



Research

Cite this article: Gustafson GT, Bybee SM, Cardenas CR, Gauthier J, Toussaint EFA. 2026 Phylogenomics of Manticorini tiger beetles supports ancient Gondwanan vicariance and recent American amphitropical disjunction. *Proc. R. Soc. B* **293**: 20260866. <https://doi.org/10.1098/rspb.2026.0866>

Received: 8 April 2026

Accepted: 14 May 2026

Subject Category:

Evolution

Subject Areas:

evolution, taxonomy and systematics, bioinformatics

Keywords:

ultraconserved elements, Adephaga, ancestral range reconstruction, museomics, historical biogeography

Author for correspondence:

Grey T. Gustafson

e-mails: grey.gustafson@nau.edu;

gtgustafson@gmail.com

Supplementary material is available online at

<https://doi.org/10.6084/m9.figshare.c.8552390>.

Phylogenomics of Manticorini tiger beetles supports ancient Gondwanan vicariance and recent American amphitropical disjunction

Grey T. Gustafson¹, Seth M. Bybee^{2,3}, Cody Raul Cardenas⁴, Jérémy Gauthier⁴ and Emmanuel F. A. Toussaint⁴

¹Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA

²Department of Biology, and ³Monte L Bean Life Science Museum, Brigham Young University, Provo, UT, USA

⁴Natural History Museum of Geneva, Geneva, Switzerland

GTG, 0000-0002-2014-7128; **SMB**, 0000-0001-6224-6303; **CRC**, 0000-0002-8402-6069; **JG**, 0000-0001-6666-1002; **EFAT**, 0000-0002-8439-1285

Disjunct distributions have long fascinated biologists, particularly those found in the Southern Hemisphere. Gondwanan vicariance has been invoked to explain these patterns, with relatively limited studies having phylogenetically tested this hypothesis. Another intriguing pattern of disjunction involving South America is the American amphitropical distribution, where Western Hemisphere taxa have close relatives either north or south of the tropics. While better known in plants, this pattern is rarely proposed for animals and only phylogenetically tested in a handful of studies on hymenopteran insects. The Manticorini is a tribe of large-bodied, flightless tiger beetles whose members possess a complex distribution pattern attributable to both Gondwanan vicariance and American amphitropical disjunction. Using genomic-scale data we perform phylogenetic analyses to produce a time-calibrated evolutionary history of the Manticorini. With the resultant time tree we perform ancestral range reconstruction in order to recover the historical biogeography of this group. Our results show deep divergence between most manticorine genera, contrasted with young crown ages indicative of recent diversification. Our analyses support Gondwanan vicariance and amphitropical disjunction resulting from recent dispersal as part of the historical biogeography of the tribe. These findings highlight the role of both vicariance and dispersal in shaping diversification and complex modern distributions.

1. Introduction

Naturalists have long been fascinated by Southern Hemisphere taxa with disjunct distributions [1]. With the formalization of plate tectonic theory in the 1960s and subsequent modelling of tectonic movements [2], a mechanism was provided to explain how closely related taxa could come to have disjunct distributions across continents currently separated by oceans, without invoking *ad hoc* land bridges. Vicariance resulting from the break up of the supercontinent Gondwana which began in the Early Jurassic (approx. 180 Ma) and was largely completed by the Cretaceous (approx. 80 Ma) [3,4], has been used to explain lineages with relatives currently found in South America, Africa, Madagascar and Australia, but missing from intervening regions. Gondwanan vicariance should have a distinct signature including ancient divergences (older than 80 Ma), larger ancestral ranges, and modern taxa with disjunct distributions across southern landmasses. Disjunct

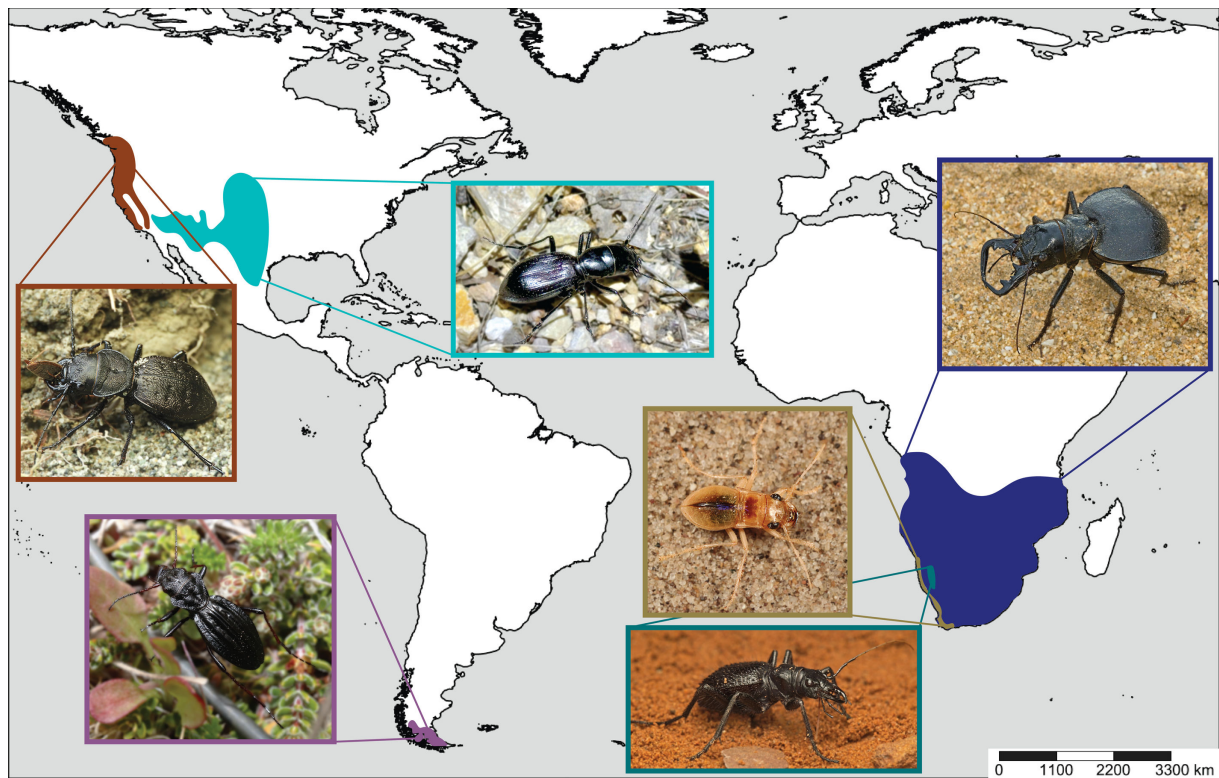


Figure 1. Global distribution and habitus of tiger beetle genera currently in the tribe Manticorini. From left to right and top to bottom, with colour denoting range depiction: *Omus*, brown; *Amblycheila*, teal; *Manticora*, dark blue; *Picrochile*, purple; *Platychile*, beige; *Mantica*, dark green. Image credits from left to right and top to bottom: Ming-Hsun Chou, Ted MacRae, Petr Mückstein, Michael Weymann, Ye Liu, Petr Mückstein.

distributions can also result from dispersal, wherein a lineage comes to occupy a previously unoccupied area, serving as an alternative hypothesis to vicariance [5]. Unlike vicariance, dispersal can potentially occur at any point throughout a lineage's history, including ancient range expansions with subsequent contraction via regional extinction, or recent long-distance dispersal. However, the timing of such events dictates potential routes and barriers encountered, as well as the likelihood of either scenario. For some lineages, both vicariance and dispersal may have played significant roles in shaping the diversification and modern distributions of taxa [6–9]. Thus, a key aspect of inferring historical biogeography is identifying the influence of these different factors in forging a lineage's evolutionary history, wherein timing plays a critical role.

Following the rise of molecular data and Bayesian phylogenetic inference, the geologic timing of lineage origination and divergences between taxa can be estimated using the fossil record with increasing precision [10–13]. Combined with model-based approaches to ancestral range reconstruction [14,15], the likelihood of different historical biogeographic scenarios can be assessed quantitatively. Despite these advances and considering the number of taxa proposed to exhibit Gondwanan distributions, relatively few studies have tested Gondwanan vicariance hypotheses using molecular phylogenetics, divergence time estimation and ancestral state reconstruction. Phylogenetically based support for Gondwanan vicariant origins has been demonstrated in several arthropod groups (e.g. scarab beetles [16,17], water beetles [18–20], centipedes [21], harvestmen arachnids [22,23]), plants [24–26] and some vertebrate lineages (e.g. lungfish [27] and geckos [28]). Other Gondwanan distributions have been demonstrated to be the result of long-distance dispersal, post supercontinent breakup (e.g. clusioid plants [29] cichlid fish [30], Malagasy iguanas [31], Australian tarantulas [32]) or even coincidentally (e.g. osteoglossiform fishes [33]).

A far less common biogeographic pattern is American amphitropical disjunction, where sister taxa are found either south or north of the Western Hemisphere tropics [34–36]. This phenomenon is most well known in plant taxa, where approximately 200 examples have been identified, but again relatively few studies have tested this pattern phylogenetically, finding it to be the result of Cenozoic long-distance dispersal (reviewed in [36]) rather than vicariance [35]. Unlike plant taxa, a very limited number of purported examples of animal taxa exhibit this type of disjunct distribution (reviewed in [34]). Notably those that have been proposed are temperate insect lineages, particularly among Hymenoptera (bees and ants [37]) as well as predaceous ground beetles (Carabidae and Trachypachidae [38]). However, to date only a handful of studies (five to our knowledge), all focused on Hymenoptera, used phylogenetic analysis to test the existence of this type of disjunction within animal taxa [39–43].

