

A comprehensive molecular phylogeny of tiger beetles (Coleoptera, Carabidae, Cicindelinae)

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Abstract. Tiger beetles are a remarkable group that captivates amateur entomologists, taxonomists and evolutionary biologists alike. This diverse clade of beetles comprises about 2300 currently described species found across the globe. Despite the charisma and scientific interest of this lineage, remarkably few studies have examined its phylogenetic relationships with large taxon sampling. Prior phylogenetic studies have focused on relationships within cicindeline tribes or genera, and none of the studies have included sufficient taxon sampling to conclusively examine broad species patterns across the entire subfamily. Studies that have attempted to reconstruct higher-level relationships of Cicindelinae have yielded conflicting results. Here, we present the first taxonomically comprehensive molecular phylogeny of Cicindelinae to date, with the goal of creating a framework for future studies focusing on this important insect lineage. We utilized all available published molecular data, generating a final concatenated dataset including 328 cicindeline species, with molecular data sampled from six protein-coding gene fragments and three ribosomal gene fragments. Our maximum-likelihood phylogenetic inferences recover Cicindelinae as sister to the wrinkled bark beetles of the subfamily Rhysodinae. This new phylogenetic hypothesis for Cicindelinae contradicts our current understanding of tiger beetle phylogenetic relationships, with several tribes, subtribes and genera being inferred as paraphyletic. Most notably, the tribe Manticorini is recovered nested within Platychilini including the genera *Amblycheila* Say, *Omus* Eschscholtz, *Picnochile* Motschulsky and *Platychile* Macleay. The tribe Megacephalini is recovered as paraphyletic due to the placement of the monophyletic subtribe Oxycheilina as sister to Cicindelini, whereas the monophyletic Megacephalina is inferred as sister to Oxycheilina, Cicindelini and Collyridini. The tribe Collyridini is paraphyletic with the subtribes Collyridina and Tricondylina in one clade, and Ctenostomina in a second one. The tribe Cicindelini is recovered as monophyletic although several genera are inferred as para- or polyphyletic. Our results provide a novel phylogenetic framework to revise the classification of tiger beetles and to encourage the generation of focused molecular datasets that will permit investigation of the evolutionary history of this lineage through space and time.

Introduction

Tiger beetles (Coleoptera, Adephaga, Carabidae, Cicindelinae) are some of the most charismatic insects within Coleoptera,

known for using vision and speed to hunt smaller invertebrates. These beetles occupy nearly all terrestrial ecosystems, and are distributed across the globe aside from Antarctica, Greenland, Tasmania and some small oceanic islands (Pearson & Vogler, 2001). The approximately 2300 described species are concentrated in the Oriental region, from India to Indonesia, where roughly half of the diversity is found, as well as in the

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Afrotropics and Neotropics (Cassola & Pearson, 2000) (Fig. 1). Tiger beetles are predominantly found in open ecosystems, but forest floor and arboreal species are common in the tropics (Vogler & Pearson, 1996; Pearson & Vogler, 2001). Although generally regarded as diurnal, some species are strictly nocturnal, and many are cathemeral (Pearson, 1988). Tiger beetles are united by several morphological synapomorphies which include an expanded labrum that extends laterally beyond the dorsomedial antennal insertions, long curved mandibles possessing multiple teeth, and a lack of longitudinal striations or umbilicated series on the elytra (Cassola, 2001). The eruciform larvae dig burrows in which they hide and ambush prey. Many species are metallic and colourful, and some can be large, reaching nearly 5 cm in body length (e.g. *Manticora* Fabricius) (Mareš, 2002).

The systematics of tiger beetles have been studied extensively using both morphological and molecular characters. Horn (1915) used external morphology to classify tiger beetles as a subfamily of Carabidae and further divided tiger beetles into the platysternal (tribes Manticorini, Megacephalini and Cicindelini) and the alocosternal (Collyridini). Rivalier (1950, 1954, 1957, 1961, 1963, 1969, 1970, 1971) revised the group based on genitalic characters, erecting 50 subgenera within the genus *Cicindela* Linné and dividing Cicindelinae into four tribes (Cicindelini, Collyridini, Megacephalini and Manticorini). Since the advent of molecular phylogenies, Horn's platysternal and alocosternal groupings have been largely abandoned, and tiger beetles have been further split into five, six or even seven tribes (Vogler & Pearson, 1996; Galián *et al.*, 2002; López-López & Vogler, 2017). Below, we give a summary of the most recent classification within tiger beetles (Fig. 2). For this study, we relied upon the classification established by Wiesner (1992) at the generic and species levels. This is the most recent checklist of worldwide tiger beetles to date. However, we also take into consideration the wealth of more recent morphological and molecular studies that have developed Wiesner's classification, or shed light on inconsistencies at different taxonomic levels (e.g. Vogler & Pearson, 1996; Galián *et al.*, 2002, 2007; Moravec, 2002, 2007, 2010; Proença *et al.*, 2005; Zerm *et al.*, 2007; Ball *et al.*, 2011).

The tribe Manticorini includes two elusive flightless genera, *Mantica* Kolbe and *Manticora*, endemic to southern Africa (Mareš, 2002; Franzen & Heinz, 2005). Species of these two genera are the largest known tiger beetles and are among the largest ground beetles (Carabidae). The adults are crepuscular and in some cases are active during overcast days or during full moons, only emerging after long periods of drought (Werner & Wiesner, 1995; Oberprieler & Arndt, 2000). They have disproportionately enlarged mandibles used to capture prey and are involved in copulatory behaviour (Oberprieler & Arndt, 2000).

All other giant tiger beetle genera were initially placed within the tribe Megacephalini (in the subtribes Omini and Platychilina), before molecular studies showed that the tribe was not monophyletic (e.g. Galián *et al.*, 2002). As a result, the tribes Amblycheilini, Omini and Platychilini were erected to encompass the giant tiger beetle genera *Amblycheila*, *Omus*, *Picnochile* and *Platychile*. The flightless nocturnal genus *Amblycheila* comprises seven species of giant tiger beetles, the largest in the

western hemisphere, distributed from southwestern U.S.A. to Mexico. The genus *Omus* comprises five nocturnal, flightless species distributed across the Pacific Northwest in the U.S.A. The monotypic genus *Picnochile* only comprises the flightless species *P. fallaciosa* Chevrolat distributed in the southernmost parts of Argentina (Tierra del Fuego) and Chile (Magallanes) (Wiesner & Bandinelli, 2014). Finally, the flightless monotypic genus *Platychile* comprises the unique species *P. pallida* Fabricius, found in southern Africa. A study focused on the mandibles and labrum-epipharynx across tiger beetles tentatively lumped *Amblycheila*, *Omus* and *Picnochile* into the tribe Amblycheilini (Fig. 2). However, this grouping does not reflect the most recent molecular phylogenetic hypothesis including the four genera (Galián *et al.*, 2002), that supports the monophyly of Amblycheilini + *Platychile*. Note that Galián *et al.* (2002) erroneously named this clade Omini in their study. Following the concept of priority, the name of the tribe representing this generic assemblage should be Platychilini (Ball *et al.*, 2011).

The tribe Megacephalini *sensu* Wiesner (1992) is not a natural group (see Galián *et al.*, 2002), but the subtribe Megacephalina is largely accepted as monophyletic (see Zerm *et al.*, 2007). This clade originally comprised the two genera *Aniara* Hope and *Megacephala* Latreille (Wiesner, 1992). However, some subgenera have since been reinstated as valid genera based on morphological revisions (Huber, 1994; Naviaux, 2007). The group currently comprises the genera *Aniara* (monotypic, one species in South America), *Australicapitona* Sumlin (nine species in Australia), *Grammognatha* Motschulsky (monotypic, one species in the Palaearctic region), *Megacephala* (11 species in Africa), *Metriocheila* Thomson (monotypic, one species in South America), *Phaeoxantha* Chaudoir (11 species in South America), *Pseudotetracha* Fleutiaux (19 species in Australia) and *Tetracha* Hope (55 species in North and South America). Megacephalini (>100 species) is a pantropical tribe of beetles which, unlike the tribes described above, are often brightly coloured. The Central and South American genera *Cheiloxya* Guerin-Meneville, *Oxycheila* Dejean and *Pseudoxycheila* Guerin-Meneville, originally placed in Megacephalina, have since been excluded based on their phylogenetic placement and sex chromosome system (Vogler & Pearson, 1996; Galián *et al.*, 2002; Proença *et al.*, 2005). These three genera have not been moved to another taxonomic clade to date, despite their distinctiveness. Species of the genera *Cheiloxya* (two species), *Oxycheila* (47 species) and *Pseudoxycheila* (22 species) are all Neotropical (Wiesner, 1992, 2003; Cassola, 1997; Perger & Guerra, 2012).

