

RESEARCH PAPER

Phylogeny, diversity and biogeography of flightless amphipacific lymanthine weevils (Coleoptera: Curculionidae: Molytinae)

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Abstract. We use DNA sequence data to generate the first phylogenetic hypothesis for the weevil tribe Lymanthini. These are leaf litter inhabiting beetles generally regarded as restricted to the New World and taxonomically arranged in two subtribes, 11 genera and some 150 named species. An additional genus of questionable affinities to the tribe, *Devernodes* Grebennikov, 2018, has five described species in Southeastern Asia. All these beetles are flightless and some have eyes reduced in size or absent, traits normally associated with limited dispersal capacity. We performed a phylogenetic analysis of 153 terminals (50 of them belong to Lymanthini representing *Devernodes* and all but three named genera) based on 4,174 bp alignment of one mitochondrial (cox1) and two nuclear fragments (ITS2 and 28S). We find that both Lymanthini subtribes Lymanthina and Caecossosina are monophyletic, the latter sister to the amphipacific tribe Anchonini. The Asian genus *Devernodes* is deeply nested among American Lymanthina. The clade of Anchonini plus Lymanthini is consistently recovered outside of the CCCMS clade of “higher” weevils (Curculioninae, Conoderinae, Cossoninae, Molytinae and Scolytinae). We hypothesize that the polished head capsule of adult beetles is an apomorphy of Anchonini and Lymanthini, the 8-segmented antennal funicle is an apomorphy of Anchonini plus Caecossosina. We attribute the origin of the currently observed amphipacific distribution of Lymanthina to normal ecological dispersal facilitated by the warmer periods of the Cenozoic such as the Eocene, and by presently submerged Arctic land bridges. Using parsimony we hypothesize a North American origin for the Anchonini plus Lymanthini crown group, as well as that of Lymanthina. We argue that *Bronchotibia adunatus* Poinar & Legalov, 2021, a Dominican amber adult weevil fossil, is not a member of Lymanthini and re-classify it as Curculionidae *incertae sedis*. We present an image gallery of 28 Lymanthini specimens to document the morphological diversity of the tribe. We hypothesize the existence of unnamed American genera of Lymanthina and make public the DNA-barcode dataset of 89 Lymanthini specimens.

Key words. Coleoptera, Anchonini, Caecossosina, Lymanthina, DNA barcode, ITS2, 28S, phylogeny, forest litter, biogeography

Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:C9E0D0F0-F4F7-4946-B2B2-83E1F9F706E2>

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Introduction

Lymanthini, the focal group of this paper, are small to medium-sized elongate weevils (Figs 1, 2) distributed between the USA and Bolivia, including the West Indies (Fig. 3). Taxonomic boundaries and placement of these beetles have always been, and remain, murky (e.g., HOWDEN 1992). As most recently defined (ALONSO-ZARAZAGA & LYAL 1999, LYAL 2014) and excluding the subsequently discovered Asian genus *Devernodes* Grebennikov, 2018, extant Lymanthini diversity is composed of two subtribes, 11

valid genera, and some 150 described species, almost 100 of these placed in the genus *Theognete* Champion, 1902. Adult Lymanthini are flightless, have eyes variously reduced in size or absent, and are collected in primary forests by sifting leaf litter, or in the soil, or rarely, in caves. Immature stages of Lymanthini have been described only once, as larvae of an unknown genus “near *Ithaura* Pascoe and *Dioptrophorus* Faust” found in sweet potatoes in Mexico (ANDERSON 1952). No reliable fossil records of the tribe are known. Assignment to the tribe of the monotypic genus



Bronchotibia Poinar & Legalov, 2021 described based on a Dominican amber fossil (POINAR & LEGALOV 2021) was based on non-informative characters employed outside of the phylogenetic framework and must be re-interpreted (see Discussion).

The weevil tribe Lymantini has at least three scientifically intriguing peculiarities. Firstly, the monophyly of the tribe remains untested and the sister group unknown. Secondly, the number of named Lymantini species is likely highly underestimated. Thirdly, although exclusively flightless, often with reduced eyes, and biologically linked with primary wet forests (and, therefore, presumably severely restricted in their dispersal capacity), this New World taxon has been recently tentatively reported from Southeastern Asia (GREBENNIKOV 2018) implying an amphi-Pacific distribution for the tribe. This paper is our attempt to shed the first evolutionary light on all these issues.

The monophyly of the tribe Lymantini, although never explicitly challenged, has never been tested in a formal phylogenetic analysis. The taxonomic recognition of the tribe implicitly suggesting its monophyly was historically pivoted on the biological association of these weevils with the forest leaf litter or the soil, on their coherent North American distribution, and two potential morphological apomorphies (Fig. 4). Firstly, at least the eyed members of Lymantini are immediately recognizable among almost all weevils by having their eyes "... placed on the rostral part of the head, which is often sharply delimited from the main head capsule, sometimes by a dorsal, lateral, and even ventral groove" (LYAL 2014; a similar condition is also found in some Cycloterini, Phrynixini and Orthorhinini; LYAL 2014). Three Lymantini genera forming the subtribe Caecossionina, as well two cave species of the genus *Lymantes* Schoenherr, 1838, although possessing the transverse rostral groove, are eyeless. Secondly, all Lymantini examined in this respect have the female hemisternites IX undivided by a transverse membrane. This character state was previously called "fused coxite-stylus" (HOWDEN 1992) or "lack styli on the coxites" (ANDERSON 2016). If indeed monophyletic, the sister group of the tribe Lymantini is entirely unknown, while its taxonomic assignment oscillates between Molytinae and Cossoninae (reviewed in HOWDEN 1992). Remarkably, the tribe's putative sole Asian genus *Devernodes* was resolved as a sister to the primarily American tribe Anchonini (GREBENNIKOV & ANDERSON 2021a) although this was without the inclusion of data about undescribed Lymantini presented here. Even more surprising, this moderately supported clade in a molecular phylogeny was placed outside of the large and strongly supported CCCMS clade of "higher" weevils (Curculioninae, Conoderinae, Cossoninae, Molytinae and Scolytinae), to which both Lymantini and Anchonini are assigned taxonomically.

