Onymacris* and *Physadesmia globosa* Haag-Rutenberg, 1875. This follows Penrith's (1986) predictions of the 3 genera being closely related, based on her observation that all 3 genera are composed of psammophilous, long-legged, cursorial (running) species (Penrith 1979, 1986).

Palearctic Adesmiini constitutes the most neglected component of the tribe from a phylogenetic perspective. Despite being represented by a single genus *Adesmia*, this lineage holds a substantial portion of the species diversity of adesmiine beetles (Iwan et al. 2020). In the only phylogenetic analysis of the group, Mas-Peinado et al. (2015) analyzed haplotypes of *Adesmia (Macradesmia) cancellata* Solier, 1835 to determine species polymorphism and diversification. Their study also provided some insights into *Adesmia* and concluded the genus is paraphyletic since the northern African taxa group with southern African *Onymacris* species. Regardless, there has been no large-scale study of Palearctic Adesmiini taxonomy.

Discrepancies exist regarding the sister tribe of Adesmiini. Originally, Tentyriini Eschscholtz, 1831 was thought to be the most closely related taxon based on an enlarged mentum shared by both tribes (Penrith 1986). However, the tribes Erodiini Billberg, 1820, Asidini Fleming, 1821, Adelostomini Solier, 1834, and Zophosini Solier, 1834 share this character as well. Penrith (1986) considered Tentyriini as the sister tribe to Adesmiini based on the presence of a mandibular process in the adesmiine genera *Alogenius* and *Epiphysa* and some Tentyriini species. *Alogenius* and *Epiphysa* are also nocturnal, as are most Tentyriini. Based on their nocturnal behavior (unlike most Adesmiini taxa) and the presence of a mandibular process, Penrith (1986) hypothesized that *Alogenius* and *Epiphysa* were basal lineages within Adesmiini and supported the tribe's close relationship to Tentyriini.

More recently, the primarily diurnal tribe Zophosini was proposed as the sister tribe to Adesmiini and Adelostomini based on a combined phylogenetic analysis of morphological and molecular data (Steckel et al. 2010). However, this study only included Zophosini, Adelostomini, and Adesmiini representatives, with *Pimelia* Fabricius, 1775 as the outgroup. To their credit, Steckel et al.'s (2010) main goal was to explore relationships within Zophosini and test the monophyly of the monogeneric tribe; tribal relationships of the other Namib darkling beetles were only mentioned briefly. Additionally, an in-depth morphological analysis of female terminalia further supports the close relationship between Zophosini and Adesmiini (Kamiński et al. 2022a). Both tribes share the following key features of the ovipositor: coxite plate c4 is inwardly rotated and ventrally bent, and coxite plate c2 is membranous and folded under the coxite plate c1. The relationship between Zophosini and Adesmiini remains to be tested with additional data.

Even with decades of interest surrounding this Afrotropical and Palearctic tribe, this paper is the first study to use modern phylogenetic methods to assess relationships within and across nearly all adesmiine genera, and thus help inform Adesmiini systematics and evolution, particularly in regard to diurnal activity within the tribe. Understanding the evolutionary history of adesmiines is important as they are a subject of research interest for many researchers outside of systematics, (ex. ecologists and engineers working on biomimicry, see Bhushan 2020, Wan et al. 2021) and current genera may be established from characters heavily influenced by species ecology (ex. longer legs and larger eyes associated with diurnal life histories). In this study, 529 low-copy nuclear protein-coding loci were analyzed from 10 of the 11 Adesmiini genera (41 species), excluding the monotypic genus *Orientacara*, to reconstruct evolutionary relationships and explore the evolution of diurnal activity patterns within the tribe.