The tropical tribe Collyridini comprises three subtribes: Collyridina, Ctenostomina and Tricondylina (Wiesner, 1992; Naviaux, 1994). Tiger beetles in this tribe are arboreal and their larvae create burrows in the branches of trees and other vegetation (Zikan, 1929; Naviaux, 1996). Most adults are diurnal, but some species of *Ctenostoma* Klug are attracted to light traps (Pearson & Vogler, 2001). The subtribe Collyridina comprises the genera *Collyris* Fabricius (ten species), *Neocollyris* Horn (>200 species) and *Protocollyris* Mandl (17 species). Species of these genera are arboreal, with a derived morphology, and are found across the Oriental region from India to the Moluccas

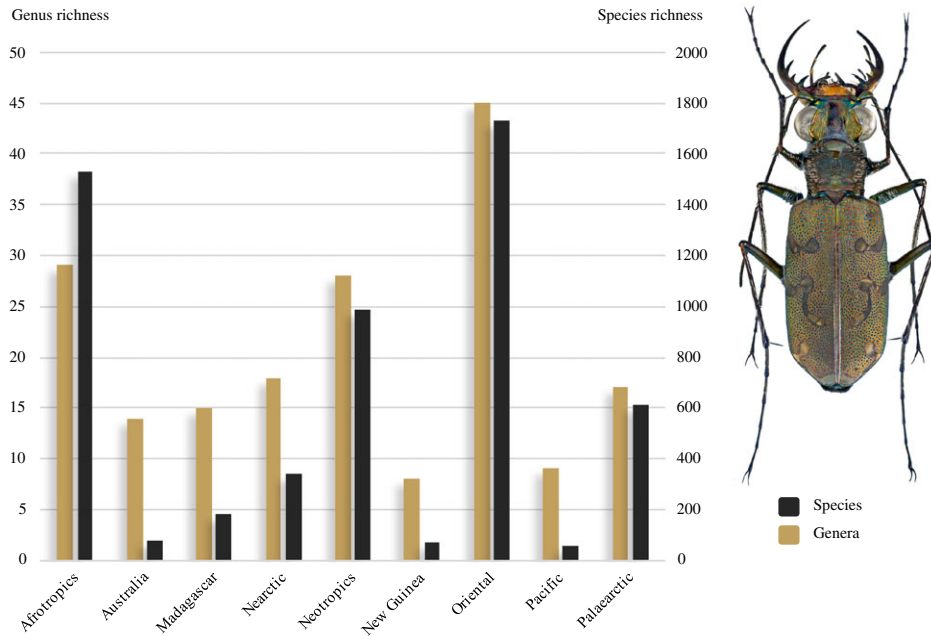


Fig. 1. World distribution of tiger beetle diversity. Approximate repartition of species and genus richness in Cicindelinae across major biogeographical regions and landmasses. The numbers are extrapolated from Pearson & Cassola (1992) and Carabidae of the World (<http://www.carabidae.org>). The reported species and genus richness of each country was summed for each major biogeographical region or landmass and plotted as a histogram. A photograph of *Cylindera mutata* Fleutiaux is presented on the right side (photo credit: Udo Schmidt). [Colour figure can be viewed at wileyonlinelibrary.com].

(Naviaux & Pinratana, 2004). The subtribe Ctenostomina comprises the arboreal genera *Ctenostoma* (>100 species) from Central and South America and *Pogonostoma* Klug (>100 species) endemic to Madagascar (Moravec, 2007). The third subtribe Tricondylina comprises the arboreal genera *Derocrania* Chaudoir (16 species) and *Tricondyla* Latreille (47 species) distributed from Southeast Asia to Australia (Naviaux, 1996, 2002).

Finally, the tribe Cicindelini is divided into the subtribes Cicindelina, Iresina, Prothymina and Theratina (Wiesner, 1992). The bulk of the taxonomic diversity within Cicindelinae is encompassed by Cicindelini, with >1500 species belonging to >80 genera distributed across all continents but Antarctica (Pearson & Vogler, 2001). The generic recognition of multiple clades within this tribe and especially within Cicindelina has been controversial for decades, but a consensus seems to be attainable due to prolonged molecular and morphological efforts (e.g. Wiesner, 1992; Erwin & Pearson, 2008).

Previous phylogenetic studies to determine the relationships between these tribes and subtribes lack consensus around a robust phylogenetic hypothesis. In an attempt to provide an overview of the current classification and nomenclatural inconsistencies between studies, the phylogenetic trees derived from the most comprehensive studies to date are summarized in Fig. 2. In addition to these studies focusing on deeper-level relationships among tiger beetles, others have focused on intra-generic relationships (e.g. Vogler & DeSalle, 1994; Cardoso & Vogler, 2005; Pons *et al.*, 2006; Pons *et al.*, 2011; Sota *et al.*, 2011; López-López *et al.*, 2016) or generic relationships

within tribes (Barraclough & Vogler, 2002; Pons *et al.*, 2004; Zerm *et al.*, 2007; Tsuji *et al.*, 2016). There is therefore a wealth of molecular data that has been generated over the past two decades, but assembling these data into a broad-scale phylogenetic tree of tiger beetles has not been attempted to date. An updated phylogeny of the group is critical to understanding biogeographical, ecological (e.g. nocturnal/diurnal, terrestrial/arboreal), genetic (Vogler & Pearson, 1996; Galián *et al.*, 2002; Proença *et al.*, 2005; Galián *et al.*, 2007) as well as morphological evolution in Cicindelinae. Here we present the most complete phylogeny of Cicindelinae to date using all available published data in a concatenated matrix of nine molecular markers.

Materials and methods

Supermatrix approach

We used a supermatrix approach in order to leverage the large amount of molecular data publicly available for tiger beetles. Inherent to this approach is uneven gene coverage which results in large amounts of missing data in the final matrix. Although studies have demonstrated adverse effects of missing data on phylogenetic reconstruction (Sanderson *et al.*, 2010; Dell'Ampio *et al.*, 2014), other studies have argued that these issues are dataset-specific and can be overcome (Gatesy *et al.*, 2004; de Queiroz & Gatesy, 2007; Winterton *et al.*, 2016; Beaulieu & O'Meara, 2018). Although it has some drawbacks,