Besides uncertain monophyly and phylogenetic placement, Lymantini are likely acutely under-sampled, understudied, and, therefore, remain largely unknown to science. During the 30+ years of Lymantini studies, one of us (RA) accumulated specimens of multiple unnamed species and perhaps genera. The assumption of under representation

was corroborated by the recent revision of the Mesoamerican genus *Theognete*, which increased the number of named species from one to 94 (ANDERSON 2010). If the same ratio remains true throughout the rest of the tribe, Lymantini extant diversity might rival that of amphibians (about 5,700 species) or mammals (about 5,400 species).

Two recent developments triggered our study. Firstly, the newly described genus *Devernodes* containing five new species from Southern China, Vietnam and Malaysia was tentatively assigned to the otherwise exclusively American tribe Lymantini (GREBENNIKOV 2018). Consistent with the rest of Lymantini, all species of *Devernodes* are wingless and found by sifting forest leaf litter. Moreover, all species of *Devernodes* have both putative Lymantini morphological synapomorphies: the peculiar constriction separating the eye-bearing rostrum from the head capsule, as well as the undivided female hemisternite IX (Fig. 4). At the time of the discovery of *Devernodes*, no Mesoamerican Lymantini were available for DNA sequencing and, therefore, assignment of this Asian genus to the tribe was made based on similarities, rather than on a formal phylogenetic analysis. Secondly, this genus of questionable relationship to Lymantini was resolved as a moderately supported sister to the re-defined, monophyletic, and primarily Mesoamerican flightless tribe Anchonini (GREBENNIKOV & ANDERSON 2021a). The latter clade is morphologically supported by the antennal funicle consisting of eight (not seven or less) antennomeres. Curiously, the same trait is also diagnostic for the sympatric Lymantini subtribe Caecossionina uniting all eyeless members of the latter tribe (excepting two convergent eyeless cave *Lymantes* species) and, therefore, "bridging the gap" between both Anchonini and Lymantini. Lacking any Mesoamerican Lymantini in the analysis, and assuming *Devernodes* represented Lymantini, we suggested (GREBENNIKOV & ANDERSON 2021a) that *Devernodes*, Lymantina, Caecossionina and Anchonini might form a clade supported by at least one morphological apomorphy: the polished head capsule of adult beetles. Remarkably, so defined, this group corresponds to "Anchonina" by CHAMPION (1902: 66, 1903). This author emphasised the same morphological character ("... recognizable by their globose, deeply inserted, almost smooth head...") and provided two large plates of high-quality Anchonini and Lymantini illustrations. In 2021, however, we lacked sufficient DNA data and, therefore, were unable to test the monophyly of CHAMPION's "Anchonina".

Results of GREBENNIKOV (2018) and GREBENNIKOV & ANDERSON (2021a), therefore, strongly suggested a Lymantini-focused phylogenetic analysis designed to test the following predictions:

- 1) All Mesoamerican Lymantini family- and genus-group taxa, as defined in LYAL (2014), that is the tribe, both subtribes and all non-monotypic genera, are monophyletic.
- 2) Monophyletic Asian *Devernodes* has its sister among American Lymantini and if so, then a plausible interpretation might be offered to explain the disjunct amphi-Pacific distribution of these low-dispersing terrestrial animals.
- 3) The polished head capsule is a synapomorphy of Anchonini and Lymantini (= "Anchonina" of CHAMPION 1902, 1903).

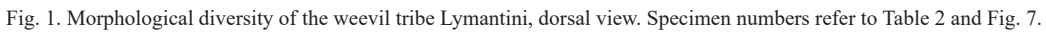




Fig. 2. Morphological diversity of the weevil tribe Lymanitini, lateral view. Specimen numbers refer to Table 2 and Fig. 7.