Methods

Specimens used in this study were collected by the authors in Namibia or South Africa (permits in acknowledgments) or contributed by collaborators. Identifications were made using publications of Penrith (1979, 1986), Koch (1944), or Reitter (1916) and comparisons to identified material, primarily in the Ditsong Museum of Natural History (Pretoria, South Africa). Voucher specimens from DNA extractions are preserved in the Purdue Entomological Research Collection with unique identifiers (TB#s) tied to sequence data in the Sequence Read Archive (NCBI-SRA). Photographs of selected specimens were taken using a Canon 1000D body with extension rings and a Canon Macro Lens EF 100 mm. Scanning microscope (SEM) images were obtained with a Hitachi S-3400N system in the Museum and Institute of Zoology, PAS (Warsaw, Poland). Resulting shots were subsequently colored in Adobe Photoshop (ver. 21.0.1).

DNA extractions were performed on 43 adesmiine and 11 outgroup specimens by disarticulating the head from the body and, in most cases, coxa from the thorax for soft tissue digestion. Large specimens (>15mm) also had their thoracic cavity scraped for additional muscle tissue. Tissue digestion and DNA extraction were conducted using QIAGEN DNEasy Blood and Tissue kits. An Invitrogen Qubit dsDNA assay was used to determine the DNA concentration in extractions and those with a DNA mass of over 1,000 ng were applicable for sequencing. Adesmiine samples, except for *Stenocara gracilis* Solier, 1835 and the outgroup taxa, were then sent to Daicel Arbor Biosciences for library preparation, targeted enrichment using custom MyBaits probes designed to capture 631 genetic loci from Pimeliinae (Kanda 2017), and DNA sequencing on a NovaSeq 6000 system for 150 bp paired end runs. Library preparation and targeted enrichment were done inhouse for *Stenocara gracilis* and some outgroup species using NEBNext Ultra DNA Library Prep Kits for Illumina and the same MyBaits custom probe kit was used to capture 631 loci. Inhouse libraries were sequenced at the University of Arizona's Genomic and Technology Core Facility (UAGC) on an Illumina NextSeq 550 using 150 bp paired end runs.

Read quality was assessed using FastQC v.0.11.9 (Andrews 2010). Reads with an average sequence quality across any 4 bases below 20, using the sliding window approach, were removed from further analyses with Trimmomatic (Bolger et al. 2014), reads were mapped in BWA and assembled in SPAdes v.3.15.2 (Prjibelski et al. 2020) within the HybPiper v.1.3.1 (Johnson et al. 2016) bioinformatic pipeline using the bait probe markers for ortholog annotation. The pipeline was dependent on Biopython (Cock et al. 2009). Loci nucleotide sequences were translated to amino acids and then aligned using MAFFT with the L-INS-I algorithm (Katoh et al. 2005). The nucleotide sequences were mapped back to the aligned peptide sequences resulting in aligned nucleotide and amino acid sequences for each locus. Low-quality amino acid sequence sites were masked and sequences with over 50% gaps per locus were trimmed out using trimAl (Capella-Gutiérrez et al. 2009). Amino acid sequences had both low yield sites and taxa trimmed for each locus using trimAl with the same parameters as the nucleotide sequences. Sequences were then concatenated by taxon using FASConCAT(Kück and Meusemann 2010) into 1 partitioned dataset. Low yielding loci (those with under 8 taxa in the concatenated dataset) were manually discarded. After the trimming and discarding steps, a dataset of 529 loci spanning 159,740 amino acids for 43 Adesmiini OTUs (operational taxonomic units, specimens in this case), spanning 10 of the 11 adesmiine genera and 39 species (Supplementary Table 1), and 11 outgroup species from the tribes Erodiini, Tentyriini, and Zophosiini were analyzed. Included in the dataset are type species from 6 of the 10 genera (*Epiphysa flavicollis* Fabricius, 1794, *Alogenius favosus* Erichson, 1843, *Renatiella reticulata* Gerstaecker, 1854, *Stenocara longipes* Olivier, 1795, *Metriopus hoffmannseggi* Solier, 1835, and *Stenodesia globulum* Haag, 1875) (Penrith, 1979). The taxa are mainly from southern Africa, but 2 Palearctic *Adesmia* representatives from Iran were also included, i.e., *Adesmia cancellata* Solier, 1835 and *Adesmia montana* Klug, 1830.