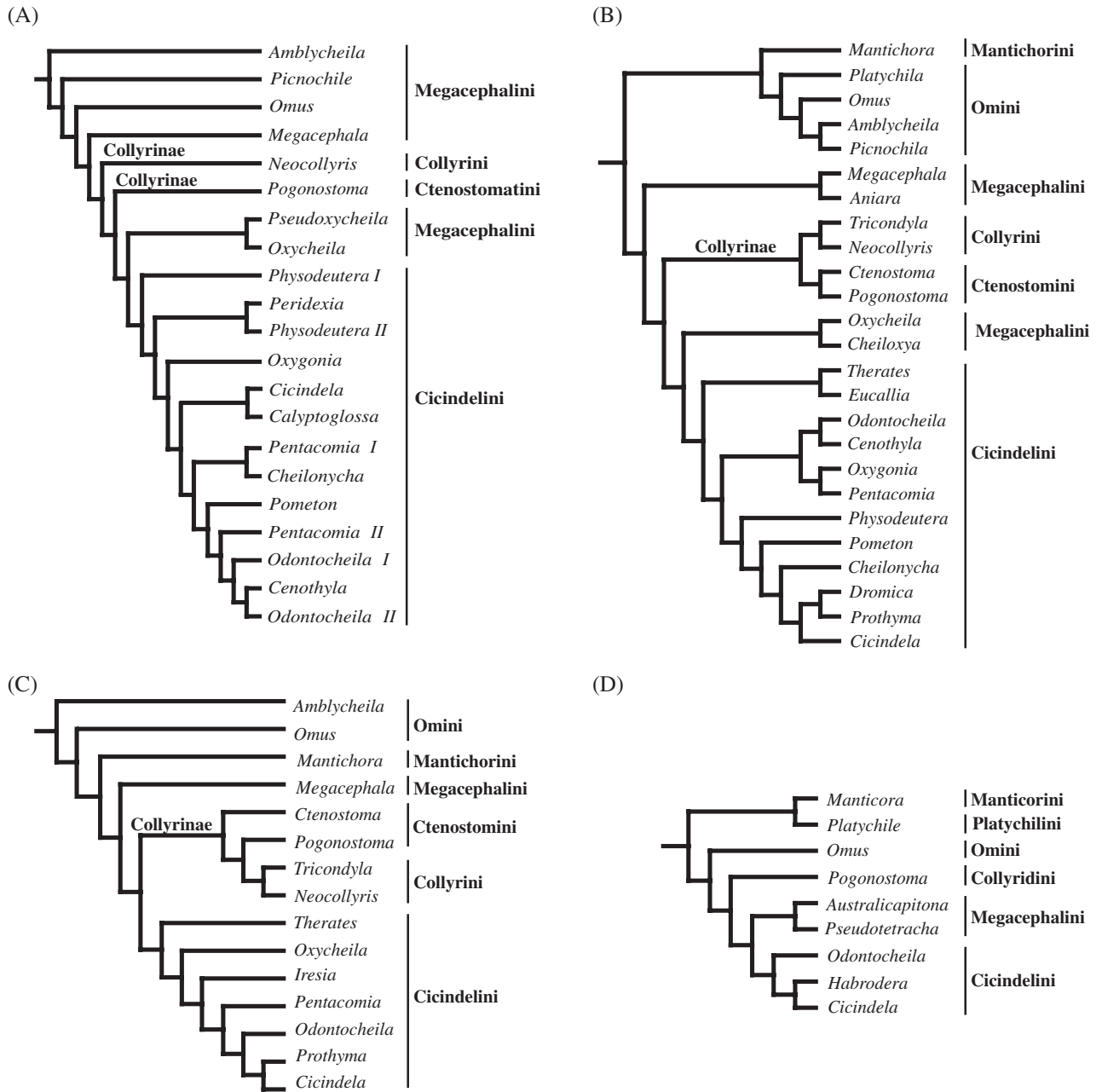


Fig. 2. Previous hypotheses of phylogenetic relationships among tiger beetles (Coleoptera, Carabidae, Cicindelinae). (a) Phylogenetic hypothesis inferred in Vogler & Pearson (1996) based on the combined analysis of the mitochondrial *16S* gene and nuclear *18S* gene (including hypervariable regions). (b) Phylogenetic hypothesis inferred in Galián *et al.* (2002) based on the analysis of the *18S* gene (including hypervariable regions). (c) Phylogenetic hypothesis from Vogler & Barraclough (1998) based on the combined analysis of the mitochondrial *16S* gene, nuclear *18S* gene (including hypervariable regions) and 34 morphological characters derived from Arndt & Putchkov (1997). All tip labels correspond to the original labelling of the different studies showcased in this figure, with the exception of obvious typos (e.g. Galián *et al.* (2002), in order to illustrate the instability of tiger beetle taxonomy over the years. (d) Phylogenetic hypothesis inferred in López-López & Vogler (2017) based on the combined analysis of mitogenomes and nuclear *18S* gene (including or excluding hypervariable regions).

the supermatrix approach continues to be used to generate phylogenies for many clades because it allows for the inclusion of data from multiple sources and larger numbers of taxa than is feasible with other methods (Thomson & Shaffer, 2010; Hedtke *et al.*,

2013; Pyron *et al.*, 2013; Burleigh *et al.*, 2015; Shin *et al.*, 2017; Toussaint & Gillett, 2018; Beaulieu & O'Meara, 2018). As such, it is a promising avenue for the future of molecular systematics and for the overarching goal to infer a comprehensive tree-of-life

Table 1. Comparison of the molecular datasets used in this study, examining the percentage of missing taxa and GC content. Length refers to the total number of base pairs.

Alignment	Length (bp)	Taxa included	Missing taxa (%)	GC content (%)
<i>COX1 5'</i>	657	99	72.6	36.4
<i>COX1 3'</i>	774	186	48.5	32.6
<i>COX3</i>	486	163	54.8	36.5
<i>CytB</i>	408	163	54.8	33.7
<i>16S</i>	823	222	38.5	26.6
<i>18S</i>	2722	103	71.5	45.3
<i>28S</i>	1684	113	68.7	36.6
<i>EF1</i>	751	58	83.9	45.0
<i>MP20</i>	1943	55	84.8	35.9
<i>Wg</i>	507	89	75.3	49.2
Comp_DT	10 755	361	0	36.3
GBlocks_DT	7295	361	0	36.9

(e.g. Delsuc *et al.*, 2005). Although generating large amounts of genomic data for all organisms on Earth and placing these in a phylogenetic framework is the ultimate goal (Lewin *et al.*, 2018), the supermatrix approach remains – in the meantime – a powerful way to combine new robust phylogenomic backbones with various densely sampled datasets comprising loci that have been traditionally sequenced in the past ('legacy genes'; e.g. Branstetter *et al.*, 2017; Kawahara *et al.* accepted pending minor revisions).

Taxon sampling

This study sampled 328 species, from all tribes and most subtribes of Cicindelinae as recognized in this study (see Introduction). This represents the largest comprehensive taxonomic sampling for any phylogenetic study of Cicindelinae to date. The final concatenated dataset included nine molecular markers, totalling 10 755 bp (Table 1). The pipeline used to construct the dataset for phylogenetic analyses is outlined below.

All DNA sequences used in this study but two (see below) were searched using the key-words 'Cicindelinae' and 'Cicindelidae' and downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>, accessed in September 2017) and Barcode Of Life Data (BOLD) Systems v4 (<http://www.boldsystems.org/>, accessed in September 2017). The sequences were subsequently imported directly into GENEIOUS R8.1.8 (Biomatters, USA) as FASTA files. Only sequences published in peer-reviewed journals or with detailed specimen information (e.g. with a specimen image or collection locality) were considered for inclusion in the study. Sequences were labelled according to the taxonomic information provided on GenBank and clustered by gene fragment. Taxonomic validity of the sequence was verified by checking each species and genus name to Wiesner (1992). Valid taxonomic changes since 1992 also were followed by checking recent taxonomic revisions and studies (see Introduction) and using the database Carabidae of the World (<http://www.carabidae.org>). All sequences with incorrect

names and typos were checked individually, and either kept or discarded depending if a valid name could be attributed or not. If multiple sequences of the same gene fragment existed for a single species, the copies were aligned and checked for incongruence. The longest matching representative sequence was selected. All species from the Cicindelinae were considered for alignment, as well as 33 outgroups based on the most recent phylogenies of Carabidae (Maddison *et al.*, 1999; Ober, 2002; Beutel *et al.*, 2008; Ober & Maddison, 2008; Maddison *et al.*, 2009; Ober & Heider, 2010; Hogan, 2012; Moore & Robertson, 2014; López-López & Vogler, 2017). We sampled six species of Brachininae, seven of Harpalinae, one of Loricarinae, nine of Paussinae, and three of Psydrinae, Rhysodinae and Scaritinae respectively, to test the phylogenetic placement of Cicindelinae within Carabidae. The phylogeny was rooted using *Bembidion transversale* Dejean (Trechinae). Unpublished sequences of *Distipsidera flavipes* MacLeay (Cicindelini, Iresina) and *Myriochila semicineta* Brulle (Cicindelini, Cicindelina) were kindly provided by Graeme Cocks.

All species that passed the first stage of selection (removal of contaminated or short sequences, and of duplicates) were initially aligned using MUSCLE (Edgar, 2004) with default options. Resulting alignments were screened for irregularities. Specifically, sequences which were of poor quality due to stop codons (in protein-coding genes), or those that may have arisen from sequencing errors or contamination were removed. Preliminary gene trees were inferred in a maximum-likelihood (ML) framework using FASTTREE 2.1.5 (Price *et al.*, 2010) in GENEIOUS R8.1.8 with a GTR model. The placement of sequences within the resulting topologies were then checked against the current taxonomy and widely supported monophyletic groups (typically supported by extraneous evidence such as concerted morphological characters) and compared by eye across gene trees to detect rogue taxa that can reveal contamination, misidentification, mislabelling or paralogues. Once these steps were completed, gene fragments with low taxonomic and/or genetic coverage were discarded to improve the overall supermatrix composition. The gene fragments that were conserved are the following: mitochondrial *cytochrome oxidase c subunit 1 (COX1)* in two fragments; 5' ('barcode') and 3', *cytochrome oxidase c subunit 3 (COX3)*, *cytochrome b (CytB)* and ribosomal *16S (16S)*, and nuclear ribosomal *18S (18S)*, ribosomal *28S (28S)*, *elongation factor 1 alpha (EF1)*, *muscle specific protein 20 (MP20)* and *wingless (Wg)*. Taxon sampling and gene coverage for each species are given in Appendix S1.

The final gene alignments were aligned using MUSCLE (Edgar, 2004) for the protein-coding gene fragments (*COX1*, *COX3*, *CytB*, *EF1*, *MP20*, *Wg*) and MAFFT 7.017 (Katoh & Standley, 2013) for the ribosomal gene fragments (*16S*, *18S*, *28S*). MUSCLE was run with a maximum of eight iterations and other options left to default. MAFFT was run with the E-INS-i algorithm to take into account the presence of numerous gaps in ribosomal gene fragments. All alignments were then trimmed to optimize the genetic coverage of the different gene fragment matrices. The ribosomal gene fragment alignments were not edited manually to avoid subjective manipulation of the data

in hypervariable regions. Similarly, intron regions within *EF1*, *MP20* and *Wg* were left untouched.