The tiger beetle tribe Manticorini (Coleoptera, Cicindelidae) currently [44], consists of large-bodied (over 10 mm), flightless, predatory beetles [45]. Their present-day distribution may reflect a Gondwanan vicariance (figure 1), with most genera found in southern Africa, one in Patagonia, and two Nearctic representatives [45]. Furthermore, a sister relationship between the Patagonian genus *Picrochile*, and the Nearctic *Amblycheila* (figure 1) was previously recovered using molecular phylogenetic evidence [46,47], suggesting the rare American amphitropical disjunction may be present in this tribe. Similar to other tiger beetles, the larval stage of Manticorini is a highly specialized, sedentary ambush predator, attacking prey from its burrow [45,48]. Phylogenetic analysis of gene fragments all supported members of this tribe as sister to all other tiger beetles, albeit differing relationships, and none with complete generic taxon sampling [47]. Altogether, the extremely limited dispersal capabilities in all life stages, potential presence of two different disjunct distributions among extant taxa, and sister-placement to

all other cicindelids make the Manticorini an ideal model to test the hypothesis of Gondwanan vicariant origins and existence of an American amphitropical disjunction. Furthermore, these genera and the tiger beetle family as a whole, have not been subject to a focused phylogenomic study. Prior phylogenomic studies on the suborder Adephaga to which Cicindelidae belongs, have incorporated cicindelid species [49,50] but none had complete tribal representation involving two or more species. Thus, monophyly of many tribes, including the Manticorini, have yet to be tested using genomic-scale data. As mentioned above, evidence from the fossil record is essential for reliable divergence time estimation [12]. Unfortunately, there is currently no support for crown Cicindelidae fossil placement below the family level [51], thus no direct evidence regarding divergence times associated with Manticorini. The most extensively sampled phylogenomic study for Cicindelidae, Cardenas *et al.* [50], included only two representatives of the tribe while inferring a time-tree using dense fossil sampling from across the suborder Adephaga. While ideal for supporting outgroup fossil placement and comparative purposes, it does not estimate divergence times for critical Southern Hemisphere genera.

Here we assemble a phylogenomic dataset for the following purposes: (i) to test the monophyly of Manticorini [47] in relation to all other cicindelid tribes; (ii) to robustly infer relationships among manticorine genera; (iii) to produce a time-calibrated phylogeny of Manticorini for divergence time estimation; and (iv) for ancestral range reconstruction to test the hypothesis that the Southern Hemisphere disjunct distribution exhibited by some genera is the result of Gondwanan vicariance, and for the presence of an American amphitropical disjunction.

2. Material and methods

(a) Taxon sampling

Ingroup sampling consisted of 39 Cicindelidae (electronic supplementary material, table S1), prioritizing the tribe Manticorini as currently defined [44,52]. Sampling for Manticorini was complete at the genus-level, with the following species-level sampling of non-monotypic genera: four of eight *Amblycheila* species, four of 15 *Manticora*, and all five currently recognized species of *Omus* [52]. For monotypic genera, a single individual of the extremely rare *Mantica horni* was sampled, with multiple individuals of *Picnochile fallaciosa* (three) and *Platychile pallida* (two). However, while establishing our preferred tree topology (i.e. the one recovered across most analyses), only the individual sample with highest locus recovery was included (electronic supplementary material, table S1). Sampling was complete for cicindelid tribes, each represented by at least two taxa, with increased representation of Cicidelini given its diversity. Outgroup sampling comprised 12 members of Carabidae and two Trachypachidae (electronic supplementary material, table S1). The relatively dense outgroup sampling was selected in order to: (i) test monophyly of the family Cicindelidae; (ii) allow dense fossil calibrations based on Cardenas *et al.* [50]; (iii) strongly test placement of members of Manticorini previously proposed as sister to all other cicindelids [47].

(b) Data matrix assembly

Data sources included both novel high throughput sequencing reads as well as existing raw read data (electronic supplementary material, table S1). For new data, equimolar pooled libraries were prepared for Illumina sequencing by: technicians at Rapid Genomics (RG, now part of LGC Biosearch Technologies) following their workflow with proprietary chemistry; or generated in-house at the Natural History Museum of Geneva (NHMG) using a SRSly NanoPlus Uracil+library preparation kit (Claret Bioscience), and the University of Kansas with an xGen EZ Library Prep Kit (Integrated DNA Technologies) and xGen UDI indices. To generate ultraconserved element (UCE) read data, libraries at RG were enriched with the full Adephaga 2.9Kv1 probe set [53], then sequenced using 150 base pair (bp) paired-end reads (pe) on a NovaSeq 6000 at RG; those at NHMG were enriched for the GeaSub-2.9Kv1 probe set [50] via a myBaits custom hybridization capture kits (Arbor Biosciences) then sequenced with 100 bp pe reads on a NovaSeq 6000 at the Institute of Genetics and Genomics in Geneva (iGE3). Low-coverage whole genome data was produced by performing 150 bp pe sequencing on a NovaSeq 6000 at RG, and 150 bp pe sequencing with a NovaSeq X at the Oklahoma Medical Research Foundation (OMRF).

All raw reads were trimmed using fastP version (ver.) 0.32.2 [54] and the commands: `q 20 l 30 w 10 --detect_adapter_for_pe --overrepresentation_analysis -g`. Trimmed reads were inspected with FastQC ver. 0.11.9 [55] to verify they were free of contamination and overrepresented sequences. As needed, subsequent trimming of sequences was performed with Cutadapt ver. 3.2 [56]. For some cleaned reads, additional quality filtering was implemented via bbduk ver. 39.01 [57] under default settings, to aid assembly. Assembly of cleaned reads into contigs was done in SPAdes 3.15.5 [58] under default settings. For new whole genome data, standard assembly metrics were generated via BUSCO ver. 5.7.1 [59] and QUAST ver. 5.2.0 [60] (electronic supplementary material, table S2).

Post assembly, the Phyluce ver. 1.7.3 pipeline [61] was primarily used to process the data. First, the Adephaga 2.9Kv1 probe set was aligned to the assembled transcriptomic and genome contigs using the command `phyluce_probe_run_multiple_lastz_sqlite` with minimum identity set to 80% and coverage at 50%, to prevent potential off target sequence identification [62]. Identified UCE loci were then extracted using the commands `phyluce_probe_slice_sequence_from_genomes` with flank set to 400 following Cardenas *et al.* [50], and subsequently placed alongside targeted capture assemblies. Together, all contigs were matched to the Adephaga 2.9Kv1 probe set using the commands `phyluce_assembly_match_contigs_to_probes` with minimum identity set to 75% and coverage at 70% to improve locus recovery. The identified UCE loci (electronic supplementary material, table S1) were extracted using `phyluce_assembly_get_fastas_from_match_counts` into a uniform ('monolithic') matrix containing all loci found across all taxa. This uniform matrix containing all UCE loci was separated into individual

loci (phyluce_assembly_explode_get_fastas_file) and aligned outside of Phyluce using MAFFT ver. 7.475 [63] and the -auto command. Aligned loci were then trimmed using Gblocks [64] under the default settings within Phyluce. Finally, two different completeness matrices were constructed by Phyluce: a 55% complete matrix (hereafter 55% CM) with a minimum of 45% taxon occupancy per locus, and a 65% complete matrix (hereafter 65 perc) with a minimum of 35% taxon occupancy per locus. AMAS [65] was used to compute standard summary statistics on the two matrices following concatenation (electronic supplementary material, table S3), and custom R-scripts by Alexander [66] were implemented to estimate missing data on a per taxon basis for each matrix (electronic supplementary material, table S1).

(c) Phylogenomic analyses

Bayesian inference (BI) was implemented with ExaBayes ver. 1.5.1 [67] on both concatenated, unpartitioned matrices, performing two independent runs with four coupled chains for either 10 million generations, or until the average standard deviation of split frequencies was ≤ 5 indicating convergence. Tracer ver. 1.7.2 [68] was used to visualize Markov chain Monte Carlo (MCMC) chain behaviour and verify effective sample sizes were ≥ 200 , indicating stationarity had been achieved. Posterior probability for topological support was established using the posterior distribution generated by the MCMC process associated with tree search. A posterior probability (pp) of ≥ 0.95 was considered as strong topological support [69]. Maximum likelihood analysis (ML) was conducted in IQ-TREE ver. 2.4.0 (IQ-TREE) [70] on both concatenated matrices that had been partitioned in PartitionFinder ver. 2.7 [71] via the sliding-window sites characteristics based on entropy (SWSC-en) model [72]. Topological support measures were established using 1000 ultrafast bootstrap (UFB) replicates [73]. An (UFB) value of ≥ 95 was considered as strong support [73]. Gene- and corrected site-based concordance factors [74,75] using the 55% CM were implemented in IQ-TREE on our preferred tree to assess congruence of recovered relationships with the underlying data.