ModelFinder (Kalyaanamoorthy et al. 2017), as implemented in IQ-TREE 2 (Minh et al. 2020) was used to infer optimal substitution models for the dataset partitioned by locus. IQ-TREE 2 was then used to run maximum likelihood analyses using an edge-proportional partition model (-spp), with the dataset partitioned by loci and the models for each locus applied from ModelFinder. Support for the resulting topology was assessed using 10,000 UltraFast Bootstrap (Hoang et al. 2018) iterations. IQ-TREE 2 was also used to infer 529 gene trees and reassess model selection for

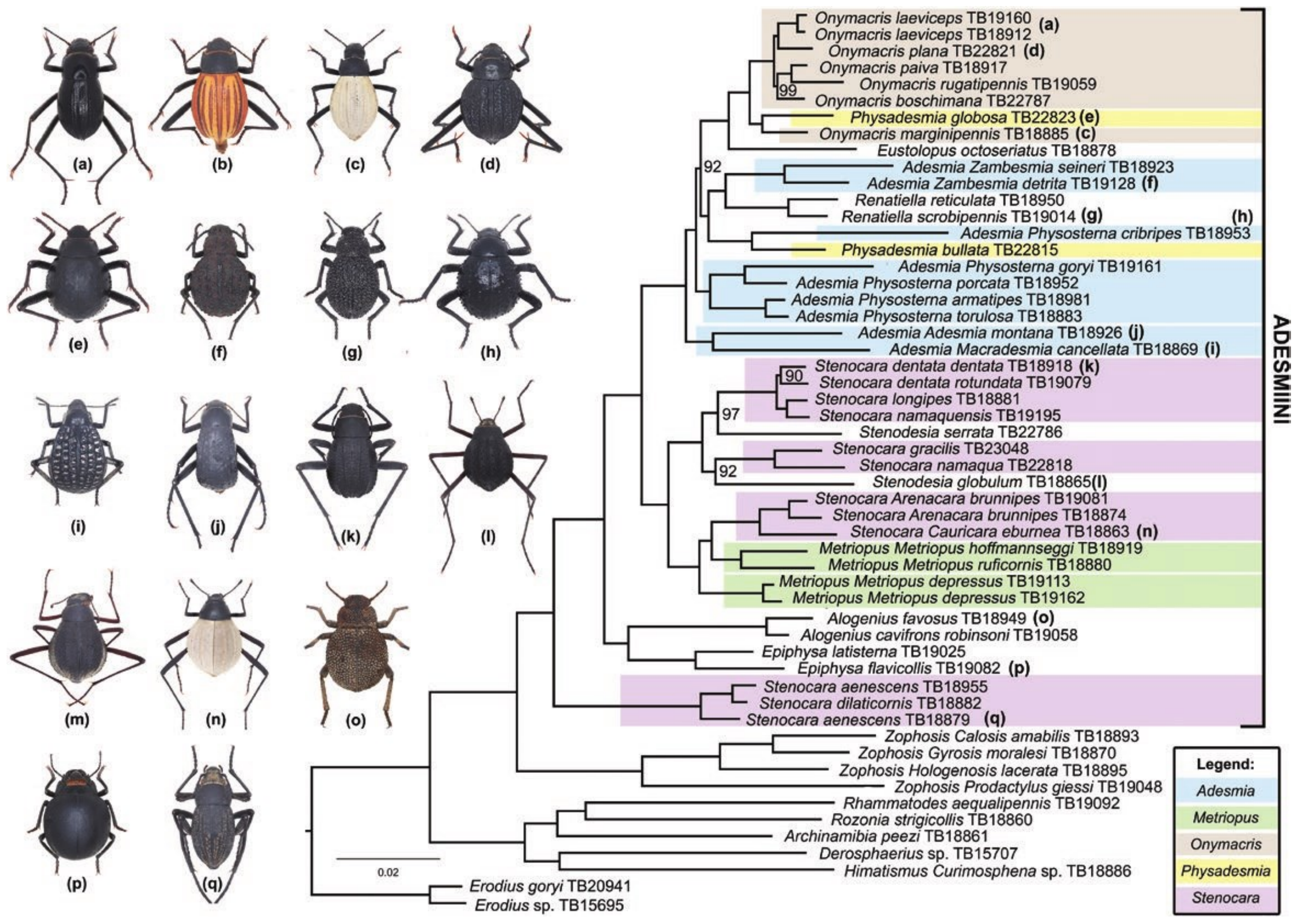

Fig. 1. Phylogeny of Adesmiini. Topology obtained in analysis of 529 amino acid loci. Statistical support when not specified equals 1.0 (posterior probability) or 100 (bootstrap). Paraphyletic genera are colored. Representatives of Adesmiini: *Onymacris laeviceps* (a), *Onymacris langi* (b), *Onymacris marginipennis* (c), *Onymacris plana* (d), *Physadesmia globosa* (e), *Adesmia detrita* (f), *Renatiella scrobipennis* (g), *Adesmia cribripes* (h), *Adesmia cancellata* (i), *Adesmia montana* (j), *Stenocara dentata* (k), *Stenodesia globulum* (l), *Stenocara phalangium* (m), *Stenocara eburnea* (n), *Alogenius favosus* (o), *Epiphysa flavicollis* (p), *Stenocara aenescens* (q).

each. All sequence assembly and IQ-TREE 2 analyses were performed on Purdue University's community cluster, Bell, within ITaP Research Computing (McCartney et al. 2014). The dataset, with the same partitions, was also analyzed using ExaBayes 1.5.1 (Aberer et al. 2014) run through the CIPRES portal (Miller et al. 2010). Two independent runs of 2 million generations, each with 1 cold chain and 2 heated chains, were performed with burn-in of 0.25 and the FLU prior for each partition and amino-acid exchange rate matrices based on empirical values. The standard deviation of split frequencies (<0.00%) between runs was compared post burn-in, and ESS values (>200) were examined in Tracer v1.7.2 (Rambaut et al. 2018)