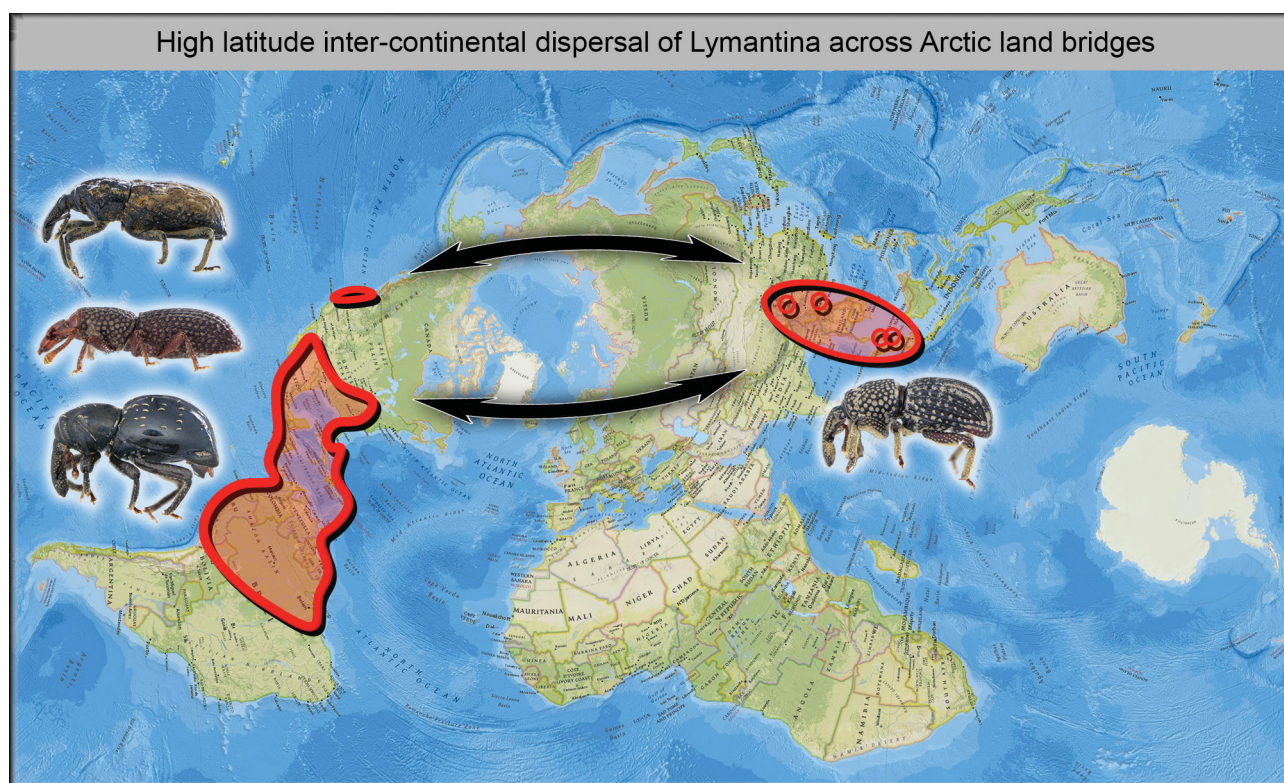


Fig. 3. Geographical distribution and hypothesized overland dispersal routes of recent Lymantrina.

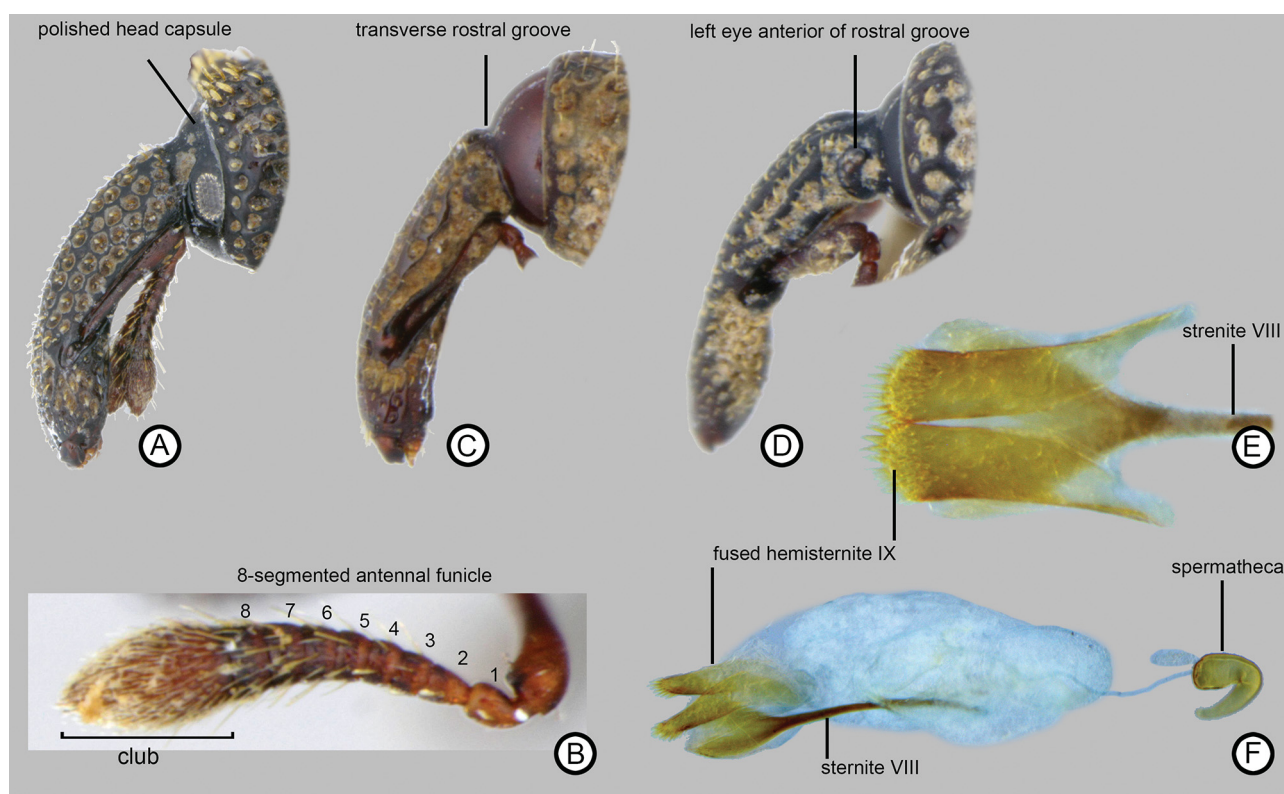


Fig. 4. Morphological diagnostic features and possible apomorphies of Anchonini (A, B) and Lymantrini (C–F). A, C, D: head, left lateral view; B: left antenna; E, F: female genitalia and apical sclerites (E: ventral, F: right dorso-lateral). A: *Titilayo geiseri* Cristóvão & Lyal, 2018; B: *T. barclayi* Cristóvão & Lyal, 2018; C: *Lymantrina scrobicollis* Gyllenhal, 1838; D–F: *Devernodes chthonia* Grebennikov, 2018. A, B: from GREBENNIKOV & ANDERSON (2021a); E, F: from GREBENNIKOV (2018).