To account for incomplete lineage sorting [76,77], we took a summary-based coalescent approach to generate a species tree using ASTRAL-III ver. 5.7.4 (ASTRAL) [78]. Locus trees for analysis by ASTRAL were generated with IQ-TREE ver. 2.4.0 using ModelFinder [79] to establish the best model and partitioning scheme for ML based on the Bayesian information criterion (i.e. MFP+MERGE), for each locus, for both completeness matrices. ASTRAL topological support was estimated using local posterior probability, wherein a recovered value of ≥ 0.95 indicates high confidence [80].

(d) Time-calibration approach

We used BEAST ver. 1.10.5 [81] to perform relaxed-clock divergence time estimation in a Bayesian framework on our preferred tree topology. Carabid outgroups were constrained to the relationships in Cardenas *et al.* [50] in order to apply comparable fossil calibrations. To make our data set computationally tractable in BEAST, we used a 'gene-shopping' approach with SortaDate [82]. Details of our time-calibration methods are provided in the electronic supplementary material, appendix.

(e) Historical biogeographic reconstruction

Ancestral range states were inferred using the resultant BEAST time tree (electronic supplementary material, figure S10), the R ver. 4.4.3 programme [83] and the R package BioGeoBEARS ver. 1.1.3 [84]. The chronogram was pruned to remove all non-Cicindelidae taxa for all analyses. Two different time trees and corresponding datasets were established: one with full Cicindelidae (FC) sampling; and Manticorini only (MO), where all non-manticorine (as newly defined below) cicindelid taxa were also pruned. Regions of known distribution were included in analyses and taxa coded as present (1) or absent (0) based on specimen label data and the literature [53] (see electronic supplementary material). The following models for ancestral range estimation were deployed in a likelihood framework: dispersal extinction cladogenesis (DEC) [14,85], dispersal-vicariance analysis (DIVALIKE) [86] and Bayesian analysis of biogeography (BAYAREALIKE) [87]. We also ran analyses with and without the +j parameter used to model founder event speciation [15,88]. All inferences were time stratified, being divided into five time slices with corresponding dispersal rate modifiers and area adjacency matrices (see electronic supplementary material) to account for plate tectonic movement. These time slices were: 0–20 Ma, 20–40 Ma, 40–80 Ma, 80–120 Ma and 120–165 Ma. Calculations for dispersal modification and establishment of area adjacency primarily followed Toussaint *et al.* [19], given similarity in focal taxa' ranges and overlap in time slices. North and South America were the exception, and were not coded as adjacent during the 80–120 Ma and 40–80 Ma time slices in our analyses. These two land masses were widely separated after 140 Ma and only come back into contact post 70 Ma (see §4 below). Comparisons of model fit were performed in BioGeoBEARS using AICc weights.

3. Results

(a) UCE data recovery for analysis

A total of 2887 UCE loci was recovered among our 53 taxa using the Adephaga 2.9Kv1 probe set. Among our ingroup the highest number of loci recovered was 2204 loci in the genome of *A. schwarzi*, and the lowest was 227 from a museum specimen of *Platycheile pallida* (electronic supplementary material, table S1). Our 55% CM consisted of 1699 total UCE loci with median locus recovery at 1073 loci and a range of 485–1679 (electronic supplementary material, table S1). The total concatenated

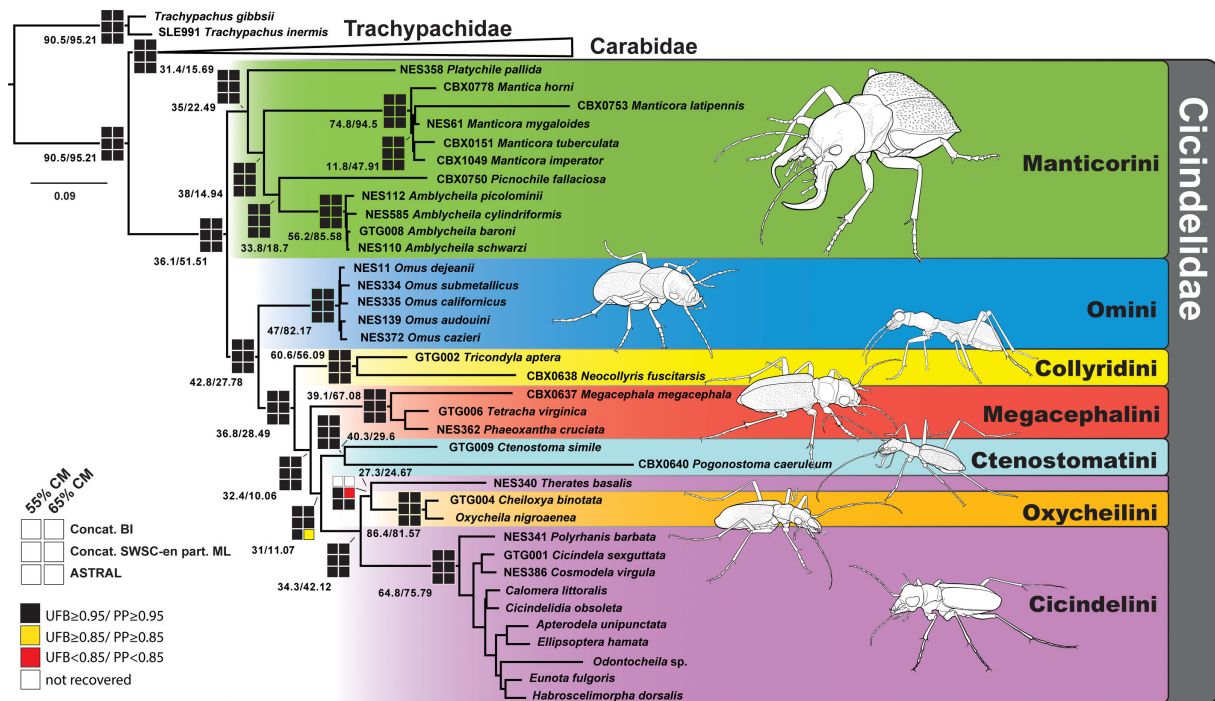


Figure 2. Phylogenetic relationships among tribes of Cicindelidae based on ultraconserved element (UCE) data. Numbers at nodes are site- and gene concordance factors, respectively. Boxes at nodes allow comparison across analyses, with position identifying the analysis and support for shown relationship indicated by colour in key in lower left. Scale bar below the tree in the top left shows expected number of substitutions per site. Abbreviations: CM, complete matrix; Concat., concatenated; BI, Bayesian inference; SWSC-en part., sliding widow sites characteristics based on entropy partitioning scheme; ML, maximum likelihood; UFB, ultrafast bootstrap; PP, posterior probability.

alignment length of the 55% CM was 489 380 nucleotides (electronic supplementary material, table S3). The 65% CM had a total of 1056 loci, a median recovery of 780 loci and range of 333–1047 (electronic supplementary material, table S1). Concatenated alignment length for the 65% CM was 316 428 nucleotides (electronic supplementary material, table S3). Further information for both concatenated matrices is available in electronic supplementary material, table S3. Taxon-specific locus recovery information is available in electronic supplementary material, table S1.

(b) Phylogenomic inference

All phylogenetic analyses produced highly resolved trees, with the majority of relationships strongly supported and largely congruent (figure 2), regardless of inference method (i.e. BI: electronic supplementary material, figures S1–S2; ML: electronic supplementary material, figures S3–S4; ASTRAL: electronic supplementary material, figures S5–S6). All analyses unambiguously rejected monophyly of Manticorini *sensu* Duran & Gough [44]. *Omus* was strongly supported as monophyletic (figure 2, electronic supplementary material, figures S7–S8) and sister to all other tiger beetles, rather than closely related to *Amblycheila*, *Mantica*, *Manticora*, *Picnochile* and *Platychile*, which form a separate, strongly supported clade (figure 2), the Manticorini *sensu novo*. Relationships within Manticorini *s. nov.* were fully resolved and strongly supported, with *Platychile* sister to all other genera (figure 2), and *Mantica*+*Manticora* reciprocally monophyletic (figure 2) and sister to the New World genera *Amblycheila*+*Picnochile* (figure 2). This clade is hereafter referred to as the MMPA clade. All analyses strongly supported monophyly of the remaining tribes of Cicindelidae as currently defined, with the exception of Cicindelini (figure 2). This tribe was paraphyletic with respect to Oxycheilini in all but one analysis. Results differed only regarding placement of *Therates*: either as sister to Oxycheilini alone (i.e. all ML and ASTRAL analyses: electronic supplementary material, figures S3–S6), sister to Oxycheilini + the remaining Cicindelini (BI 55% CM: electronic supplementary material, figure S3; BI: electronic supplementary material, figures S1–S2), or sister to all other Cicindelini (BI 65% CM: electronic supplementary material; figure S2).

(c) Divergence time estimation

We recovered crown Cicindelidae as originating during the Late Jurassic, approximately 161 Ma (138–186 Ma 95% highest posterior density—HPD; electronic supplementary material, figure S10). The most recent common ancestor (MRCA) of Manticorini *s. nov.* likely evolved by at least the Early Cretaceous (figure 3) with our median estimate being approximately 135 Ma (111–159 Ma 95% HPD), but potentially as early as the Late Jurassic (electronic supplementary material, figure S10). The common ancestor of the MMPA clade originated approximately 115 Ma during the Cretaceous. However, the split between the New World *Picnochile* and *Amblycheila* is estimated to be much older than that of the African *Mantica* and *Manticora*, at around 100 Ma (99.6 Ma) as compared to 17.7 Ma. The most diverse genera in the tribe, *Manticora* and *Amblycheila*, are recovered with relatively young crown ages, having evolved during the Neogene at 22.6 Ma and 4.4 Ma, respectively (figure 3; electronic supplementary material, figure S10). The common ancestor of *Omus* and all other tiger beetles likely originated approximately

140 Ma, with *Omus* having a young crown age, comparable with that of *Amblycheila* at 5.8 Ma (electronic supplementary material, figure S10), and a very deep divergence from its sister clade.