Species activity patterns, diurnal versus nocturnal/crepuscular, were based on literature records and collecting events by the authors (Supplementary Table 1). Activity pattern evolution was reconstructed as a discrete trait (diurnal or nocturnal/crepuscular) using the likelihood ancestral state reconstruction method (Maddison and Maddison 2006) in Mesquite (Maddison and Maddison 2021). In addition, the ancestral state was reconstructed with Phytools using 200 stochastic character maps (Revell 2012). Crepuscular taxa were included in the nocturnal group in order to delimit them from the extremely thermophilic species (diurnal group) that are active during the warmest times of the day.

Phylogenies were rooted with Erodiini based on their placement as relatively distant from Adesmiini based on relationships between tribes within more taxon-rich tenebrionid datasets (Kergoat et al. 2014, Smith et al. unpublished). The resulting topologies from concatenated and coalescent analyses were edited in Adobe Photoshop 2020, with taxa and branches colored by genus.

Results

A single topology was recovered from the partitioned ExaBayes and IQ-TREE 2 ML analyses, which uncovered multiple clades that do not conform to the current generic classification of Adesmiini (Fig. 1). The genera *Renatiella*, *Alogenius*, and *Epiphysa* (each represented by 2 species in this study) were recovered as monophyletic. The monophyly of *Eustolopus*, a genus with only 2 species, could not be definitively determined as only *Eustolopus octoseriatus* was included in analyses. The remaining 6 genera included in this study were not recovered as monophyletic.