Fig. 5. Morphological diversity of the weevil tribe Lymantini, antennae. Specimen numbers refer to Table 2 and Fig. 7.

4) the 8-segmented antennal funicle is a synapomorphy of Anchonini and Caecossosina.

5) The tribe Lymantini is outside the CCCMS clade of “higher” weevils.

6) The tribe Lymantini contains unnamed genera.

This paper is our attempt to test all these predictions using the newly constructed first phylogenetic tree of American Lymantini and their relatives, itself based on the newly generated DNA data. Our more inclusive goal is to establish a baseline for the further research of these and related organisms by releasing their genetic, morphological and geographical data. Specifically, we want to document the morphological diversity of Lymantini, output an on-line DNA-barcode (HEBERT et al. 2003) dataset of these organisms, and generate their first phylogenetic tree, the latter likely including representatives of unnamed genera awaiting formal description. Overall we designed this paper to trigger and facilitate further evolutionary research of these morphologically distinct, diverse, and acutely understudied organisms.

Material and methods

Sampling of Mesoamerican Lymantini. Herein newly sequenced adult specimens of Mesoamerican Lymantini were sifted from forest leaf litter using hand-held sifters, with subsequent extraction of live specimens using suspended Winkler funnels. Live adults were preserved in 96% ethanol and subsequently sorted, imaged, and processed for DNA barcoding, mounted on pins, and stored in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC, Ottawa) or the Canadian Museum of Nature (CMN, Ottawa). Images and geographic data of each herein reported 50 Lymantini specimens (and of all non-Lymantini outgroups used in the analysis, Table 2) are available online in the public datasets of the Barcode of Life Data System (BOLD, RATNASINGHAM & HEBERT 2007); see below.

DNA sequencing. Three DNA fragments were sequenced and analyzed (Table 1, fragment abbreviations are in brackets): mitochondrial cytochrome c oxidase subunit I (COI, the DNA barcode fragment), nuclear internal transcribed spacer 2 (ITS2) and nuclear 28S ribosomal DNA (28S). Sequencing of DNA was made at the Canadian Centre for DNA Barcode (<http://ccdb.ca/>) using standard protocols. The primers are listed in Table 1 in GREBENNIKOV (2017). All details of the lab work (such as DNA extraction, amplification, PCR protocols), as well as images of the original electropherograms for all specimens, are available online

in BOLD, in two public datasets, each pertaining to one of two herein implemented analyses (see below).

DNA barcode dataset of Lymantini. Our first analysis was to generate and make public the DNA barcode dataset of Lymantini, following the currently accepted tribal limits (even if perhaps non-monophyletic; see Results). By doing this, we wanted to document the genetic, morphological and geographic diversity of Lymantini available to us, even if many of them represent unnamed and/or unidentified genera and/or species. This DNA barcode dataset is designed to facilitate future taxonomic and other research of these beetles by allowing direct online comparison between our specimens and those of others. This dataset contains 89 DNA barcodes of Lymantini, each of them longer than 350 base pairs (bp) and most of them 658 bp. The dataset includes 26 specimens of the Asian genus *Devernodes* (their DNA barcodes first released in GREBENNIKOV 2018), plus 63 newly generated DNA barcodes of American Lymantini. We subjected these DNA barcodes to the standard analytical pipeline procedure implemented in the BOLD website (<http://www.boldsystems.org/>) by clustering them into an unrooted topology using the Neighbour Joining (=NJ) algorithm (BOLD commands “Sequence Analysis: taxon ID tree”). For this purpose, we used the default Kimura 2 model of nucleotide substitutions and selected “BOLD Aligner” for the “Align Sequences” parameter. In this analysis we used the Barcode Index Numbers (BINs, RATNASINGHAM & HEBERT 2013), to identify minimal evolutionary significant units. The resulting topology with GenBank accession numbers of all 89 DNA barcodes of Lymantini are in Supplementary File. The entire dataset is available online as a BOLD public dataset at dx.doi.org/10.5883/DS-VGDS25.

Selection of terminals for a phylogenetic analysis. Our second analysis was a phylogenetic one, based on a three-marker DNA dataset of Lymantini, and designed to test all six predictions made in the Introduction. The ingroup was formed by 45 newly sequenced representatives of Mesoamerican Lymantini (41 of Lymantina and four of Caecossosina) plus five terminals representing all five valid species of the Asian genus *Devernodes*. We used the DNA barcode tree as a guide to maximizing the phylogenetic diversity of the ingroup. The nearest outgroup was formed by 17 representatives of the tribe Anchonini, as suggested by the recovery of *Devernodes* sister to this tribe (GREBENNIKOV & ANDERSON 2021a). The more distant outgroup was formed by 60 representatives of the CCCMS clade other than Anchonini, Lymantini, or *Devernodes*, as well as by 14 representatives of the CEGH clade (Cyclominae, Entiminae, Gonipterini and Hyperinae, SHIN et al. 2017), which forms the sister to the CCCMS clade (SHIN et al. 2017). We specifically included five representatives of the predominantly Australian and New Zealand tribe Phrynixini (Molytinae) because of similarly to Lymantini as at least some Phrynixini have their eye positioned at the base of the rostrum (LYAL 2014). Since the monophyletic subfamily Dryophthorinae consistently branches outside the CCCMS plus CEGH clade, five representatives of this subfamily were added as more distant outgroups. Consi-

Table 1. DNA fragments used in the phylogenetic analyses of Lymantini weevils, followed by total number of sequenced terminals, minimal, maximal, and aligned length of each fragment, and the first and the last position of each aligned fragment in the concatenated matrix.