(d) Ancestral range reconstruction

Analysis of full Cicindelidae (FC) sampling gave different ancestral state reconstruction results (electronic supplementary material, figures S11–S16) than Manticorini only (MO) (electronic supplementary material, figures S17–S22; figure 3). The greatest differences in ancestral state reconstruction involved inclusion of the +j parameter (figure 3; electronic supplementary material, figures S23–S34). Adding this resulted in identical reconstructions regardless of underlying model or sampling strategy (i.e. FC versus MO) (electronic supplementary material, figures S23–S34). Comparisons of model fit under both FC and MO sampling identified the DIVALIKE+j model as being most fit, with DEC+j second, and BAYAREALIKE+j third (electronic supplementary material, table S5). The models without the +j parameter proceeded in the same order for both FC and MO sampling, with DIVALIKE identified as the best fit, including during separate testing without any +j parameter models (electronic supplementary material, table S5).

4. Discussion

(a) Phylogeny of the Manticorini

Our phylogenomic analyses produced trees that were primarily congruent and strongly supported (figure 2). The main topological differences were associated with the Cicindelini, specifically the relationship of *Therates* to Oxycheilini and the rest of the cicindelina taxa, with most trees suggesting paraphyly of Cicindelini as currently defined (figure 2; electronic supplementary material, figures S1–S6). Previous studies [49,50] have placed *Therates* as sister to Oxycheilini, the primary result recovered here (figure 2; electronic supplementary material, figures S3–S6). Relationships among the tribes of Cicindelidae recovered here differ from all previous studies with complete tribal sampling [46,47]. However, our focus was testing the monophyly of Manticorini, not inferring the phylogeny of the family, which will require more extensive sampling.

Our results completely reject the monophyly of Manticorini *sensu* Duran & Gough [44], as *Omus* was strongly supported as being sister to all other tiger beetles across all analyses (figure 2). This necessitates resurrection of the monotypic tribe Omini (figure 2). With the separation of *Omus*, Manticorini *sensu nov.* now consists primarily of Southern Hemisphere species (with the exception of *Amblycheila*), all of which are united by features associated with the larval stage (i.e. a triangular ligula and two pairs of hooks on abdominal segment V [48]). Relationships within the Manticorini differ significantly from previous studies, with the exception of the sister group relationship between the New World *Picnochile* and *Amblycheila* [46,47]. We consistently recover *Platychile* as sister to all other manticorines with strong support (figure 2). This monotypic genus contains a single southwest African coastal beach dwelling species, *P. pallida* (figure 1). This species is estimated to have diverged around 131 million years ago and represents the sister lineage to all Manticorini (figure 3; electronic supplementary material, figure S10). Thus, *Platychile pallida* is an interesting relictual paleoendemic taxon with a highly specialized ecology [90,91]. Given invasion of sandy beach habitats has been demonstrated to occur numerous times independently in other beetle lineages like carabids and staphylinids [92,93]; it is likely that tiger beetles have as well, as beach dwelling forms occur in several different genera in other tribes. This makes it likely that the beach dwelling nature of *P. pallida* is a derived, rather than ancestral, feature for all Manticorini. Sandy beaches, while dynamic, are among the most resilient types of coastline [94], potentially affording the evolutionary persistence of this unique representative of such an ancient lineage. Despite its derived ecology, which likely produced its light colouration relative to other manticorines (figure 1), there are plesiomorphic character states not found in any other manticorine genera, supporting its placement as sister. These include retention of a vestigial lacinia in the larva [95] and the adult mandibles having two terebral teeth (three in both sexes of *Mantica*, all *Manticora* males and some females) with a monocuspitate terebral tooth 1 (tooth 1 triscuspitate in *Amblycheila* and *Picnochile*) [96].

This study represents the first molecular phylogeny to include both *Mantica* and *Manticora*. The close relationship between these two genera has always been hypothesized based on morphology (figure 1) and is confirmed here (figure 2). Recovery of the MMPA clade is novel and strongly congruent with the underlying genomic data, receiving site concordance factors (figure 2; electronic supplementary material, figure S7) higher than for the entire tribe itself. Morphologically, the MMPA clade is united by a larval feature consisting of a derived pattern of stemmata reduction [48]. The close relationship between the Western Hemisphere genera *Amblycheila* and *Picnochile* had been inferred previously through morphology [96] and gene fragment analysis [47], and is here highly supported using genomic-scale data (figure 2). Interestingly, the two most diverse genera, *Amblycheila* and *Manticora* have comparatively young crown ages (22.6 and 4.4 Ma, respectively) with late Cenozoic diversification, but represent ancient lineages that diverged from their most recent common ancestor with other genera (excluding *Mantica*) nearly a hundred million years ago (figure 3).

(b) Historical biogeography of the Manticorini

Our divergence time estimates for crown Cicindelidae and crown Manticorini at approximately 161 Ma and approximately 135 Ma, respectively were similar to those of Cardenas *et al.* [50] (166 Ma and 135 Ma, respectively), placing the origin of Manticorini in the Early Cretaceous, prior to the breakup of West Gondwana (figure 3) [3]. Based on model comparison, the DIVALIKE+j

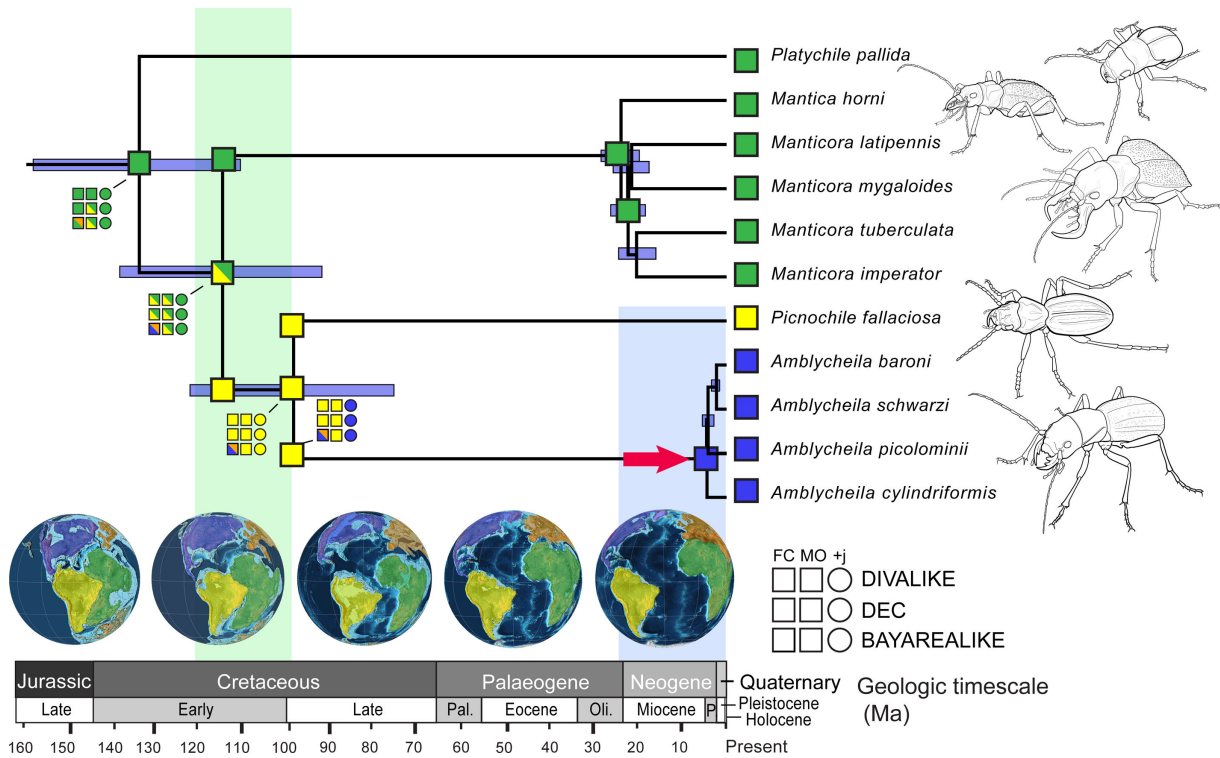


Figure 3. Historical biogeography of Manticorini. Blue bars at nodes within time tree depict 95% highest posterior density for ages. Squares at tips display present distribution of species, those at nodes show most likely range occupied by the ancestor. For particular nodes, results across all reconstructions are depicted, with a key to analyses in the bottom right. Red arrow indicates inferred dispersal event. Paleogeographic maps modified from Scotese [4]. Geographic range reconstruction colours correspond to continental colours in maps: dark green, Africa; yellow, South America; dark blue, North America; orange, Palaearctic region. Light green rectangle in back denotes timeframe for break of Gondwana according to Seton *et al.* [3]. Light blue rectangle depicts timeframe for collision of South America with North America [89]. Abbreviations: FC, full-Cicindelidae sampling; MO, Manticorini-only sampling; +j, the jump-dispersal parameter.