Eustolopus was recovered as a sister to a clade containing all *Onymacris* taxa in the analyses and *Physadesmia globosa*. *Physadesmia globosa* was recovered within the *Onymacris* clade, thus rendering *Onymacris* paraphyletic. The genus *Adesmia* was recovered as polyphyletic with respect to *Renatiella*, *Physadesmia*, and the *Eustolopus* + (*Physadesmia* + *Onymacris*) clade. The subgenus *Physosterna* was not recovered as monophyletic, with *A.* (*Physosterna*) *cribripes* sister to *Physadesmia bullata* and these

2 taxa were not sister to the rest of the *A*. (*Physosterna*) taxa included in the dataset. The 2 included *Adesmia* (*Zambesmia*) species were placed as sisters to the 2 included *Renatiella* species. The Palearctic *Adesmia* representatives, *A*. (*Macradesmia*) *cancellata* and *A*. (*Macropoda*) *montana*, grouped together and were sisters to the clade containing *Onymacris*, *Physadesmia*, *Eustolopus*, and the African *Adesmia* subgenera.

Stenocara was recovered as polyphyletic with 4 separate clades. The first one, including the type species for the genus (*Stenocara longipes*), was recovered sister to *Stenodesia serrata*. This grouping was projected sister to the second *Stenocara* clade containing *Stenocara namaqua* and *S. gracilis* sister to *Stenodesia globulum*. The third was recovered within a clade containing all sampled *Metriopus* species, thus rendering *Metriopus* paraphyletic. While *Epiphysa* and *Alogenius* were recovered as sister genera, they were not placed as the basal lineage of Adesmiini with respect to the outgroup taxa. Instead, the last *Stenocara* clade was recovered as a clade sister to the rest of the tribe. From the sampled outgroups, the tribe Zophosini was strongly supported as the sister tribe to Adesmiini.

The ancestral state reconstruction analysis for activity patterns indicated that the most recent common ancestor of Adesmiini was most probably diurnal (posterior probability = 65.30%). Within the phylogeny, *Adesmia* (*Physosterna*) *armatipes* + *torulosa*, *Renatiella* + *Adesmia* (*Zambesmia*), *Adesmia* (*Physosterna*) *cribripes*, and *Alogenius* + *Epiphysa* constitute 4 independent lineages with shifts to nocturnal or crepuscular activity patterns and morphologies (Fig. 2). The clades consisting of *Onymacris*, *Physadesmia globosa*, *Eustolopus*, *Stenocara*, *Stenodesia*, and *Metriopus* contain species that are most active during the warmest times of the day. Details on ancestral states for particular nodes are presented in Fig. 2. A morphological overview of the representatives of nocturnal clades revealed previously unreported traits indicating independent transitions of some lineages from diurnal activity. Namely, the narrowing of the eyes within the *Alogenius* + *Epiphysa* clade is established by the extension of the temples, while in the other clades the eyes are noticeably shifted by the expanding canthi (Fig. 2).

Discussion

Penrith's (1986) revisionary work on the southern African Adesmiini was thorough and remains useful, but her cladistic analysis was based on limited external morphological characters and does not reflect the phylogenetic relations accurately. We have demonstrated that the genera *Adesmia*, *Metriopus*, *Onymacris*, *Physadesmia*, and *Stenocara* are either para- or polyphyletic (Fig. 1), highlighting the need for generic-level revision of Adesmiini to align their taxonomy with recovered evolutionary history.

In terms of generic relationships, we confirm that *Physadesmia globosa* is integrated within *Onymacris*, with *Eustolopus* sister to this clade, as stated by Lamb and Bond (2013). Therefore, the assumption from Penrith (1986) and Lamb and Bond (2013) that the 3 genera, *Onymacris*, *Physadesmia*, and *Eustolopus* are more closely related to each other than to other adesmiine taxa is supported by this phylogeny (Fig. 1). However, *Physadesmia* is shown to be paraphyletic, with *Physadesmia bullata* sister to *Adesmia cribripes*; therefore, the genus still needs revision.