Fragment	#	min	max	aligned	positions
COI-5P	152	353	658	658	1 to 658
ITS2	133	223	763	2645	659 to 3303
28S	152	341	607	871	3304 to 4174

Table 2. DNA fragments and their GenBank accession numbers of 153 weevil (Coleoptera) specimens used in the three marker phylogenetic analysis of the tribe Lymanini (including 137 newly sequenced fragments shown in **bold**: OL671058–OL671194).

Voucher	Subfamily	Tribe	Genus and/or species	Country	COI	ITS2	28S
431	Molytinae	Molytini	<i>Anchondium unguiculare</i>	Morocco	HM417678	none	KY110382
434	Dryophthorinae	Rhynchophorini	<i>Sphenophorus parumpunctatus</i>	Morocco	HM417724	KY110320	KY110384
487	Molytinae	Emphyastini	<i>Thalasselephas maximus</i>	Russia	HM417677	KY110313	KY110375
703	Molytinae	Pissodini	<i>Pissodes punctatus</i>	China	HQ987002	none	KY110366
704	Molytinae	Ithyporini	<i>Ectatorhinus adamsii</i>	China	HQ987003	KY110315	KY110377
861	Molytinae	none	<i>Zembris perseus</i>	China	HQ987100	MG648823	MG648736
1678	Cossoninae	Rhyncolini	<i>Himatium</i>	Tanzania	JN265954	KY110323	KY110388
1791	Cossoninae	Dryotribini	<i>Trichopentarthrum uluguricus</i>	Tanzania	JN265975	KY110327	KY110392
2288	Molytinae	Lymanini	<i>Devernodes alkippe</i>	China	MH034387	MH034357	MH034414
2533	Molytinae	Aminyopini	<i>Niphadonyx</i>	China	MG648752	MG648826	MG648738
2640	Molytinae	Anchoniini	<i>Himalanchnomus</i>	China	MT889126	MT889147	MT889172
2676	Molytinae	none	<i>Aater gashanensis</i>	China	MG648761	MG648835	MG648747
2723	Molytinae	Aminyopini	<i>Niphades</i>	China	MG648751	MG648825	MG648737
2731	Molytinae	Molytini	<i>Niphadomimus maia</i>	China	KJ427744	KY110324	KY110389
2735	Dryophthorinae	Rhynchophorini	<i>Sitophilus zeamais</i>	China	KJ672255	MG968837	MG968894
2955	Molytinae	Molytini	<i>Lobosoma rausense</i>	Russia	KJ427738	KY110316	KY110378
2968	Entiminae	Alophini	<i>Trichalophus alternatus</i>	Canada	KM538666	MW536413	MW536465
2970	Cossoninae	Rhyncolini	<i>Carphonotus testaceus</i>	Canada	KY110606	KY110309	KY110371
3060	Molytinae	Molytini	<i>Lupangus asterius</i>	Tanzania	KY034280	KY250485	KY250480
3280	Molytinae	Cycloterini	<i>Prothrombosternus tarsalis</i>	Tanzania	KU748541	KY110337	KY110402
3561	Dryophthorinae	Dryophthorini	<i>Dryophthorus</i>	Tanzania	MG968913	MG968814	MG968871
4118	Molytinae	Molytini	<i>Microplinthus</i>	China	MG648755	MG648829	MG648741
4337	Molytinae	Lymanini	<i>Devernodes asteria</i>	Vietnam	MH034376	MH034352	MH034409
4339	Molytinae	Lymanini	<i>Devernodes chthonia</i>	Vietnam	MH034400	MH034364	MH034421
4353	Molytinae	Lithinini	<i>Seleuca</i>	Vietnam	MG648754	MG648828	MG648740
4355	Molytinae	none	<i>Otibazo polyphemus</i>	Vietnam	KJ841732	KY110328	KY110393
4402	Dryophthorinae	Stromboscerini	<i>Nephys argus</i>	Vietnam	MH034380	MH034354	MH034411
4537	Molytinae	Molytini	<i>Morimotoles ismene</i>	China	KJ871649	KY110338	KY110403
4846	Molytinae	Cycloterini	<i>Thrombosternus cucullatus</i>	Tanzania	KJ445714	KY110335	KY110400
4991	Molytinae	Aminyopini	<i>Niphadonothus gentilis</i>	Tanzania	KX360489	KY110336	KY110401
5001	Molytinae	Molytini	<i>Aparopionella elliptica</i>	Tanzania	KX360455	KY110318	KY110381