In order to consider possible nonhomologous regions in the *16S*, *18S*, *28S*, *EF1*, *MP20* and *Wg* alignments, and account for the possible impact of hypervariable regions on phylogenetic inference within Carabidae (López-López & Vogler, 2017), we generated two datasets. The first dataset ‘Comp_DT’ was generated by concatenating all resulting gene fragment alignments into a supermatrix. The second dataset ‘GBlocks_DT’ was generated after running GBLOCKS 0.91b (Castresana, 2000) on the *16S*, *18S*, *28S* and *MP20* gene alignments. GBLOCKS searches and deletes large segments of contiguous nonconserved positions, gap positions and nonconserved flanking positions, thereby reducing the need to manually edit ribosomal alignments for instance. This method has proven very useful in increasing phylogenetic accuracy for complex molecular datasets (e.g. Talavera *et al.*, 2007). We used the default stringent parameters to run GBLOCKS, disallowing smaller final blocks, gap positions and nonconserved flanking positions. Resulting alignments were then imported back into GENEIOUS with the original alignments of *COXI* (3' and 5'), *COX3*, *CytB* and with the alignments of *EF1* and *Wg* without their intronic regions that were removed manually in GENEIOUS for this particular dataset. The individual alignments were then concatenated to generate the GBlocks_DT dataset. The final two matrices (Comp_DT and GBlocks_DT) are provided in Appendices S3 and S7 and their compositions are given in Table 1.

Phylogenetic analyses

We inferred phylogenetic relationships in a ML framework using IQ-TREE 1.5.4 (Nguyen *et al.* 2015). The partitioning schemes for the Comp_DT and GBlocks_DT datasets were selected using PARTITIONFINDER 2.1.1 (Lanfear *et al.*, 2017) with the greedy algorithm, across all available models of nucleotide substitution (‘models=all’ option) and model selection based on the corrected Akaike Information Criterion (AICc). Protein-coding gene fragments were divided by codon positions and non protein-coding ribosomal gene fragments were left unpartitioned before running PartitionFinder. The *COXI* gene fragments (3' and 5') were treated independently because they have been shown to have different rates of evolution (e.g. Andújar *et al.*, 2012). Each intronic region was treated as a separate partition. The PARTITIONFINDER analysis recovered a scheme including 23 and 16 partitions respectively for the Comp_DT and GBlocks_DT datasets (see Appendices S4, S5 and S8, S9 for more details). The resulting partitioning schemes were used as inputs in IQ-TREE, and models of nucleotide substitution were estimated *de novo* across all available models including the ones relaxing the assumption of gamma-distributed rates (‘+R FreeRate’ option; Soubrier *et al.*, 2012). We performed 1000 ultrafast bootstraps (UFBoot; Minh *et al.*, 2013) as well as 1000 SH-aLRT tests (Guindon *et al.*, 2010; Minh *et al.*, 2013) to investigate nodal support across the topology. The consensus tree of all bootstrap trees was used to

map the nodal support values. All analyses were performed on the HiPERGATOR 2.0 cluster at the University of Florida.

Results and Discussion

Role of hypervariable and intronic regions in tiger beetle phylogenetics

Using GBLOCKS resulted in a much smaller dataset than the Comp_DT (Table 1). The analyses based on the Comp_DT and GBlocks_DT datasets resulted in some inconsistencies both in the outgroup relationships with tiger beetles and within Cicindelinae. The phylogenetic inference based on the GBlocks_DT dataset had generally lower nodal support values across the topology (See Appendices S2 and S6). The phylogenetic inference based on the full dataset (Comp_DT) is presented in Figs 3 and 4. We summarized the main discrepancies between the two phylogenetic hypotheses in Appendix S10. We recovered Rhysodinae as sister to Cicindelinae although with low nodal support (UFBoot = 86 / SH-aLRT = 39) (Fig. 3). The monophyly of Cicindelinae + Paussinae + Rhysodinae + Scaritinae (CPRS quartet) was, however, strongly supported (UFBoot = 99 / SH-aLRT = 100) as recovered in other studies focusing on carabid phylogenetics using different datasets (e.g. Maddison *et al.*, 1999; Beutel *et al.*, 2008; Maddison *et al.*, 2009; McKenna *et al.*, 2015). The GBlocks phylogenetic hypothesis also recovers Rhysodinae as sister to Cicindelinae with strong nodal support (UFBoot = 100 / SH-aLRT = 95.7), but does not recover the monophyly of the CPRS quartet due to the inclusion of Loricarinae as sister to Scaritinae (Appendices S6 and S10).

Recently, López-López & Vogler (2017) investigated the placement of tiger beetles within Carabidae using mitochondrial genomes (*c.* 14 kb) in combination with nuclear ribosomal genes (*18S* and *28S*). They concluded that the placement of tiger beetles as described above is mainly driven by the hypervariable regions found in these nuclear ribosomal genes (but see McKenna *et al.* (2015) for an example of a phylogenetic hypothesis recovering the CPRS quartet without ribosomal gene fragments). In our study, the relationships between outgroups changed slightly between datasets, but our inferences do not support the view developed in López-López & Vogler (2017). On the contrary, our analyses indicate that some of the data removed using GBLOCKS is most likely crucial to resolve the tiger beetle phylogeny. For instance, within Cicindelinae, some taxa are clearly misplaced from morphological and taxonomic points of view when using the GBlocks_DT dataset, but correctly placed using Comp_DT. These include for instance, several lineages for which only a unique representative is available such as *Caledonica* Chaudoir, *Distipsidera* Westwood, *Dromica* Dejean, *Eurymorpha* Hope or *Rivacindela* Nidek. These taxa alone are responsible for a large fraction of the apparent inconsistency between the two topologies (Appendix S10). These taxa whose placement remains uncertain, are represented in the matrix solely by *18S* sequences (except *Distipsidera* that had only a *COXI* 5' sequence), which explains the pattern seen in our analyses. Considering their correct placement with respect to

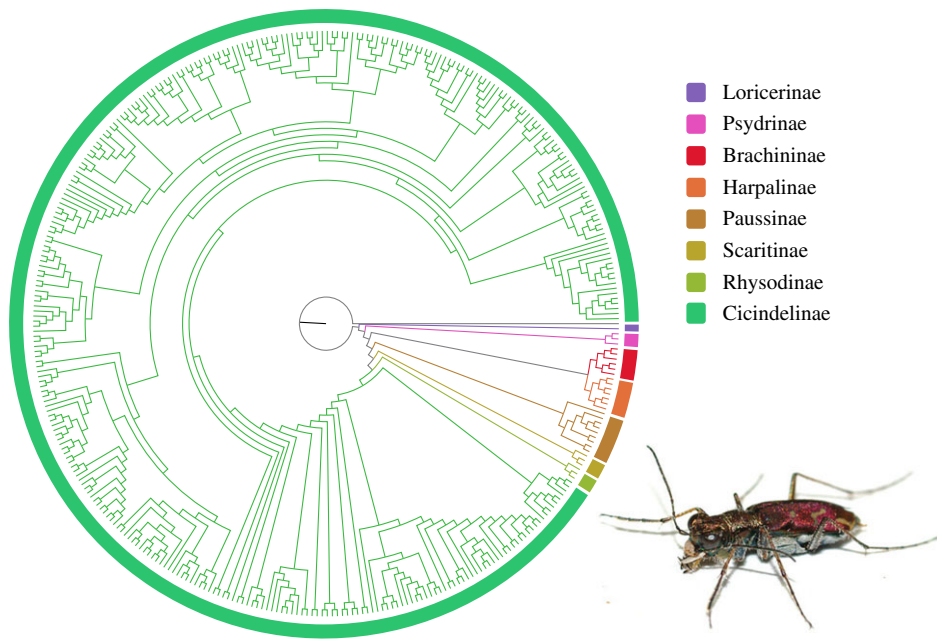


Fig. 3. Maximum-likelihood phylogenetic hypothesis for the placement of tiger beetles within Carabidae. Circular cladogram representing the maximum-likelihood phylogeny inferred in IQ-TREE using the Comp_DT dataset comprising nine gene fragments and about 11 kb of molecular data. The branch lengths have been modified to ease the visualization of relationships between subfamilies within Carabidae. A photograph of *Brasiella wickhami* Horn is presented at the bottom of the figure (photo credit: Margarethe Brummermann). [Colour figure can be viewed at wileyonlinelibrary.com].

morphology and historical classification when using hypervariable and intronic regions (Comp_DT dataset), we hypothesize that removing the latter results in a significant loss of phylogenetic signal. We argue that conserving these regions for phylogenetic inference is important to reconstruct the most likely phylogeny of tiger beetles. Most major groupings that are moderately to strongly supported with the Comp_DT dataset are usually consistent with the GBlocks_DT dataset when ignoring these artificially rogue lineages. Additional gene sampling, possibly using phylogenomic methods (anchored hybrid enrichment, e.g. Haddad *et al.*, 2017; transcriptomes, e.g. Misof *et al.*, 2014; and/or ultra-conserved elements, e.g. Baca *et al.*, 2017) will help to resolve long-standing questions regarding the placement of tiger beetles within Carabidae and deep nodes within Cicindelinae. Based on our results, we only discuss below the phylogenetic relationships as recovered in the tree inferred using the Comp_DT dataset (see Appendix S6 for more details on the phylogenetic hypothesis reconstructed using the GBlocks dataset).