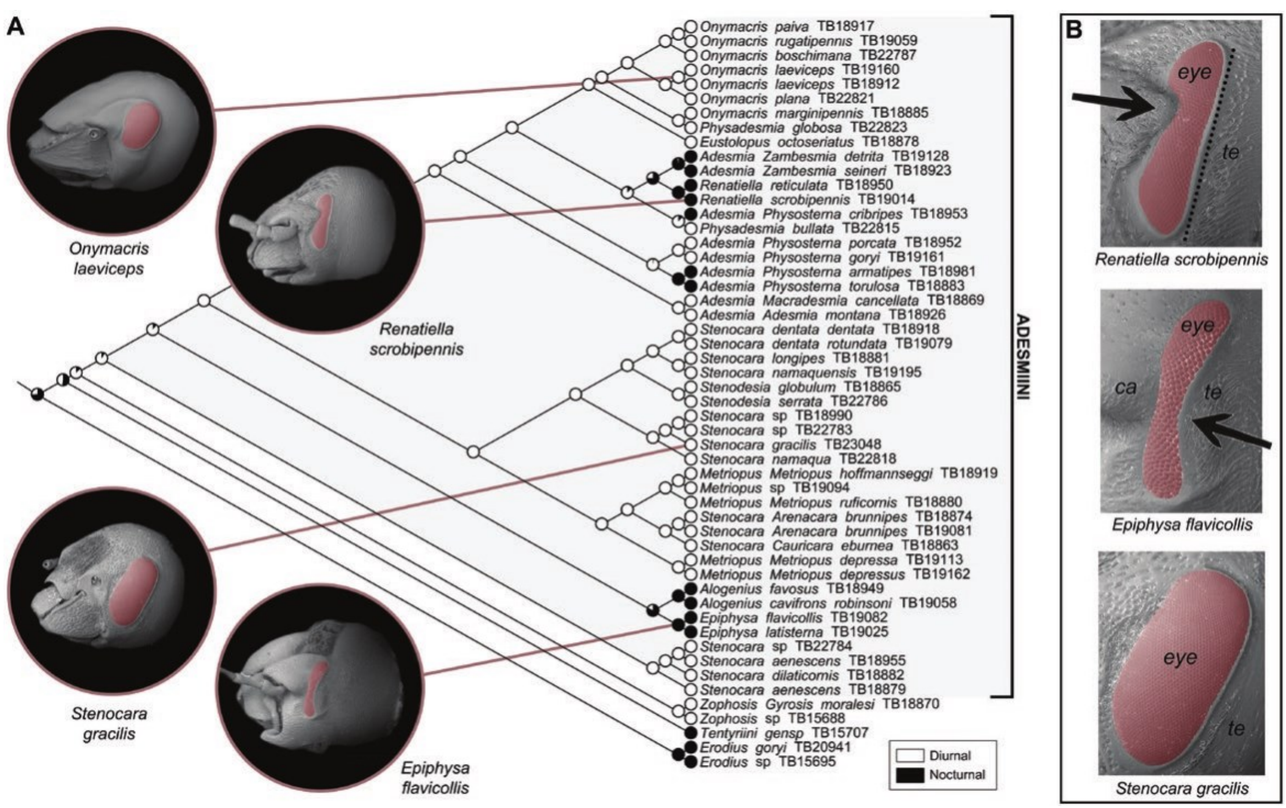

Fig. 2. The evolutionary history of diel activity patterns of Adesmiini darkling beetles. Pie charts at nodes denote posterior probabilities for each of the strategies (diurnal or nocturnal). Crepuscular taxa were included in the nocturnal group in order to separate them from thermophilic species (diurnal group) that are active during the warmest times of the day. Differences in eye morphology between diurnal and nocturnal clades have been illustrated by SEM images. Abbreviations: ca – canthus, te – temple.

Alogenius and *Epiphysa*, as the 2 adesmiine genera with mandibular processes, were confirmed to be sister taxa. However, they were not rendered as the most basal genera of Adesmiini counter to Penrith's hypothesis (1986). Instead, a *Stenocara* clade was recovered as sister to the rest of the Adesmiini, followed by a clade containing the above mentioned *Epiphysa* and *Alogenius*, as sister to the rest of the sampled adesmiines (Fig. 1).