5402	Entiminae	Cneorhinini	<i>Catapionus mopsus</i>	China	KU748534	MW536396	MW536448
5848	Molytinae	Molytini	<i>Adexius scrobipennis</i>	Poland	KJ445686	KY110305	KY110367
5954	Molytinae	Lymanini	<i>Devernodes drimo</i>	Malaysia	MH034401	MH034365	MH034422
5975	Molytinae	Lymanini	<i>Devernodes methone</i>	Malaysia	MH034390	MH034360	MH034417
6485	Molytinae	Molytini	<i>Plinthus amplicollis</i>	Georgia	KY110617	KY110331	KY110396
6552	Molytinae	Molytini	<i>Aparopion costatum</i>	Georgia	KJ445700	none	KY110387
6608	Molytinae	Molytini	<i>Leiosoma reitteri</i>	Georgia	KJ445698	KY110322	KY110386
6683	Molytinae	Molytini	<i>Euthycus</i>	Taiwan	KJ445702	KY110325	KY110390
6858	Molytinae	Lithinini	<i>Seleuca</i>	Taiwan	KY110611	KY110317	KY110380
7166	Molytinae	Molytini	<i>Typoderus antennarius</i>	Tanzania	KY250487	KY250484	KY250479
7281	Molytinae	Cycloterini	<i>Alloccyloterus circellariceps</i>	Tanzania	MK813366	MK813357	MK813361
7530	Cryptorhynchinae	Cryptorhynchini	<i>Cryptorhynchus lapathi</i>	Russia	KY110605	KY110303	KY110365
7531	Molytinae	Aminyopini	<i>Niphades verrucosus</i>	Russia	KY110610	KY110314	KY110376
8046	Molytinae	Aminyopini	<i>Niphades</i>	Tanzania	MG648748	MG648821	MG648734
8317	Molytinae	Aminyopini	<i>Niphades</i>	Cameroon	MG648749	MG648822	MG648735
8474	Molytinae	Lepyriini	<i>Lepyrus palustris</i>	Poland	KX360483	KY110332	KY110397
8480	Molytinae	Molytini	<i>Leiosoma deflexum</i>	Poland	KY110614	KY110326	KY110391
8484	Molytinae	Trachodini	<i>Trachodes hispidus</i>	Poland	KX360436	KY110307	KY110369
8489	Brachycerinae	Eirrhiniini	<i>Notaris scirpi</i>	Poland	KR736279	MW201453	MW201464
8578	Brachycerinae	Eirrhiniini	<i>Tournotaris bimaculata</i>	Poland	KR736283	MW201456	MW201467
8721	Molytinae	Aminyopini	<i>Oreoscutus</i>	Ethiopia	MG648760	MG648834	MG648746
8878	Molytinae	Molytini	<i>Microplinthus emeishanicus</i>	China	MG648757	MG648831	MG648743
8912	Entiminae	Alophini	<i>Graptus weberi</i>	Czech Rep.	MW536361	MW536409	MW536461
8915	Molytinae	Paipalesomini	<i>Peribleptus</i>	Vietnam	KY110615	KY110329	KY110394
8936	Molytinae	Trachodini	<i>Acicnemis albofasciata</i>	Russia	KY110609	KY110312	KY110374
9056	Entiminae	Nastini	<i>Nastus</i>	Kazakhstan	KY110618	KY110334	KY110399
9187	Molytinae	Anchoniini	<i>Aethiopacorep africanus</i>	Eq. Guinea	MT889122	MT889144	MT889168
9190	Molytinae	Anchoniini	<i>Aethiopacorep africanus</i>	Eq. Guinea	MT889120	MT889142	MT889166
9254	Molytinae	Anchoniini		Eq. Guinea	MT889123	MT889145	MT889169
9337	Molytinae	none	<i>Tazarcus aenea</i>	Tanzania	MK813371	MK813359	MK813363
9542	Molytinae	Anchoniini		Cameroon	MT889109	MT889133	MT889155
9750	Hyperinae	Hyperini	<i>Hypera</i>	Kazakhstan	MW201362	MW201462	MW201475
9802	Molytinae	Anchoniini	<i>Acorep spinosus</i>	Guadeloupe	MT889127	MT889148	MT889173
9804	Molytinae	Anchoniini	<i>Acorep piliger</i>	Guadeloupe	MT889125	none	MT889171
9806	Molytinae	Anchoniini	<i>Ixanchnomus hustachei</i>	Guadeloupe	MT889128	MT889149	MT889174
9807	Molytinae	Anchoniini	<i>Geobysrsa trossula</i>	Guadeloupe	MT889117	MT889139	MT889163
9816	Molytinae	Anchoniini	<i>Leprosomus</i>	Colombia	MT889107	none	MT889153