Systematics of major tiger beetle lineages

The ML tree derived from the analysis of the Comp_DT dataset showed strong support (UFBoot ≥ 95 / SH-aLRT ≥ 80) for all intertribal relationships. The tribe Manticorini was recovered nested within the tribe Platychilini including the genera *Amblycheila*, *Omus*, *Picnochile* and *Platychile* (Fig. 4). In their study, Galián *et al.* (2002) recovered *Manticora* as sister

to Platychilini with the monophyly of Manticorini+Platychilini strongly supported. López-López & Vogler (2017) found *Manticora* as part of a clade containing *Platychile* but excluding *Omus*. Our topology renders Platychilini paraphyletic due to the inclusion of *Manticora*. Because the extremely rare African genus *Mantica* was not sampled in this study, the monophyly of Platychilini and the inclusion of Manticorini should be revisited in the future with additional data. Within Platychilini, the two North American genera *Amblycheila* and *Omus* were not closely related. The close relationship between the African *Manticora* and *Platychile*, and the South American *Picnochile* could represent the traces of an ancient Gondwanan distribution (Cassola, 2001).

The tribe Megacephalini was recovered as paraphyletic due to the placement of the monophyletic subtribe Oxycheilina as sister to the tribe Cicindelini (Fig. 4). The latter relationship, recovered with strong support (UFBoot = 100 / SH-aLRT = 98.8), is in line with Vogler & Pearson (1996) and Galián *et al.* (2002). The placement of Megacephalina as sister to the Cicindelini, Oxycheilini and Collyridini (UFBoot = 100 / SH-aLRT = 98.2), agrees with Vogler & Pearson (1996), Vogler & Barraclough (1998) and Galián *et al.* (2002) but is at odds with López-López & Vogler (2017) who found Megacephalina as the sister-group to Cicindelini with strong support. Monophyly of Megacephalina was highly supported in our analysis (UFBoot = 100 / SH-aLRT = 99.7), with the subtribe split into two major clades whose sister lineage is the Palaearctic species *Grammognatha euphratica* Dejean (Fig. 4). One clade contains the African species *Megacephala regalis* Boheman as sister to