ancestral range reconstruction under MO sampling had the highest overall log likelihood and best fit based on AICc weight, with DEC+j and BAYAREALIKE+j under this sampling regime being the second and third highest, respectively (electronic supplementary material, table S5). The application of the +j parameter which models founder event speciation [15], has been the subject of some controversy [97,98]. Our results are consistent with previous observations [15,97] that models with the +j parameter receive consistently higher likelihoods than those without the parameter (electronic supplementary material, table S5). Concerningly, inclusion of the +j parameter produced identical reconstructions, regardless of the underlying model and sampling strategy (figure 3; electronic supplementary material, figures S23–S34). Importantly, the biogeographic history inferred for the Manticorini under the +j parameter was biologically unrealistic, a trend also noted in a published critique [97]. The +j model infers a founder speciation event in North America within the stem lineage of *Amblycheila* involving dispersal out of South America at approximately 100 Ma (figure 3). At this point in time, North America as part of Laurasia, had fully separated from South America by 140 Ma and the Caribbean Arc had yet to accrete (this does not occur until after 70 Ma) [3], resulting in these two continents being widely separated (figure 3). Given this, and that all modern manticorines are highly dispersal limited at each life stage, that particular founder event scenario is unlikely. It has been demonstrated in scenarios where several extant taxa are limited to a single biogeographic area, models including the +j parameter are usually the best fitting [15,98]. Additionally, the +j parameter exacerbates the issue of limited anagenetic modelling present within both it and the DEC model, resulting in cladogenetic changes being favoured [97], as seen in our results (figure 3). Thus, we find our dataset where: (i) all taxa are highly dispersal limited, (ii) occupy distinct biogeographic areas, and (iii) have numerous successive long branches creating extensive opportunity for anagenetic range evolution, presents a particular scenario where the +j parameter fits the data better, but is unlikely to result in an accurate ancestral range reconstruction. Therefore, we do not consider any model including the +j parameter for ancestral range reconstruction, despite a greater model fit.

Among the models without the +j parameter, DIVALIKE with FC sampling attained the overall highest corrected Akaike criterion weight (AICcW) at 0.927 (electronic supplementary material, table S5). While AICcW cannot be directly compared between the different datasets (FC and MO), AICcW does measure the probability that a model is the best model given the data, with a score of >0.90 considered as identifying a single best model [99]. Only the DIVALIKE model under FC sampling achieved identification as the single best model by AICcW (electronic supplementary material, table S5) and is therefore selected as our preferred reconstruction (figure 3). AICcW comparison of all other models, including those with the +j parameter, failed to achieve support as a single best model among those tested (electronic supplementary material, table S5). Furthermore, the DIVALIKE model with FC sampling reconstruction inferred the most ancestral ranges in common with all other models across sampling schemes (figure 3), while also being the most biologically realistic.

Under our preferred ancestral state reconstruction (figure 3), the common ancestor of Manticorini was present in Africa with subsequent range expansion to include South America, resulting in the common ancestor of the MMPA clade being distributed across West Gondwana at the beginning of its break-up, with the vicariant event resulting in the stem lineage

Mantica + *Manticora* becoming isolated on Africa and stem *Picnochile* + *Amblycheila* on South America. The common ancestor of *Picnochile* + *Amblycheila* is reconstructed as having been distributed in South America alone around 100 Ma. Notably the stem lineage leading to *Amblycheila* is also inferred as being initially present within South America, invoking dispersal to North America sometime between approximately 100 Ma and approximately 4.5 Ma as the MRCA of *Amblycheila* is inferred to have been North American (figure 3). Thus, under this scenario, the American amphitropical disjunct distribution between *Amblycheila* and *Picnochile* (figure 1) is the result of some form of dispersal. While there is no direct evidence to support the precise timing or exact nature of the dispersal event in the ancestor of *Amblycheila*, using inferences from other taxa we can propose a most likely scenario.

American amphitropical disjunction (hereafter AAD) has been documented most often in plant taxa, with few proposed cases in animals [34–36]. Among animals, insects form the majority of taxa exhibiting this distribution [37,38]. Two primary hypotheses to explain the origin of these disjunctions are: (i) long-distance dispersal; (ii) range expansion with subsequent fragmentation from regional extinction [34,100]. The majority of phylogenetically based ancestral range reconstruction studies come from plants, which support long-distance dispersal from North to South America sometime during the Pliocene, particularly for temperate taxa [35,36,100]. Even fewer phylogenetically based studies of AAD in animals are available; these include: *Diadasia* bees [39], eucerine bees [40], andrenine bees [43] and *Dorymyrmex* ants [41,42]. In most investigations, the origin of the disjunction in these arid-adapted species is the Miocene and the directionality is primarily from South America to North. This pattern of south to north AAD occurring later during the Miocene is also seen in arid-adapted plants as well, a pattern in contrast to temperate plants with AAD distributions [36]. Further differing from the pattern in plants, these insect studies concluded northward range expansions associated with favourable cooling temperatures and expansion of open arid environments in South America during the Miocene as the most likely explanation [39–41]. Stepping-stone dispersal along the eastern slope of the Andes has been proposed as a way to facilitate such northward range expansion in arid adapted taxa found south of the Amazon [34,101]. However, empirical support for this Andean corridor in association with AAD has been inconclusive [102] or lacking [100]. The habitat fragmentation model provides testable corollaries in that stepping-stone distributions should be evident by (i) the presence of extinct forms in the fossil record, (ii) persistence of relictual lineages near or within the corridor, and (iii) disjunct sister taxa situated close to the tropical barrier. Unlike the hymenopteran taxa above, which Simpson [36] would categorize as having distributions that significantly enter the tropical regions in both North and South America, therefore exhibiting (iii) in support of some form of stepping-stone range expansion, *Picnochile* and *Amblycheila* are an example of a classic arid-adapted AAD taxon where the South American taxon is found in the temperate steppe of Patagonia and the North American taxon in subtropical steppe, outside the tropical barrier with no known intervening taxa (figure 1) [36]. Given a much older relictual taxon has survived in Africa, long persistence time of lineages within this tribe (figure 3), and proximity of *Picnochile* to the southern Andes (figure 1), it seems unlikely that a single representative from such a stepping-stone dispersal scenario would not have persisted somewhere along the cordilleran corridor between Patagonia and Northern Mexico (figure 1), had such an event occurred. Considering the popularity of tiger beetles, large size of extant manticorine species, and extensive collecting efforts in South America, we similarly find the existence of an undiscovered manticorine lineage somewhere along the base of the Andes unlikely. However, this possibility cannot be entirely ruled out. Therefore, the present AAD in Manticorini does not exhibit any empirical evidence in support of the stepping-stone habitat fragmentation model.

Another important difference between the Hymenoptera AAD examples which have winged adults and our taxa, is that all extant adult manticorines are large-bodied (over 10 mm) and flightless, making them relatively more dispersal limited. Furthermore, the larval stage of all species is a burrowing, primarily sedentary, ambush predator, seemingly highly dependent upon the surrounding soil composition. While it is possible that similar to ratite birds [103,104], the manticorine ancestor was fully winged, given *Platychile* is completely apterous, as likely are all other genera (see electronic supplementary material), it is also possible that aptery is the ancestral state for the tribe. Bird-mediated dispersal is a potential mechanism for passive long-distance dispersal in flightless insects, particularly beetles [105,106]. Larvae [107] and eggs—including those from predated gravid females [108], have been demonstrated to survive the digestive tract of birds, in support of this, and birds serve as significant predators of both adult and larval tiger beetles [45], including *Amblycheila* (see electronic supplementary material). Bird-mediated dispersal, including by ingestion (endozoochory), is also considered the most likely mechanism for long-distance dispersal in desert plants which show the most similar AAD pattern [36]. Therefore, we ultimately find a single long-distance dispersal event to North America sometime after 20 Ma during the Miocene as the most likely scenario, given: the lack of evidence for range expansion, strong similarity of the AAD pattern to desert plants, the young age of crown *Amblycheila*, and that this time period coincides with emerging land mass between North America and South America associated with the uplift of the Panama Arc [109] following collision of North American and South American tectonic plates between 23 and 25 Ma [89].