Onymacris, *Physadesmia*, and *Eustolopus* were recovered as more recently diverging lineages. This is flipped from the assumptions of Penrith (1986), whose analysis placed *Stenodesia*, *Orientacara*, *Metriopus*, and *Stenocara* as derived members of the tribe, while the psammophilous *Onymacris*, *Physadesmia*, and *Eustolopus*, were considered early diverging (Penrith 1979).

The Palearctic *Adesmia* species, *A. cancellata* and *A. montana*, are deeply nested within the southern African Adesmiini. They are sisters to genera *Onymacris*, *Physadesmia*, *Renatiella*, and other *Adesmia*, confirming Mas-Peinado et al.'s (2015) view that the genus is not monophyletic. Additional taxon sampling focused on Palearctic subgenera and species is necessary to investigate the northern range of Adesmia. Multiple dispersal events could potentially shape the evolutionary history of the groups (see Kamiński et al. 2022b).

The Namib Desert is one of the driest regions on Earth. While subject to extreme variability seasonally, average precipitation in Namib can vary regionally from 5-100 mm, and mainly originates from sparse thunderstorms (Eckardt et al. 2013). These infrequent storms influence an activity pulse-response in adesmiine taxa conditional to the season the storm occurs. Activity increases of uncommon species, such as *Epiphysa arenicola* (Penrith 1979), are greatly influenced by heavy summer rains, and their populations drastically decrease following extremely dry years. Meanwhile, *Stenocara velox* (Péringuey, 1886) and *Stenocara eburnea* (Pascoe, 1866) population irruptions are only triggered by winter rains. However, not all adesmiines are as dependent on seasonal storms, and periods of little precipitation still see thriving Namib tenebrionids. For example, *M. depressus* and *Adesmia cribripes* (Haag-Rutenberg, 1875) are active year-round independent of precipitation (Henschel 2021). Cursorial adesmiines, including *Onymacris*, are more resistant to heat and lower water availability than other desert taxa by maintaining their metabolic rates even in high temperatures. These psammophilic adesmiines produce metabolic water while they are actively running to replace water lost by evaporative cooling, enabling them to be active when other animals, including predators, are forced to seek shelter from the high temperatures (Duncan 2021). Additionally, cursorial fog-basking beetle (*Onymacris unguicularis)* populations remain constant during the dry months by actively collecting the Atlantic fog which rolls over the Namib dunes (Hamilton and Seely 1976).

While it is easier to categorize animals as diurnal or nocturnal taxa, the time of activity is difficult to determine as there is not always strict delimitation between the 2. Species can be dusk and dawn active (crepuscular) or activity can be based on factors such as thermal constraints rather than strict time partitioning (cathemerality). Thermal constraints, such as the harsh environment of the Namib Desert, alter the behavior of its inhabitants when temperatures fall outside of their functional range; either too high during the day or too low during the night (Bennie et al. 2014). For example, *Metriopus depressus* is known to settle beneath rocks when temperatures are not manageable (Duncan 2021). While *Metriopus* was listed as diurnal (Penrith 1979), it may fall into the cathemeral category if environmental factors fall outside of the beetle's tolerance, and physiological costs outweigh the benefits of diurnal activity (Cloudsley-Thompson 1963, Wharton 1980, Bennie et al. 2014, Maeno et al. 2014).

Tenebrionids, prevalent in deserts worldwide, are generally nocturnal or crepuscular (Cloudsley-Thompson et al. 1985); however, shifts in activity time have occurred across the family. Certain tenebrionid tribes contain multiple diurnal species, including Adesmiini, Zophosini (Duncan 2021, Henschel 2021), Sepidiini (e.g., *Somaticus*, Koch, 1953). Behavioral adaptations are selected based on multiple variables including niche competition, diet availability and quality, and avoiding predators. Many putative predators of darkling beetles are ancestrally and commonly nocturnal in Southern Africa due to high temperatures (Bennie et al. 2014). Therefore, there is likely pressure on tenebrionids to avoid predation through diurnal activity (Wharton 1980).