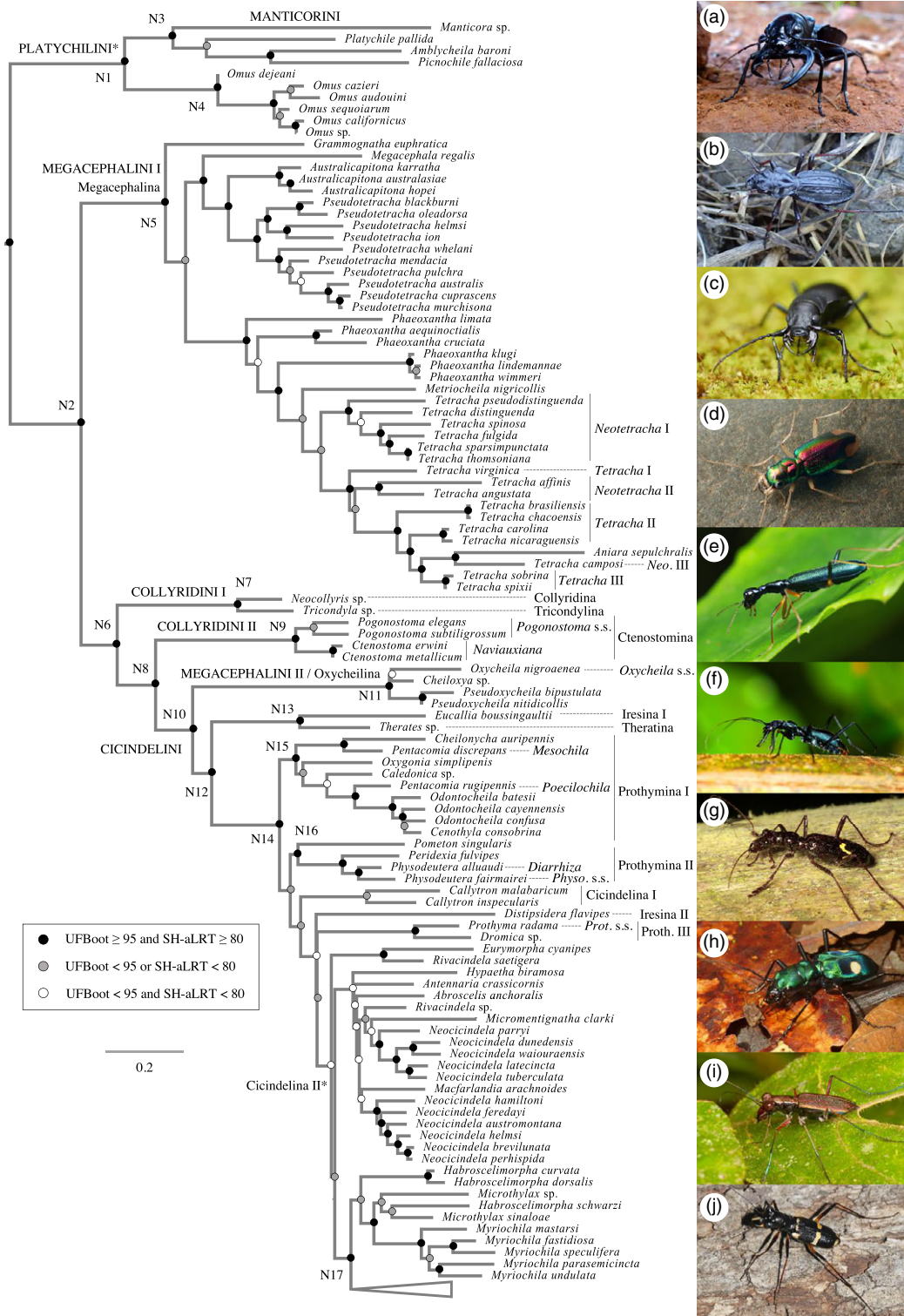


Fig. 4. Continued. Legend on page 11

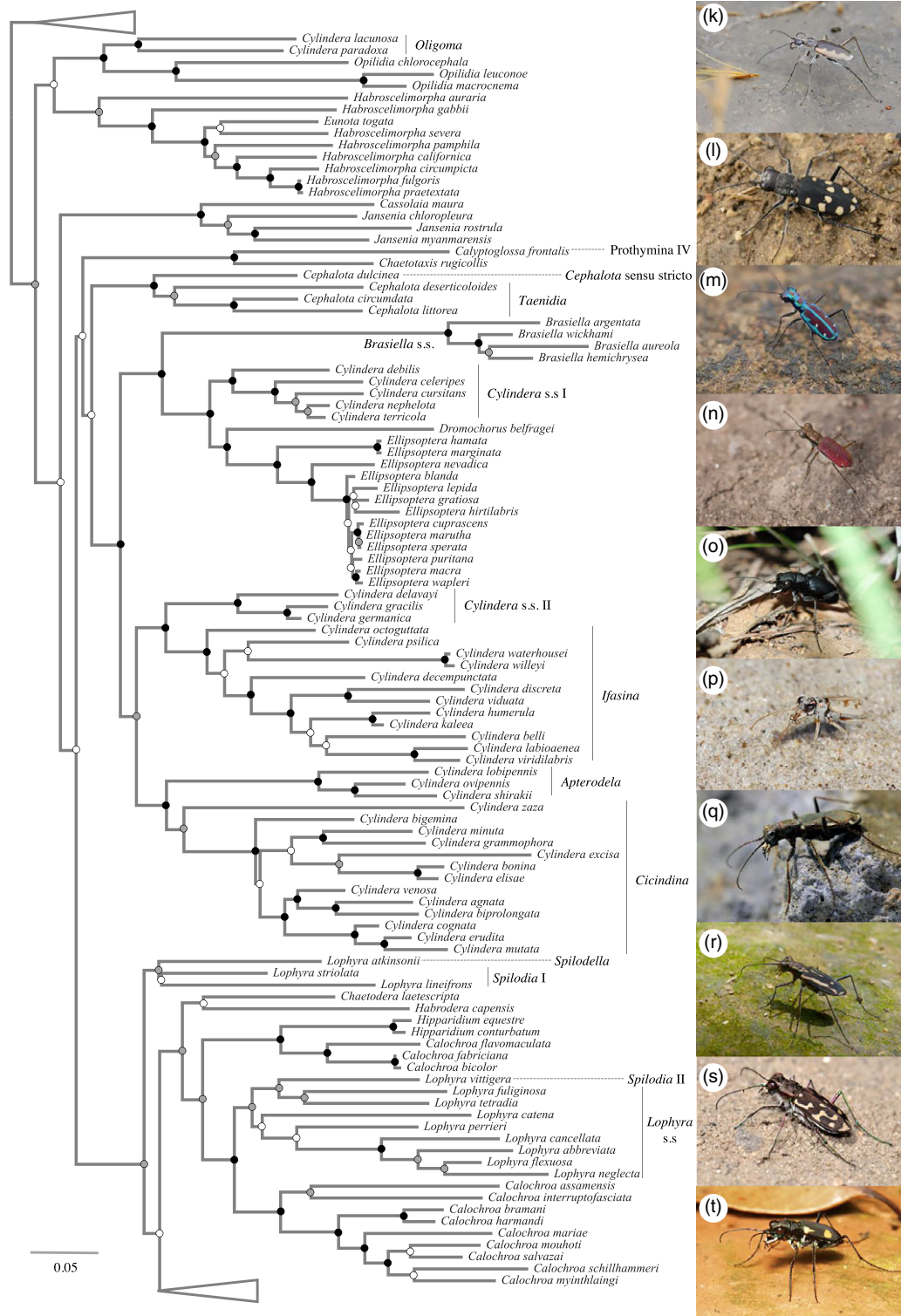


Fig. 4. Continued. Legend on page 11

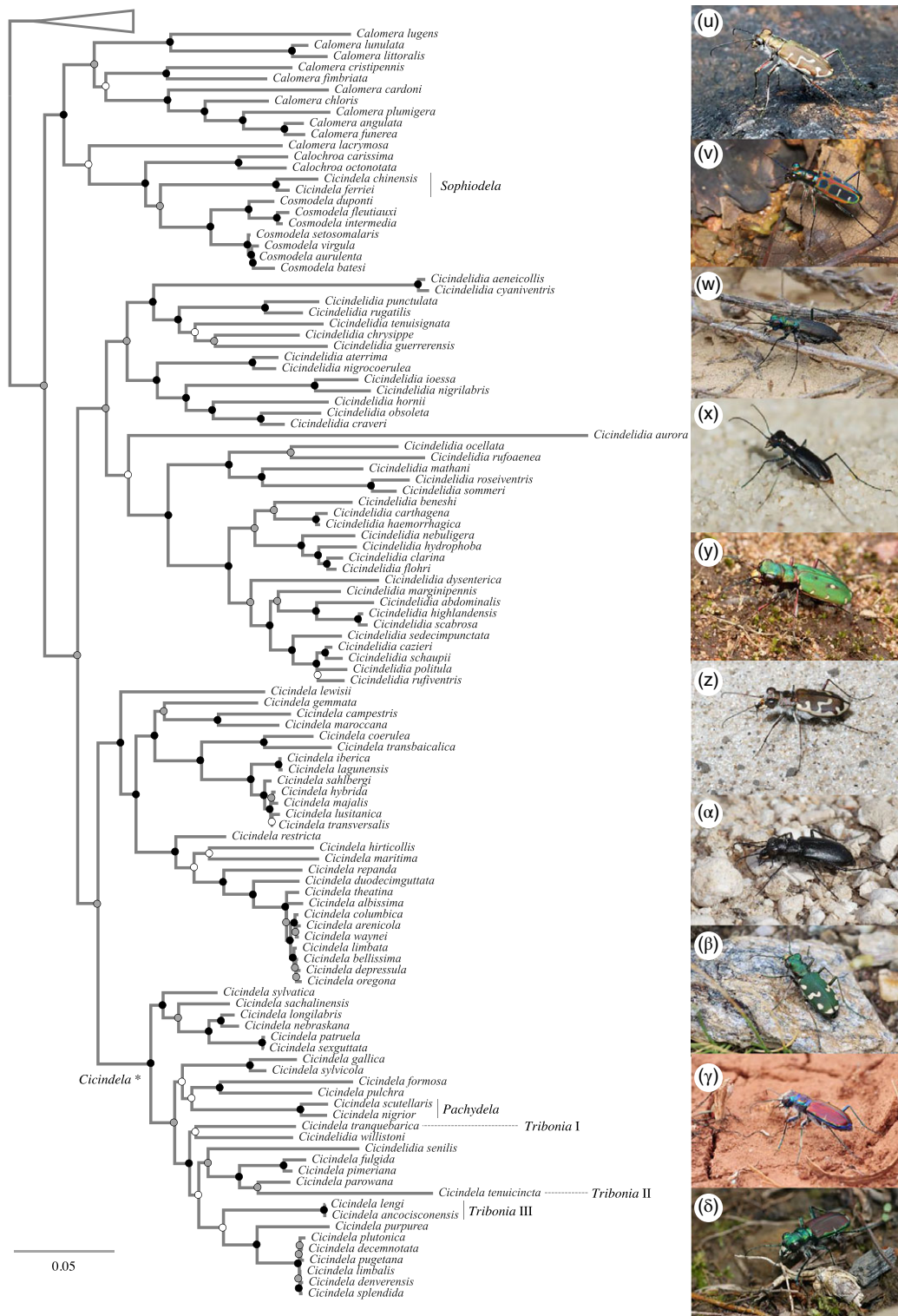


Fig. 4. Continued. Legend on next page

the reciprocally monophyletic Australian genera *Australicapitona* and *Pseudotetracha*. The other was composed entirely of New World species with *Anaria sepulchralis* Fabricius nested within *Tetracha*. The genus *Phaeoxantha* was recovered as polyphyletic, in contrast to the result of Zerm *et al.* (2007) who found this genus to be monophyletic. The genus *Metriocheila* was recovered as sister to *Tetracha*, within which the subgenera *Neotetracha* and *Tetracha* s.s., recognized by Naviaux (2007), were not recovered as monophyletic (Fig. 4).

Collyridini was paraphyletic in the present study (UFBoot = 99 / SH-aLRT = 91.3), with Collyridina and Tricondyliina in one clade, and Ctenostomina in another (Fig. 4). This result was strongly supported and is congruent with Vogler & Pearson (1996), but conflicts with the trees of Vogler & Barraclough (1998) and Galián *et al.* (2002), the latter two of which recovered a monophyletic Collyridini. The monophyly of the different subgenera erected in *Ctenostoma* and *Pogonostoma* (Naviaux, 1998; Moravec, 2007; Erwin & Pearson, 2008) could not be tested in this study because we sampled only representatives of one subgenus for each clade (*Naviauxiana* Erwin and *Pogonostoma* s.s., respectively).

The remainder of Cicindelini was recovered as monophyletic with strong support (UFBoot = 98 / SH-aLRT = 79.8). The Southeast Asian subtribe Theratina was represented by a single specimen of the unique genus *Therates* Latreille (>100 species) and was found in a strongly supported clade (UFBoot = 100 / SH-aLRT = 99.9) with the Neotropical monotypic genus *Eucallia* Guérin-Meneville of the subtribe Iresina. The Australian genus *Distipsidera* (12 species) was the only other representative of Iresina in our analysis and its placement was poorly supported (UFBoot = 83 / SH-aLRT = 50.3). The apparent paraphyly of Iresina was artefactual as *Distipsidera* and *Eucallia* share no gene fragments in our alignment (Appendix S1). The placement of *Distipsidera* also was uncertain because few included taxa have been sequenced for the barcode gene fragment (*COXI* 5'; Appendix S1). Moreover, the subtribe Iresina comprises several additional genera (*Diastrophella* Rivalier, *Euprosopus* Dejean, *Iresia* Dejean, *Langea* Horn, *Megalomma* Westwood, *Nickerlea* Horn, *Rhysopleura* Sloane and *Rhytidophaena* Bates) that were

not included in this study. Therefore, any conclusion regarding the monophyly or placement of Iresina within Cicindelini is premature.