(continues on the next page)

Table 2. DNA fragments and their GenBank accession numbers of 153 weevil (Coleoptera) specimens used in the three marker phylogenetic analysis of the tribe Lymanini (including 137 newly sequenced fragments shown in **bold**: OL671058–OL671194).

Voucher	Subfamily	Tribe	Genus and/or species	Country	COI	ITS2	28S
9817	Molytinae	Lymantini	<i>Lymanthes scrobicollis</i>	United States	OL671066	OL671163	OL671115
9819	Molytinae	Lymantini	<i>Epibaenus pinicola</i>	Mexico	OL671067	OL671164	OL671116
9821	Molytinae	Lymantini	<i>Theognete cozari</i>	Mexico	OL671065	OL671162	OL671114
9828	Molytinae	Lymantini	<i>Theognete chiapaneca</i>	Mexico	OL671064	OL671161	OL671113
9829	Molytinae	Lymantini	<i>Theognete galvezi</i>	Mexico	OL671081	OL671174	OL671129
9831	Molytinae	Lymantini	<i>Theognete montana</i>	Mexico	OL671105	OL671193	OL671154
9832	Molytinae	Anchonini	<i>Anchonus</i>	Mexico	MT889111	MT889135	MT889157
9834	Molytinae	Anchonini	<i>Anchonus</i>	Mexico	MT889113	none	MT889159
9934	Lixinae	Lixini	<i>Bangasternus orientalis</i>	Tajikistan	MW726818	MW726727	MW726908
9960	Molytinae	Anchonini	<i>Anchonus blatchleyi</i>	Cuba	MT889108	MT889132	MT889154
9968	Molytinae	Cycloterini	<i>Dufauella</i>	Cuba	MT889130	MT889151	MT889176
9972	Dryophthorinae	Stromboscerini	<i>Allaotes niger</i>	Cuba	MN621866	MN621859	MN621862
9985	Lixinae	Cleonini	<i>Leucophyes pedestris</i>	Russia	MW726742	MW726665	MW726832
9989	Lixinae	Cleonini	<i>Pachycerus segnis</i>	Russia	MW726753	MW726674	MW726843
10060	Molytinae	Lymantini		Mexico	OL671072	none	OL671121
10067	Molytinae	Lymantini		Mexico	OL671076	none	OL671125
10070	Molytinae	Cycloterini	<i>Paranchonus</i>	Costa Rica	MT889131	MT889152	MT889177
10071	Molytinae	Anchonini	<i>Anchonus</i>	Costa Rica	MT889114	none	MT889160
10074	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671099	OL671189	OL671148
10075	Molytinae	Lymantini		Mexico	OL671068	OL671165	OL671117
10077	Molytinae	Lymantini		Mexico	OL671074	OL671168	OL671123
10079	Molytinae	Lymantini		Mexico	OL671061	OL671158	OL671110
10080	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671096	OL671186	OL671144
10082	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671070	OL671166	OL671119
10086	Molytinae	Lymantini	<i>Lymanthes</i>	Mexico	OL671058	OL671156	OL671107
10089	Molytinae	Lymantini		Mexico	OL671093	OL671184	OL671141
10092	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671102	none	OL671151
10093	Molytinae	Lymantini	<i>Lymanthes</i>	Mexico	OL671092	none	OL671140
10094	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671075	OL671169	OL671124
10095	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671073	OL671167	OL671122
10101	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671059	OL671157	OL671108
10102	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671083	OL671176	OL671131
10103	Molytinae	Lymantini	<i>Epibaenus</i>	Mexico	OL671091	OL671183	OL671139
10105	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671098	OL671188	OL671147
10313	Molytinae	Conotrachelini	<i>Conotrachelus</i>	United States	MT889115	MT889137	MT889161
10315	Molytinae	Lymantini	<i>Caecossonus</i>	Belize	OL671085	OL671178	OL671133
10325	Entiminae	Sitonini	<i>Sitona</i>	Canada	MW201359	MW201459	MW201472
10326	Entiminae	Alophini	<i>Lepidophorus lineaticollis</i>	Canada	MW536368	MW536417	MW536469
10327	Entiminae	Phyllorhini	<i>Evotus naso</i>	Canada	MW536370	MW536419	MW536471
10329	Molytinae	Lymantini		Mexico	OL671089	OL671181	OL671137
10330	Brachycerinae	Raymondionymini		Mexico	MW201357	MW201458	MW201470
10331	Brachycerinae	Raymondionymini		Mexico	MW201361	MW201461	MW201474
10334	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671095	OL671185	OL671143
10335	Molytinae	Lymantini		Mexico	OL671086	OL671179	OL671134
10338	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671060	none	OL671109
10339	Brachycerinae	n/a	<i>Yagder serratus</i>	Mexico	MW201355	MW201457	MW201468
10341	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671080	OL671173	OL671128
10391	Molytinae	Anchonini	<i>Titilayo barclayi</i>	S. Tome & Pr.	MT889119	MT889141	MT889165
10393	Molytinae	Anchonini	<i>Titilayo geiseri</i>	Guinea	MT889112	MT889136	MT889158
10394	Molytinae	Phrynixini		New Zealand	OL671069	none	OL671118
10395	Molytinae	Phrynixini		New Zealand	OL671100	OL671190	OL671149
10401	Molytinae	Phrynixini		New Zealand	OL671090	OL671182	OL671138
10403	Molytinae	Phrynixini		New Zealand	OL671087	OL671180	OL671135
10404	Molytinae	Phrynixini		New Zealand	OL671084	OL671177	OL671132
10407	Curculioninae	Geochini	<i>Geochus</i>	New Zealand	MT889110	MT889134	MT889156
10443	Entiminae	Ophryastini	<i>Deracanthus</i>	Mongolia	MW536349	MW536391	MW536443
10546	Molytinae	Lymantini	<i>Ithaura</i>	Costa Rica	OL671079	OL671172	none
10548	Molytinae	Lymantini		Costa Rica	OL671078	OL671171	OL671127
10557	Molytinae	Lymantini	<i>Ithaura</i>	Costa Rica	OL671097	none	OL671145
10559	Molytinae	Lymantini		Costa Rica	OL671103	OL671192	OL671152
10584	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671077	OL671170	OL671126
10592	Molytinae	Lymantini	<i>Epibaenus</i>	Mexico	OL671094	none	OL671142
10644	Lixinae	Lixini	<i>Rhinocyllus conicus</i>	Ukraine	MW726746	MW726668	MW726836
10708	Molytinae	Lymantini	<i>Decuanellus</i>	Puerto Rico	OL671101	OL671191	OL671150
10709	Molytinae	Lymantini	<i>Decuanellus</i>	Puerto Rico	OL671082	OL671175	OL671130
10732	Molytinae	Lymantini	<i>Dioprophorus</i>	Mexico	OL671106	OL671194	OL671155
10733	Molytinae	Lymantini		Mexico	OL671088	none	OL671136
10747	Molytinae	Lymantini	<i>Caecossonus</i>	Costa Rica	OL671071	none	OL671120

(continues on the next page)

Table 2. DNA fragments and their GenBank accession numbers of 153 weevil (Coleoptera) specimens used in the three marker phylogenetic analysis of the tribe Lymanitini (including 137 newly sequenced fragments shown in **bold**: OL671058–OL671194).