The diurnal adesmiine genera, *Onymacris*, *Stenocara*, *Eustolopus*, *Metriopus*, *Physadesmia*, and *Stenodesia*, retain characteristics that benefit a diurnal lifestyle in the desert (Penrith 1979). Adesmiines which live on dunes are morphologically equipped to run across the hot sands during daylight's higher temperatures. These taxa, such as *Onymacris*, have tibial spurs (Penrith 1979, 1984), which are selected for a psammophilic lifestyle on Namib dunes (Penrith 1984). Additionally, adesmiines have 2 general eye shapes, large-ovoid or narrow (Fig. 2), which appear to relate to their activity time mapped onto the phylogeny here (as those with large eyes are diurnal whereas those with narrow eyes are nocturnal or crepuscular) (Penrith 1979, 1984). Nevertheless, our morphological analysis of eye shape suggests that the distinction between ovoid and narrow eyes is shallow, and that there are likely other phylogenetically informative traits that have been overlooked. For example, *Alogenius* and *Epiphysa* possess eyes laterally emarginate cut by the extension of temples, while other nocturnal taxa are characterized by eyes emarginated by expanding canthi (Fig. 2). Although the eyes are narrowed in both cases, they originate via independent processes and cannot be considered homologous. Similar evolutionary patterns have been observed in other darkling beetle groups (e.g., Iwan and Kamiński 2016, Lumen et al. 2020).

Based on the topology and ancestral state reconstruction, the ancestral state for Adesmiini activity patterns is likely diurnal (Fig. 2). It is worth noting that Zophosini, the sister tribe to Adesmiini, are almost entirely diurnal as well, which helps support this claim. There appears to be at least 3 shifts to nocturnal activity within Adesmiini. One each in the ancestors of the *Adesmia* (*Zambesmia*) and *Renatiella* group, the *A. torulosa* and *A. armitipes* group, and the *Alogenius* and *Epiphysa* group. This is also reflected in these adesmiine groups' morphologies. The taxa listed above follow morphological patterns retained in all crepuscular adesmiines: relatively short legs and small eyes, while the large eyes and long-running legs are reserved for diurnal adesmiines (Penrith 1979). Penrith's (1986) analysis was hindered by the nature of her chosen characters. Many are directly tied to species life history, particularly activity cycles (diurnal versus nocturnal or crepuscular), substrate types (unvegetated sand dunes versus gravel plains or Karroo), and shifts in morphology (e.g., eye size, leg length, tarsal claw length) (Koch 1955). Our ancestral state reconstruction indicates eye size and shape are not conserved with the generic relationships given by Penrith (1986). Therefore, species' life histories are nonoptimal for adesmiine systematic analyses.

Supplementary Material

Supplementary material is available at *Insect Systematics and Diversity* online.

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Author Contributions

Kali Swichtenberg (Data curation-Equal, Formal analysis-Equal, Investigation-Equal, Project administration-Equal, Writing – original draft-Equal, Writing – review & editing-Equal), Marcin Kaminski (Data curation-Equal, Formal analysis-Equal, Investigation-Equal, Resources-Equal, Visualization-Equal, Writing – review & editing-Equal), Olivia Gearner (Investigation-Equal, Software-Equal, Writing – review & editing-Equal), Ryan Lumen (Investigation-Equal, Writing – review & editing-Equal), Kojun Kanda (Methodology-Equal, Software-Equal), Aaron Smith (Conceptualization-Equal, Data curation-Equal, Formal analysis-Equal, Funding acquisition-Equal, Investigation-Equal, Project administration-Equal, Resources-Equal, Supervision-Equal, Visualization-Equal, Writing – original draft-Equal, Writing – review & editing-Equal)

Data Availability

Data from this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9kd51c5p5 (Swichtenberg et al., 2023).

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