Several genera within Cicindelini (e.g. *Odontocheila* Leporte, *Oxygonia* Mannerheim, *Pentacomia* Bates, *Pometon* Fleutiaux) have been placed in the subtribe Odontocheilina (Horn 1910). However, this subtribal name was later abandoned (Rivalier, 1969, 1971; Wiesner, 1992; but see Moravec, 2012; Moravec & Brzoska, 2014) and these genera were placed by Wiesner (1992) within Prothymina. In our study, Prothymina was recovered as polyphyletic with representative genera spread across three clades (Fig. 4). The Neotropical genera *Cenothyla* Rivalier, *Cheilonycha* Lacordaire, *Odontocheila*, *Oxygonia* and *Pentacomia* were found in a first clade (Node 15). Interestingly, the New Caledonian endemic genus *Caledonica* (14 species) was recovered nested within this clade. This placement is dubious especially because the genus *Caledonica* is morphologically closely related to the Australian genus *Distipsidera* (Deuve, 2015; Kudrna, 2016), also sampled in this study although without overlap in the sequence alignment. The phylogenetic affinities of these two Melanesian genera and their placement within Cicindelini should be tested with additional data sampling. The genus *Pentacomia* was recovered as paraphyletic with representatives of two subgenera in different parts of the clade. Additional sampling will be needed to test the monophyly of this genus. The genus *Odontocheila* was recovered as paraphyletic due to the placement of *Cenothyla consobrina* Lucas. This result is congruent with Pons *et al.* (2006). The two Madagascar endemic genera *Peridexia* Chaudoir (two species) and *Physodeutera* Lacordaire (64 species) are recovered as sister in a different clade with the Neotropical species *Pometon singularis* Fleutiaux (UFBoot = 95 / SH-aLRT = 86.9). The African genus *Dromica* (>160 species) and the Old World genus *Prothyma* Hope (41 species) were recovered as sister in a separate clade (UFBoot = 100 / SH-aLRT = 97). The latter renders the subtribe Cicindelina paraphyletic with respect to the Oriental genus *Callytron* Gistel (Fig. 4). The remainder of Cicindelina also was recovered as paraphyletic due to the placement of the Madagascar endemic genus *Calyptoglossa* Jeannel as sister to

Fig. 4. Maximum-likelihood phylogenetic hypothesis for tiger beetles. Maximum-likelihood phylogenetic tree inferred in IQ-TREE using the Comp_DT dataset comprising nine gene fragments and about 11 kb of molecular data. Nodal support values are reported for each node following the caption inserted in the first panel of the figure. Major taxonomic groups are indicated and numbered when not monophyletic. Abbreviations: *Cicindela**, *Cicindela* s.s. + *Cicindelidia senilis* + *Cicindelidia willin* *Pachylida* + *Tribonia*; N, node; Neo., *Neotetracha*; Physo., *Physodeutera*; Platychilini*, Platychilini + Manticorini; Prot., *Porthyma*; Porth., Porthymina. Photographs of tiger beetle lineages are presented on the right side of the figure. From top to bottom: (a) *Manticora scabra* Klug (photo credit: Bernard Dupont), (b) *Picnochile fallaciosa* (photo credit: Yasuoki Takami), (c) *Omus californicus* Eschscholtz (photo credit: Ken Hickman), (d) *Tetracha carolina* Linné (photo credit: David Maddison), (e) *Neocollyris* sp. (photo credit: Tyus Ma), (f) *Pogonostoma* sp. (photo credit: Michel Candel), (g) *Ctenostoma ecuadorensis* Naviaux (photo credit: Andreas Kay), (h) *Pseudoxycheila* sp (photo credit: Andreas Kay), (i) *Odontocheila* sp (photo credit: Andreas Kay), (j) *Distipsidera flavipes* (photo credit: Malcolm Tattersall), (k) *Eunota togata* LaFerte-Senectere (photo credit: Dave Rogers), (l) *Cephalota maura* Linné (photo credit: Costán Escuer), (m) *Jansenia azureocincta* Bates (photo credit: Dinesh Valke), (n) *Brasiella wickhami* (photo credit: Jason Lambert), (o) *Dromochorus belfragei* Salle (photo credit: Josh Kouri), (p) *Ellipsoptera lepida* Dejean (photo credit: Dave Rogers), (q) *Cylindera germanica* Linné (photo credit: Jinze Noordijk), (r) *Lophyra striolata* Illiger (photo credit: Eduard Jendek), (s) *Lophyra flexuosa* Fabricius (photo credit: Jesús Tizón Taracido), (t) *Calochroa salvazai* Fleutiaux (photo credit: John Horstman / itchydogimages), (u) *Calomera angulata* Fabricius (photo credit: Len Worthington), (v) *Cosmodela duponti* Dejean (photo credit: Jee & Rani Nature Photography), (w) *Cicindelidia punctulata* Olivier (photo credit: Dave Rogers), (x) *Cicindelidia abdominalis* Fabricius (photo credit: Kevin Stohlgren), (y) *Cicindela campestris* Linné (photo credit: Jon Moore), (z) *Cicindela hirticollis* Say (photo credit: Mathew Brust), (α) *Cicindela nebraskana* Casey (photo credit: Dave Rogers), (β) *Cicindela gallica* Brulle (photo credit: Robin Holler), (γ) *Cicindela pulchra* Say (photo credit: Dave Rogers), (δ) *Cicindela splendida* Hentz (photo credit: William Hull). [Colour figure can be viewed at <http://wileyonlinelibrary.com>].

the Madagascar endemic genus *Chaetotaxis* Jeannel with strong nodal support (UFBoot = 100 / SH-aLRT = 99.4). These two genera share some morphological features that Moravec (2010) noted in his monograph of Malagasy tiger beetles.

Systematic focus on the subtribe *Cicindelina*

Over two thirds of the taxa included in our analysis occur in the subtribe *Cicindelina*. In fact, the subtribe comprises about 1000 species globally distributed (Cassola & Pearson, 2000). The relationships among genera of *Cicindelina* are poorly understood despite some earlier studies (e.g. Pons *et al.*, 2004). In our study, when ignoring the placement of *Callytron*, we recovered the African monotypic genus *Eurymorpha* and one of the two sampled species of the Australian genus *Rivacindela* (30 species, but see Pons *et al.*, 2006; this genus was used to develop the Generalized Mixed Yule Coalescent model) in a clade sister to the remainder of the subtribe (Fig. 4). Although both taxa were sequenced in Galián *et al.* (2002), it seems that *Eurymorpha* was not included in the phylogenetic tree proposed in this paper. This is a surprising relationship that, despite strong nodal support (UFBoot = 98 / SH-aLRT = 99.5), should be tested with additional data. This is particularly obvious considering that the genus *Rivacindela* was inferred as paraphyletic because both included species do not overlap genetically. However, the placement near *Micromentignatha oblongicollis* MacLeay is more in line with current understanding of phylogenetic relationships in this clade (e.g. Pons *et al.*, 2011). In a large clade with low nodal support across the topology, we recovered multiple genera of mixed geographical distributions. The New Zealand endemic genus *Neocicindela* Rivalier (12 species) was recovered as paraphyletic due to the placement of the Australian endemic genera *Macfarlandia* Sumlin and *Micromentignatha* Sumlin as well as *Rivacindela* sp. (Fig. 4). We also recovered the Australian endemic genus *Antennaria* Dokhtouroff (four species) and the two widespread Oriental/Australian genera *Abroscelis* Hope (six species) and *Hypaetha* Leconte (14 species) in this clade. However, the internal phylogenetic relationships are poorly supported and no conclusions regarding the evolutionary relationships of these genera can be derived from our inference.

We found the New World genus *Habroscelimorpha* Dokhtouroff paraphyletic with species placed in two different clades (Fig. 4). The Central American and Nearctic species *Habroscelimorpha curvata* Chevrolat, *H. dorsalis* Say (type species of the genus) and *H. schwarzi* Horn are part of a moderately supported clade (UFBoot = 90 / SH-aLRT = 81.5) that includes the paraphyletic Central American genus *Microthylax* Rivalier (three species) and the monophyletic widespread genus *Myriochila* Motschulsky (46 species). The other eight species of the genus *Habroscelimorpha* included in our analysis formed a moderately well-supported clade together with the monotypic Nearctic genus *Eunota* Rivalier (UFBoot = 75 / SH-aLRT = 89.7). This placement was noted already by Cardoso & Vogler (2005). The Central American genus *Opilidia* Rivalier (six species) was recovered as monophyletic and sister to *Cylindera lacunosa* Putzeys and *C. paradoxa* Horn, both of which belong to the

subgenus *Oligoma* Rivalier (Fig. 4). Our phylogenetic hypothesis was not strongly supported for the placement of *Oligoma* in Cicindelini. The Oriental genus *Jansenia* Chaudoir (38 species) was recovered as monophyletic and sister to the monotypic Western Mediterranean subgenus *Cephalota* Dokhtouroff (*Cassolaia* Wiesner) (Fig. 4). The predominantly Palaearctic genus *Cephalota* (22 species), in which *Cassolaia* is sometimes merged, was found monophyletic with strong nodal support (UFBoot = 98 / SH-aLRT = 93.8). Within *Cephalota*, the subgenera *Cephalota* s.s. and *Taenidia* Rivalier are sister clades, but *Cassolaia* was recovered as sister to *Jansenia*.