5. Conclusions

Phylogenomic analyses produced completely resolved trees whose relationships were strongly supported and robust to different analytical approaches (figure 2). The phylogeny supports a new definition of the tribe Manticorini whose constituents consist of Southern Hemisphere taxa with one notable exception, the North American genus *Amblycheila* (figure 1). The time tree of Manticorini *sensu novo* revealed ancient divergences between most genera, along with surprisingly young crown ages (figure 3). The monotypic genus *Platychile* is the sister lineage to all other genera, representing a relict taxon that diverged from its closest living relatives approximately 131 million years ago, and exhibits a likely derived beach-dwelling ecology, inhabiting a narrow range along the Atlantic coast of Africa (figure 1). Ancestral range reconstruction supports an African origin for

Manticorini during the Early Cretaceous, with West Gondwanan vicariance resulting in the disjunct distribution between the Patagonian taxon *Picnochile* and the southern African genera *Manticora* and *Mantica* (figure 3). Our analyses place the sole North American manticorine genus, *Amblycheila*, as sister to the Patagonian genus *Picnochile*, having been descended from a common South American ancestor. Thus, we recover an example of an American amphitropical disjunct distribution, a phenomenon rarely demonstrated in animals, particularly with phylogenetically based evidence. Similar to the few other animal examples (notably all insects), our ancestral range reconstruction supports a South American origin for stem *Amblycheila* with dispersal to North America likely happening sometime during the Miocene. There is no empirical evidence to support stepping-stone dispersal involving range expansion and fragmentation, leaving long-distance dispersal as the most likely explanation—similar to other arid-adapted taxa in plants. Ultimately, the diversification of the manticorine tiger beetles has been influenced by both ancient Gondwanan vicariance separating New versus Old World genera, as well as long-distance dispersal from South to North America with subsequent recent diversification. To our knowledge, our study on manticorine tiger beetles is the first to provide phylogenetically based support for an American amphitropical disjunction within a non-hymenopteran animal system. The existence of two distinct types of disjunctions within Manticorini, one stemming from ancient vicariance and the other from recent dispersal, highlights the importance both processes have to play in shaping both diversification and complex modern geographic distributions.

Ethics. Insect specimens used in this research were collected legally with proper permission where applicable. Specific permit information available upon request.

Data accessibility. Newly generated sequence data are available through the National Center for Biotechnology Information (NCBI), Sequence Read Archive (SRA), under BioProject PRJNA1348490. Datasets analysed to produce these results are available through Zenodo [110].

Supplementary material is available online [111].

Declaration of AI use. AI-assisted technologies were used to select the colour scheme for taxon ranges in figure 1.

Authors' contributions. G.T.G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing; S.M.B.: resources, writing—original draft, writing—review and editing; C.R.C.: data curation, resources, writing—original draft; J.G.: data curation, resources, writing—original draft; E.F.A.T.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This project was supported by funding from the National Science Foundation grant DEB# 2208620 and Swiss National Science Foundation grant 310030_200491. E.F.A.T. was also funded by an internal grant of the NHMG.

Acknowledgements. We are indebted to Stephen Baca, Kyleigh Bachelor, Julia Bilat, Ming-Hsun Chou, Rachel Glynn, H       Mottaz and Jamie Ramirez for wet lab procedures and data generation. Michael Balke, Arnaud Faille, R. Dennis Haines, Miroslav Hrd    , Mike Kippenhan, Kelly Miller, Wendy Moore, T. Will Richardson and Peter Sch       are thanked for providing specimens. Marianna Sim       is thanked for access to material from the SDEI M           (Brandenburg). Dave Pearson, J       Wiesner and Dan Duran are thanked for their knowledge and contacts. Computational analyses were run on Northern Arizona University's Monsoon computing cluster funded by Arizona's Technology and Research Initiative Fund. We appreciate Ming-Hsun Chou, Ted MacRae and Michael Weymann for free use of their images.

References

1. Hooker JD. 1844 *The botany of the Antarctic voyage of HMS Discovery ships Erebus and Terror in the years 1839–1843, under the command of captain Sir James Clark Ross*. London, UK: Reeve Brothers. See <https://doi.org/10.5962/bhl.title.16029>.
2. Palin RM, Santosh M. 2021 Plate tectonics: what, where, why, and when? *Gondwana Res.* **100**, 3–24. (doi:10.1016/j.gr.2020.11.001)
3. Seton M *et al.* 2012 Global continental and ocean basin reconstructions since 200Ma. *Earth Sci. Rev.* **113**, 212–270. (doi:10.1016/j.earscirev.2012.03.002)
4. Scotese CR. 2021 An Atlas of phanerozoic paleogeographic maps: the seas come in and the seas go out. *Annu. Rev. Earth Planet. Sci.* **49**, 679–728. (doi:10.1146/annurev-earth-081320-064052)
5. Platnick NI, Nelson G. 1978 A method of analysis for historical biogeography. *Syst. Zool.* **27**, 1. (doi:10.2307/2412808)
6. Korall P, Pryer KM. 2014 Global biogeography of scaly tree ferns (Cyatheaceae): evidence for Gondwanan vicariance and limited transoceanic dispersal. *J. Biogeogr.* **41**, 402–413. (doi:10.1111/jbi.12222)
7. Hedin M, McCormack M, Hedin M, McCormack M. 2017 Biogeographical evidence for common vicariance and rare dispersal in a southern Appalachian harvestman (Sabaconidae, *Sabacon cavicolens*). *J. Biogeogr.* **44**, 1665–1678. (doi:10.1111/jbi.12973)
8. Derkarabetian S, Baker CM, Giribet G. 2021 Complex patterns of Gondwanan biogeography revealed in a dispersal-limited arachnid. *J. Biogeogr.* **48**, 1336–1352. (doi:10.1111/jbi.14080)
9. Foley S, Krehenwinkel H, Cheng DQ, Piel WH. 2021 Phylogenomic analyses reveal a Gondwanan origin and repeated out of India colonizations into Asia by tarantulas (Araneae: Theraphosidae). *PeerJ* **9**, e11162. (doi:10.7717/peerj.11162)
10. Yang Z, Rannala B. 2006 Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Mol. Biol. Evol.* **23**, 212–226. (doi:10.1093/molbev/msj024)
11. Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006 Relaxed phylogenetics and dating with confidence. *PLoS Biol.* **4**, e88. (doi:10.1371/journal.pbio.0040088)
12. Heath TA. 2012 A hierarchical Bayesian model for calibrating estimates of species divergence times. *Syst. Biol.* **61**, 793–809. (doi:10.1093/sysbio/sys032)
13. Heath TA, Huelsenbeck JP, Stadler T. 2014 The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proc. Natl Acad. Sci. USA* **111**, E2957–E2966. (doi:10.1073/pnas.1319091111)
14. Ree RH, Smith SA. 2008 Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* **57**, 4–14. (doi:10.1080/10635150701883881)

15. Matzke NJ. 2014 Model selection in historical biogeography reveals that founder-event speciation is a crucial process in Island Clades. *Syst. Biol.* **63**, 951–970. (doi:10.1093/sysbio/syu056)
16. Eberle J, Fabrizi S, Lago P, Ahrens D. 2017 A historical biogeography of megadiverse Sericini-another story 'out of Africa'? *Cladistics* **33**, 183–197. (doi:10.1111/cla.12162)
17. Gunter NL, Monteith GB, Cameron SL, Weir TA. 2019 Evidence from Australian mesic zone dung beetles supports their Gondwanan origin and Mesozoic diversification of the Scarabaeinae. *Insect Syst. Evol.* **50**, 162–188. (doi:10.1163/1876312X-00002171)
18. Toussaint EFA, Fikáček M, Short AEZ. 2016 India–Madagascar vicariance explains cascade beetle biogeography. *Biol. J. Linn. Soc.* **118**, 982–991. (doi:10.1111/bj.12791)
19. Toussaint EFA, Bloom D, Short AEZ. 2017 Cretaceous West Gondwana vicariance shaped giant water scavenger beetle biogeography. *J. Biogeogr.* **44**, 1952–1965. (doi:10.1111/jbi.12977)
20. Baca SM, Short AEZ. 2020 Molecular phylogeny of the notomicrine water beetles (Coleoptera: Noteridae) reveals signatures of Gondwanan vicariance and ecological plasticity. *Insect Syst. Divers.* **4**, 1–11. (doi:10.1093/isd/ixaa015)
21. Joshi J, Edgecombe GD, Joshi J, Edgecombe GD. 2019 Evolutionary biogeography of the centipede genus *Ethmostigmus* from Peninsular India: testing an ancient vicariance hypothesis for Old World tropical diversity. *BMC Evol. Biol.* **19**, 41. (doi:10.1186/s12862-019-1367-6)
22. Baker CM, Boyer SL, Giribet G. 2020 A well-resolved transcriptomic phylogeny of the mite harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi) reveals signatures of Gondwanan vicariance. *J. Biogeogr.* **47**, 1345–1361. (doi:10.1111/jbi.13828)
23. Oberski JT, Sharma PP, Jay KR, Coblens MJ, Lemon KA, Johnson JE, Boyer SL. 2018 A dated molecular phylogeny of mite harvestmen (Arachnida: Opiliones: Cyphophthalmi) elucidates ancient diversification dynamics in the Australian Wet Tropics. *Mol. Phylogenet. Evol.* **127**, 813–822. (doi:10.1016/j.ympev.2018.06.029)
24. Beaulieu JM, Tank DC, Donoghue MJ. 2013 A Southern Hemisphere origin for campanulid angiosperms, with traces of the break-up of Gondwana. *BMC Evol. Biol.* **13**, 80. (doi:10.1186/1471-2148-13-80)
25. Cai L, Xi Z, Peterson K, Rushworth C, Beaulieu JM, Davis CC. 2016 Phylogeny of Elatinaceae and the tropical Gondwanan origin of the Centroplacaceae (Malpighiaceae, Elatinaceae) clade. *PLoS One* **11**, e0161881. (doi:10.1371/journal.pone.0161881)
26. Gonçalves DJP, Shimizu GH, Ortiz EM, Jansen RK, Simpson BB. 2020 Historical biogeography of Vochysiaceae reveals an unexpected perspective of plant evolution in the Neotropics. *Am. J. Bot.* **107**, 1004–1020. (doi:10.1002/ajb2.1502)
27. Brownstein CD, Harrington RC, Near TJ. 2023 The biogeography of extant lungfishes traces the breakup of Gondwana. *J. Biogeogr.* **50**, 1191–1198. (doi:10.1111/jbi.14609)
28. Gamble T, Bauer AM, Greenbaum E, Jackman TR. 2008 Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *J. Biogeogr.* **35**, 88–104. (doi:10.1111/j.1365-2699.2007.01770.x)
29. Ruhfel BR, Bove CP, Philbrick CT, Davis CC. 2016 Dispersal largely explains the Gondwanan distribution of the ancient tropical clusioid plant clade. *Am. J. Bot.* **103**, 1117–1128. (doi:10.3732/ajb.1500537)
30. Matschiner M, Böhne A, Ronco F, Salzburger W. 2020 The genomic timeline of cichlid fish diversification across continents. *Nat. Commun.* **11**, 5895. (doi:10.1038/s41467-020-17827-9)
31. Welt RS, Raxworthy CJ. 2022 Dispersal, not vicariance, explains the biogeographic origin of iguanas on Madagascar. *Mol. Phylogenet. Evol.* **167**, 107345. (doi:10.1016/j.ympev.2021.107345)
32. Briggs EJ, Foley S, Cook LG. 2025 Gondwanan relic or recent arrival? The biogeographic origins and systematics of Australian tarantulas. *Mol. Phylogenet. Evol.* **204**, 108246. (doi:10.1016/j.ympev.2024.108246)
33. Capobianco A, Friedman M, Capobianco A, Friedman M. 2024 Fossils indicate marine dispersal in osteoglossid fishes, a classic example of continental vicariance. *Proc. R. Soc. B* **291**. (doi:10.1098/rspb.2024.1293)
34. Raven PH. 1963 Amphitropical relationships in the floras of North and South America. *Q. Rev. Biol.* **38**, 151–177. (doi:10.1086/403797)
35. Wen J, Ickert-bond SM. 2009 Evolution of the Madrean–Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. *J. Syst. Evol.* **47**, 331–348. (doi:10.1111/j.1759-6831.2009.00054.x)
36. Simpson MG, Johnson LA, Villaverde T, Guillems CM. 2017 American amphitropical disjuncts: perspectives from vascular plant analyses and prospects for future research. *Am. J. Bot.* **104**, 1600–1650. (doi:10.3732/ajb.1700308)
37. Michener CD. 1979 Biogeography of the Bees. *Ann. Missouri Bot. Garden* **66**, 277. (doi:10.2307/2398833)
38. Erwin TL. 1979 Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In *Carabid beetles: their evolution, natural history and classification* (eds TL Erwin, GE Ball, DR Whitehead, AL Halpern), pp. 539–592. Dordrecht, The Netherlands: Springer. (doi:10.1007/978-94-009-9628-1_30)
39. Wilson JS, Carril OM, Sipes SD. 2014 Revisiting the Great American Biotic Interchange through analyses of amphitropical bees. *Ecography* **37**, 791–796. (doi:10.1111/ecog.00663)
40. Freitas FV, Branstetter MG, Casali DM, Aguiar AJC, Griswold T, Almeida EAB. 2022 Phylogenomic dating and Bayesian biogeography illuminate an antitropical pattern for eucerine bees. *J. Biogeogr.* **49**, 1034–1047. (doi:10.1111/jbi.14359)
41. Oberski JT. 2022 First phylogenomic assessment of the amphitropical new world ant genus *Dorymyrmex* (Hymenoptera: Formicidae), a longstanding taxonomic puzzle. *Insect Syst. Div.* **6**, 1–10. (doi:10.1093/isd/ixab022)
42. Oberski JT. 2025 Ultraconserved element (UCE) phylogenomics illuminates the evolutionary history and biogeography of *Dorymyrmex* pyramid ants. *Syst. Entomol.* **50**, 325–348. (doi:10.1111/syen.12658)
43. Ramos KS, Martins AC, Melo GAR. 2022 Evolution of andrenine bees reveals a long and complex history of faunal interchanges through the Americas during the Mesozoic and Cenozoic. *Mol. Phylogenet. Evol.* **172**, 107484. (doi:10.1016/j.ympev.2022.107484)
44. Duran DP, Gough HM. 2020 Validation of tiger beetles as distinct family (Coleoptera: Cicindelidae), review and reclassification of tribal relationships. *Syst. Entomol.* **45**, 723–729. (doi:10.1111/syen.12440)
45. Pearson DL, Vogler AP. 2001 *Tiger beetles: the evolution, ecology, and diversity of the cicindelids*. Ithaca, NY: Cornell University Press.
46. Galián J, Hogan JE, Vogler AP. 2002 The origin of multiple sex chromosomes in tiger beetles. *Mol. Biol. Evol.* **19**, 1792–1796. (doi:10.1093/oxfordjournals.molbev.a004001)
47. Gough HM, Duran DP, Kawahara AY, Toussaint EFA. 2019 A comprehensive molecular phylogeny of tiger beetles (Coleoptera, Carabidae, Cicindelinae). *Syst. Entomol.* **44**, 305–321. (doi:10.1111/syen.12324)
48. Glynn RD, Ramirez J, Chambers A, Gustafson GT. 2026 Larval description and chaetotaxic analysis of the Mojave giant Tiger beetle, *Amblycheila schwarzi* Horn (Coleoptera: Cicindelidae). *Coleopt. Bull.* **80**, 1–12. (doi:10.1649/0010-065X-80.1.1)
49. Baca SM, Gustafson GT, Alexander AM, Gough HM, Toussaint EFA. 2021 Integrative phylogenomics reveals a Permian origin of Adephaga beetles. *Syst. Entomol.* **46**, 968–990. (doi:10.1111/syen.12506)