The Caribbean/Neotropical genus *Brasiella* Rivalier (45 species) was recovered as monophyletic with strong support (UFBoot = 100 / SH-aLRT = 100) in our analysis. *Brasiella* is nested within the diverse genus *Cylindera* Westwood that was polyphyletic in our analysis (Fig. 4). We found a strongly supported clade (UFBoot = 100 / SH-aLRT = 99.8) of five North American *Cylindera* species as sister to the Nearctic genus *Dromochorus* Guerin-Meneville (4 species) and to the monophyletic Nearctic genus *Ellipsoptera* Dokhtouroff (13 species). The clade containing these four lineages was strongly supported (UFBoot = 100 / SH-aLRT = 98.1), consists exclusively of New World taxa and was sister to a predominantly Old World clade of *Cylindera* species. Although our analysis recovered the genus *Cylindera* as polyphyletic, we found moderate to strong support for the monophyly of four named subgenera *Apterodela* Rivalier, *Cicindina* Ádám & Merkl (replacement name for the pre-occupied name *Eugrapha* Rivalier, 1950, see Ádám & Merkl, 1986), *Ifasina* Jeannel and *Oligoma*, and strong support for the polyphyly of the subgenus *Cylindera* s.s. (Fig. 4). This is in line with the study of Sota *et al.* (2011) on Japanese *Cylindera* tiger beetle systematics.

The predominantly Old World genus *Lophyra* Motschulsky (74 species) was inferred as polyphyletic (Fig. 4). We recovered the Oriental subgenus *Spilodella* Matalin & Cherkasov as well as two species of the Oriental subgenus *Spilodia* Rivalier in an isolated clade with low support (UFBoot = 51 / SH-aLRT = 81.5). The remainder of sampled *Lophyra* species are found as sister to a clade of the genus *Calochroa* Hope. These belong, except for *L. vittigera* Dejean (*Spilodia*), to the widespread subgenus *Lophyra* s.s. The two African genera *Chaetodera* Jeannel (nine species) and *Habrodera* Motschulsky (six species) are found in a clade sister to the *Lophyra* + *Calochroa* clade described above, although with moderate support (UFBoot = 60 / SH-aLRT = 96.4). Our analysis found strong support for the monophyly of the predominantly African genus *Hipparidium* Jeannel (23 species), represented in this study by two species from Madagascar (Fig. 4). The genus was found as sister to another clade of the genus *Calochroa* comprising two Indian and one African species.

We also find the widespread Old World genus *Calomera* Motschulsky (20 species, the commonly encountered genus name *Lophyridia* Jeannel is a junior synonym) to be paraphyletic, due to the poorly supported placement of *C. lacrymosa* Dejean as sister to a clade that was itself sister to the rest of *Calomera* (UFBoot = 80 / SH-aLRT = 45.5).

This latter clade comprises two Oriental species of the genus *Calochroa*, two Japanese species of the genus *Cicindela* (subgenus *Sophiodela* Nakane) and the monophyletic Oriental genus *Cosmodela* Rivalier (13 species). Clearly, the most problematic lineage in this part of the tree is the genus *Calochroa*, whose polyphyly was strongly supported and in line with Tsuji *et al.* (2016). Unfortunately, the type species *C. sexpunctata* Fabricius was not sampled in our study and, therefore, it is difficult to predict which clade would hold the genus name. Additional studies are needed to clean the taxonomy of this genus, and of the closely related *Lophyra*.

The New World genus *Cicindelidia* Rivalier (69 species) and Holarctic genus *Cicindela* (75 species) are two of the taxonomically best represented genera in our analysis. The genus *Cicindelidia* was recovered as paraphyletic due to the placement of *Cicindelidia senilis* Horn and *C. willistoni* Leconte that are recovered as deeply nested within *Cicindela*. Both genera had a moderately to strongly supported internal structure with several genetically well-differentiated large clades (Fig. 4). Within the genus *Cicindela*, we recovered the subgenera *Pachydela* Rivalier and *Tribonia* Rivalier deeply nested within the subgenus *Cicindela s.s.*

Future directions in tiger beetle systematics and evolution

Our study attempts to integrate over two decades of molecular sequence data on Cicindelinae into a single phylogenetic analysis and framework. Although we recognize the limits of supermatrix approaches (e.g. no new data and a substantial amount of missing data), we believe that this new phylogenetic hypothesis of tiger beetles is a necessary primer toward the generation of more robust and taxonomically more comprehensively sampled phylogenetic trees. Although some relationships among the tribe Cicindelini are poorly supported, an emerging backbone for the subfamily is recovered with strong nodal support (Fig. 4). The biogeographical distribution of tiger beetles once mapped onto this topology reveals a striking pattern of widespread ranges even in derived clades of Cicindelinae. Although a proper dating analysis of tiger beetles is lacking, the most recent studies estimating divergence times for major lineages of beetles recover an age in line with the fossil record of tiger beetles. The oldest known tiger beetle fossil is †*Oxycheilopsis cretacicus* Cassola & Werner from the Santana Formation in Brazil and dated back to the Early Cretaceous *c.* 112 Ma (Cassola & Werner, 2004). Toussaint *et al.* (2017) using the published phylogenetic framework of McKenna *et al.* (2015) and a comprehensive set of beetle fossils, inferred a crown age of tiger beetles (represented by the genera *Cicindela* and *Omus*) in the Cretaceous (*c.* 120 Ma), an age largely congruent with the current fossil record. In their study, Toussaint *et al.* (2017) relied upon the phylogeny of McKenna *et al.* (2015) that reconstructed Cicindelinae as sister to the CPRS quartet. Toussaint *et al.* (2017) inferred a stem age of Cicindelinae (=Cicindelinae+CPRS quartet crown age) in the early Jurassic *c.* 200 Ma. Recently, Zhang *et al.* (2018) using a different set of beetle fossils and a new phylogenomic

tree of Coleoptera including a unique representative of Cicindelinae, estimated a stem age of tiger beetles in the late Jurassic (*c.* 151 Ma), with Cicindelinae inferred as sister to all other Carabidae. The discrepancies between these stem ages can be partially explained by the dating method, different set of fossils used and the placement of clades within which fossil calibrations are enforced. Although some early divergence events in the evolution of Cicindelinae could be reconciled with Gondwanan vicariance scenarios (e.g. Megacephalina, Manticatorini+Platychilini), others in different clades are clearly too recent to be explained by such geological events. It seems that the biogeographical history of tiger beetles could have been shaped by ancient vicariance as well as more recent dispersal events. Developing a more robust timetree for tiger beetles and increasing the taxon sampling would allow testing these hypotheses in a statistical framework.

Based on the topology presented in Fig. 4, it is now possible to clearly identify the priority clades in the tree that need attention in order to unravel the evolution of major clades in Cicindelinae. Future attempts at shedding light on the tiger beetle tree-of-life should focus on (i) building a robust phylogenomic/transcriptomic backbone by sampling as many tribes and subtribes of Cicindelinae as possible, (ii) assembling large phylogenomic datasets using newly developed cost-effective approaches (e.g. anchored hybrid enrichment, ultra-conserved elements) that allow the combination of Sanger-generated data with genomic data and therefore take advantage of earlier molecular studies, and (iii) inferring a robust time-tree of tiger beetles using available fossil data (e.g. Cassola & Werner, 2004; Wiesner *et al.*, 2017) that will serve as a blueprint to study the astonishing biology of tiger beetles in an evolutionary framework.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Taxon sampling with gene coverage.

Appendix S2. Maximum-likelihood tree inferred in IQ-TREE using the Comp_DT dataset.

Appendix S3. Comp_DT molecular matrix used in this study.

Appendix S4. Comp_DT gene partitions.

Appendix S5. Partitioning schemes and corresponding models of substitution used in the IQ-TREE analysis based on the Comp_DT dataset.

Appendix S6. Maximum likelihood tree inferred in IQ-TREE using the GBlocks_DT dataset.

Appendix S7. GBlock_DT molecular matrix used in this study.

Appendix S8. GBlock_DT gene partitions.

Appendix S9. Partitioning schemes and corresponding models of substitution used in the IQ-TREE analysis based on the GBlocks_DT dataset.

Appendix S10. Nodal support of major nodes across the two phylogenetic hypotheses inferred using the Comp_DT and GBlocks datasets.

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