50. Cardenas CR, Gustafson GT, Toussaint EFA. 2025 Global integration of phylogenomic data and fine-scale partitioning strategies refine the evolutionary tree of Adephaga beetles. *BSSB* **4**, 1–35. (doi:10.18061/bssb.v4i1.10345)
51. Schmidt J, Scholz S, Wiesner J, Will K. 2023 MicroCT data provide evidence correcting the previous misidentification of an Eocene amber beetle (Coleoptera, Cicindelidae) as an extant species. *Sci. Rep.* **13**, 14743. (doi:10.1038/s41598-023-39158-7)
52. Wiesner J. 2020 *Checklist of the tiger beetles of the world*, 2nd edn. Borsdorf, Germany: Edition Winterwork.
53. Gustafson GT, Alexander A, Sproul JS, Pflug JM, Maddison DR, Short AEZ. 2019 Ultraconserved element (UCE) probe set design: base genome and initial design parameters critical for optimization. *Ecol. Evol.* **9**, 6933–6948. (doi:10.1002/ece3.5260)
54. Chen S, Zhou Y, Chen Y, Gu J. 2018 fastp: an ultra-fast all-in-one FASTQ preprocessor. *Bioinformatics* **34**, i884–i890. (doi:10.1093/bioinformatics/bty560)
55. Andrews S. 2010 FastQC: a quality control tool for high throughput sequence data. See <https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>.
56. Martin M. 2011 Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet. J.* **17**, 10. (doi:10.14806/ej.17.1.200)
57. Bushnell B. 2014 BBTools software package. See <https://github.com/bbushnell/BBTools>.
58. Bankevich A *et al.* 2012 SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *J. Comput. Biol.* **19**, 455–477. (doi:10.1089/cmb.2012.0021)
59. Simão FA, Waterhouse RM, Ioannidis P, Kriventseva EV, Zdobnov EM. 2015 BUSCO: assessing genome assembly and annotation completeness with single-copy orthologs. *Bioinformatics* **31**, 3210–3212. (doi:10.1093/bioinformatics/btv351)
60. Mikhchenko A, Pribelski AD, Saveliev V, Antipov D, Gurevich A. 2018 Versatile genome assembly evaluation with QUAST-LG. *Bioinformatics* **34**, i142–i150. (doi:10.1093/bioinformatics/bty266)
61. Faircloth BC. 2016 PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* **32**, 786–788. (doi:10.1093/bioinformatics/btv646)
62. Bossert S, Danforth BN. 2018 On the universality of target-enrichment baits for phylogenomic research. *Methods Ecol. Evol.* **9**, 1453–1460. (doi:10.1111/2041-210X.12988)
63. Katoh K, Standley DM. 2013 MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780. (doi:10.1093/molbev/mst010)
64. Castresana J. 2000 Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol. Biol. Evol.* **17**, 540–552. (doi:10.1093/oxfordjournals.molbev.a026334)
65. Borowiec ML. 2016 AMAS: a fast tool for alignment and computing of summary statistics. *Pearl* **4**, e1660. (doi:10.7717/peerj.1660)
66. Alexander A. 2019 Missing_data_per_sample v0.0. See https://github.com/laninsky/Missing_data_for_UCE_loci.
67. Aberer AJ, Kobert K, Stamatakis A. 2014 ExaBayes: massively parallel Bayesian tree inference for the whole-genome era. *Mol. Biol. Evol.* **31**, 2553–2556. (doi:10.1093/molbev/msu236)
68. Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018 Posterior summarization in bayesian phylogenetics using tracer 1.7. *Syst. Biol.* **67**, 901–904. (doi:10.1093/sysbio/syy032)
69. Erixon P, Sennblad B, Britton T, Oxelman B. 2003 Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. *Syst. Biol.* **52**, 665–673. (doi:10.1080/10635150390235485)
70. Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R. 2020 IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Mol. Biol. Evol.* **37**, 1530–1534. (doi:10.1093/molbev/msaa015)
71. Lanfear R, Calcott B, Kainer D, Mayer C, Stamatakis A. 2014 Selecting optimal partitioning schemes for phylogenomic datasets. *BMC Evol. Biol.* **14**, 82. (doi:10.1186/1471-2148-14-82)
72. Tagliacollo VA, Lanfear R. 2018 Estimating improved partitioning schemes for ultraconserved elements. *Mol. Biol. Evol.* **35**, 1798–1811. (doi:10.1093/molbev/msy069)
73. Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS. 2018 UFBoot2: improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.* **35**, 518–522. (doi:10.1093/molbev/msx281)
74. Minh BQ, Hahn MW, Lanfear R. 2020 New methods to calculate concordance factors for phylogenomic datasets. *Mol. Biol. Evol.* **37**, 2727–2733. (doi:10.1093/molbev/msaa106)
75. Mo YK, Lanfear R, Hahn MW, Minh BQ. 2023 Updated site concordance factors minimize effects of homoplasy and taxon sampling. *Bioinformatics* **39**, btac741. (doi:10.1093/bioinformatics/btac741)
76. Maddison WP. 1997 Gene trees in species trees. *Syst. Biol.* **46**, 523–536. (doi:10.1093/sysbio/46.3.523)
77. Edwards SV. 2009 Is a new and general theory of molecular systematics emerging? *Evolution (N Y)* **63**, 1–19. (doi:10.1111/j.1558-5646.2008.00549.x)
78. Zhang C, Rabiee M, Sayyari E, Mirarab S. 2018 ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinform.* **19**, 153. (doi:10.1186/s12859-018-2129-y)
79. Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS. 2017 ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. Methods* **14**, 587–589. (doi:10.1038/nmeth.4285)
80. Sayyari E, Mirarab S. 2016 Fast coalescent-based computation of local branch support from quartet frequencies. *Mol. Biol. Evol.* **33**, 1654–1668. (doi:10.1093/molbev/msw079)
81. Suchard MA, Lemey P, Baele G, Ayres DL, Drummond AJ, Rambaut A. 2018 Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evol.* **4**, vey016. (doi:10.1093/ve/vey016)
82. Smith SA, Brown JW, Walker JF. 2018 So many genes, so little time: a practical approach to divergence-time estimation in the genomic era. *PLoS One* **13**, e0197433. (doi:10.1371/journal.pone.0197433)
83. R Core Team. 2025 R: a language and environment for statistical computing. R Foundation for Statistical Computing. See <https://www.r-project.org/>.
84. Matzke NJ. 2018 BioGeoBEARS: biogeography with Bayesian (and likelihood) evolutionary analysis with R scripts. Zenodo. (doi:10.5281/zenodo.1478250)
85. Ree RH, Moore BR, Webb CO, Donoghue MJ. 2005 A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution (NY)* **59**, 2299–2311.
86. Ronquist F. 1997 Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Syst. Biol.* **46**, 195–203. (doi:10.1093/sysbio/46.1.195)
87. Landis MJ, Matzke NJ, Moore BR, Huelsenbeck JP. 2013 Bayesian analysis of biogeography when the number of areas is large. *Syst. Biol.* **62**, 789–804. (doi:10.1093/sysbio/syt040)
88. Matzke NJ. 2013 Probabilistic historical biogeography: new models for founder-even speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Front. Biogeogr.* **5**, 242–248. (doi:10.21425/F5FBG19694)
89. Farris DW *et al.* 2011 Fracturing of the Panamanian Isthmus during initial collision with South America. *Geology* **39**, 1007–1010. (doi:10.1130/G32237.1)
90. Grandcolas P, Nattier R, Trewick S. 2014 Relict species: a relict concept? *Trends Ecol. Evol. (Amst.)* **29**, 655–663. (doi:10.1016/j.tree.2014.10.002)
91. Oliver PM, McDonald PJ. 2016 Young relicts and old relicts: a novel palaeoendemic vertebrate from the Australian Central Uplands. *R. Soc. Open Sci.* **3**, 160018. (doi:10.1098/rsos.160018)

92. Maddison DR, Maruyama M. 2019 Phylogenetic relationships and convergent evolution of ocean-shore ground beetles (Coleoptera: Carabidae: Trechinae: Bembidion and relatives). *Syst. Entomol.* **44**, 39–60. (doi:10.1111/syen.12307)
93. Song JH, Ahn KJ. 2013 Molecular phylogeny reveals multiple origins of seashore colonisation in the genus *Aleochara* Gravenhorst (Coleoptera: Staphylinidae: Aleocharinae). *Invertebr. Syst.* **27**, 239–244. (doi:10.1071/IS12040)
94. McLachlan A, Defeo O. 2017 *The ecology of sandy shores*, 3rd edition. San Diego, CA: Academic Press.
95. Arndt E. 1998 Larval description and natural history data of two genera of tiger beetles from southern Africa (Coleoptera, Cicindelidae). *Entomologische Blätter Für Biologie Und Systematik Der Käfer* **94**, 33–45.
96. Ball GE, Acorn JH, Shpeley D. 2011 Mandibles and labrum-epipharynx of tiger beetles: basic structure and evolution (Coleoptera, Carabidae, Cicindelidae). *Zookeys* **147**, 39–83. (doi:10.3897/zookeys.147.2052)
97. Ree RH, Sanmartin I. 2018 Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *J. Biogeogr.* **45**, 741–749. (doi:10.1111/jbi.13173)
98. Matzke NJ. 2022 Statistical comparison of DEC and DEC+J is identical to comparison of two ClaSSE submodels, and is therefore valid. *J. Biogeogr.* **49**, 1805–1824. (doi:10.1111/jbi.14346)
99. Portet S. 2020 A primer on model selection using the Akaike information criterion. *Infect. Dis. Model.* **5**, 111–128. (doi:10.1016/j.idm.2019.12.010)
100. Guillems CM, Hasenstab-Lehman KE, Mabry ME, Simpson MG. 2017 Memoirs of a frequent flier: phylogenomics reveals 18 long-distance dispersals between North America and South America in the popcorn flowers (Asteraceae: Helianthus). *Am. J. Bot.* **104**, 1717–1728. (doi:10.3732/ajb.1700369)
101. Solbrig OT. 1972 The floristic disjunctions between the 'Monte' in Argentina and the 'Sonoran Desert' in Mexico and the United States. *Ann. Missouri Bot. Garden* **59**, 218. (doi:10.2307/2394754)
102. Frost LA, Tyson SM, Lu-Irving P, O'Leary N, Olmstead RG. 2017 Origins of North American arid-land Verbenaceae: more than one way to skin a cat. *Am. J. Bot.* **104**, 1708–1716. (doi:10.3732/ajb.1700292)
103. Yonezawa T *et al.* 2017 Phylogenomics and morphology of extinct paleognaths reveal the origin and evolution of the ratites. *Curr. Biol.* **27**, 68–77. (doi:10.1016/j.cub.2016.10.029)
104. Widrig K, Alfieri F, Kuo PC, James H, Field DJ. 2025 Quantitative analysis of stem-paleognath flight capabilities sheds light on ratite dispersal and flight loss. *Biol. Lett.* **21**, 20250320. (doi:10.1098/rsbl.2025.0320)
105. Claridge EM, Gillespie RG, Brewer MS, Roderick GK. 2017 Stepping-stones across space and time: repeated radiation of Pacific flightless broad-nosed weevils (Coleoptera: Curculionidae: Entiminae: *Rhyncogonus*). *J. Biogeogr.* **44**, 784–796. (doi:10.1111/jbi.12901)
106. Baird HP, Shin S, Oberprieler RG, Hullé M, Vernon P, Moon KL, Adams RH, McKenna DD, Chown SL. 2021 Fifty million years of beetle evolution along the Antarctic Polar Front. *Proc. Natl Acad. Sci. USA* **118**, e2017384118. (doi:10.1073/pnas.2017384118)
107. Green AJ, Sánchez MI. 2006 Passive internal dispersal of insect larvae by migratory birds. *Biol. Lett.* **2**, 55–57. (doi:10.1098/rsbl.2005.0413)
108. Suetsugu K, Nozaki T, Hirota SK, Funaki S, Ito K, Isagi Y, Suyama Y, Kaneko S. 2023 Phylogeographical evidence for historical long-distance dispersal in the flightless stick insect *Ramulus mikado*. *Proc. R. Soc. B* **290**, 20231708. (doi:10.1098/rspb.2023.1708)
109. O'Dea A *et al.* 2016 Formation of the Isthmus of Panama. *Sci. Adv.* **2**, e1600883. (doi:10.1126/sciadv.1600883)
110. Gustafson G, Byee S, Cardenas C, Gauthier J, Toussaint E. 2026 Phylogenomics of Manticorini tiger beetles supports ancient Gondwanan vicariance and recent American amphitropical disjunction. Zenodo. (doi:10.5281/zenodo.19239119)
111. Gustafson G, Bybee S, Cardenas CR, Gauthier J, Toussaint EFA. 2026 Supplementary material from: Phylogenomics of Manticorini tiger beetles supports ancient Gondwanan vicariance and recent American amphitropical disjunction. Figshare. (doi:10.6084/m9.figshare.c.8552390)