Voucher	Subfamily	Tribe	Genus and/or species	Country	COI	ITS2	28S
10780	Entiminae	Cneorhini	<i>Attactagenus albinus</i>	Ukraine	MW536374	MW536424	MW536476
10785	Entiminae	Tanymecini	<i>Tanymecus palliatus</i>	Ukraine	MW536341	MW536383	MW536433
10788	Entiminae	Otiorynchini	<i>Otiorynchus albidus</i>	Ukraine	MW536379	MW536430	MW536482
10790	Entiminae	Phyllobiini	<i>Phyllobius oblongus</i>	Ukraine	MW536378	MW536429	MW536481
10801	Molytinae	Mecysolobini	<i>Sternuchopsis</i>	South Africa	MW726787	none	MW726877
10804	Molytinae	Mecysolobini	<i>Sternuchopsis</i>	Madagascar	MW726745	none	MW726835
10810	Molytinae	Anchonini		Cote d'Ivoire	MT889116	MT889138	MT889162
10811	Molytinae	Anchonini		Cote d'Ivoire	MT889129	MT889150	MT889175
10826	Brachycerinae	Raymondionymini	<i>Alaocyba</i>	Italy	MW201354	MW201455	MW201466
10827	Brachycerinae	Raymondionymini	<i>Raymondellus</i>	Italy	MW201353	MW201454	MW201465
10835	Molytinae	Lymanitini	<i>Ithaura</i>	Nicaragua	OL671104	none	OL671153
10836	Molytinae	Lymanitini		Nicaragua	OL671063	OL671160	OL671112
10837	Molytinae	Lymanitini		Nicaragua	OL671062	OL671159	OL671111
10842	Molytinae	Lymanitini	<i>Pseudolaocyba</i>	Guatemala	none	OL671187	OL671146
10853	Molytinae	Mecysolobini	<i>Sternuchopsis</i>	Madagascar	MW726750	MW726671	MW726840
11026	Lixinae	Lixini	<i>Lixus filiformis</i>	Ukraine	MW726777	MW726695	MW726867
11046	Lixinae	Lixini	<i>Lixus rubicundus</i>	Ukraine	MW726793	MW726706	MW726883

dering that either Lymanitini or Anchonini consistently emerged outside of the CCCMS clade (GREBENNIKOV 2018, GREBENNIKOV & ANDERSON 2021a,b), we widened the outgroup by including seven representatives of non-monophyletic Brachycerinae, a waste-basket taxon at least some members of which forming the twilight zone of “true weevils” (Curculionidae, SHIN et al. 2017, GREBENNIKOV & ANDERSON 2021b). To root the Curculionidae topology consistently with earlier results (SHIN et al. 2017, GREBENNIKOV & ANDERSON 2021b), we used five eyeless species of Brachycerinae, four of them belonging to the likely non-monophyletic tribe Raymondionymini (GREBENNIKOV & ANDERSON 2021b). Altogether, 153 weevil terminals constituted the matrix (Table 2 and an online BOLD public dataset dx.doi.org/10.5883/DS-VGDS24).

Three-marker Maximum Likelihood (ML) phylogenetic analysis. The methodological approach of the analysis follows those of our recent works (GREBENNIKOV & ANDERSON 2021a,b) and, therefore, is only briefly described. Alignment of all three DNA fragments was done separately using the online MAFFT Q-INS-i algorithm utilizing, when applicable, the secondary structure information (KATO et al. 2017; <https://mafft.cbrc.jp/alignment/server/>). No internal parts of DNA fragments were removed before the analysis, even if consisting mainly of indels (insertions or deletions, particularly frequent in ITS2). Inconsistently sequenced 5'-end and 3'-ends of the ITS2 alignment were trimmed of 11 and 12 positions on each side, respectively; 21 such positions were also trimmed at the 3'-end of the 28S alignment. Three aligned single-fragment datasets (Table 1) were concatenated using Mesquite 3.61 (MADDISON & MADDISON 2020) into a matrix of 4,174 positions. An unrooted topology was built using an ML approach, as implemented in CIPRES Science Gateway online platform (MILLER et al. 2010; <http://www.phylo.org/>, tool “RAXML-HPC2 on XSEDE”) and using RAXML version 8 algorithm (STAMATAKIS 2014) which applies the CAT approximation to the GTR+G nucleotide substitution model independently to each of the three partitions. Branch support values were generated based on 1000 bootstrap replicates (STAMATAKIS et al. 2008) and categorized as strong

(≥95%), moderate (<95% and ≥75%), or weak (<75%). The tree was visualized in FigTree v1.4.4. (RAMBAUT 2020).

Specimen illustration and documentation. To document the inadequately known adult morphological diversity of the tribe Lymanitini, a dedicated effort was made to illustrate these beetles. For this purpose, 26 ingroup specimens (from 50 included in the ML analysis) were imaged in five standard views (habitus dorsal, habitus left lateral, habitus left fronto-lateral, habitus ventral, antenna). Two additional specimens from two Lymanitini genera lacking DNA data and not represented in the analysis were similarly illustrated: *Gononotus angulicollis* (Suffrian, 1871) in Fig. 34 and *Kuschelaxius discifer* Howden, 1992 in Fig. 35. All five images of each of the 28 specimens, together with the specimen's number, its geographic coordinates and the most detailed currently available taxonomic assignment, were arranged into 28 plates (Figs 8–35). The only Lymanitini genus not herein illustrated (and not seen by us) is the monotypic *Pseudocaecocossus* Osella, 1977 known only from two Cuban specimens (HOWDEN 1992).

An uncertain number of segments in antennal funicle. During this study we concluded that determining the homology (and, therefore, the number) of antennomeres in a funicle (Fig. 5) of the subtribe Lymanitina is far from straightforward. It appears likely that the club of at least some Lymanitina (e.g., the genus *Theognete*) came to include the much enlarged distal (seventh) funicle antennomere. If so, this distal antennomere is likely misinterpreted as part of the club, giving the 7-segmented funicle the appearance of being 6-segmented. Presently we did not make an effort to clarify this uncertainty, but thoroughly documented antennal diversity throughout the tribe (Figs 5, 8–35). When giving the number of funicle segments in Lymanitina, we use published numbers, which might, or might not be correct.

Results

The three-marker ML analysis of 153 terminals resulted in a phylogenetic tree depicted in Figs 6 and 7. The tribe Lymanitini, the ingroup of the analysis, was rendered paraphyletic by the monophyletic tribe Anchonini. The internal

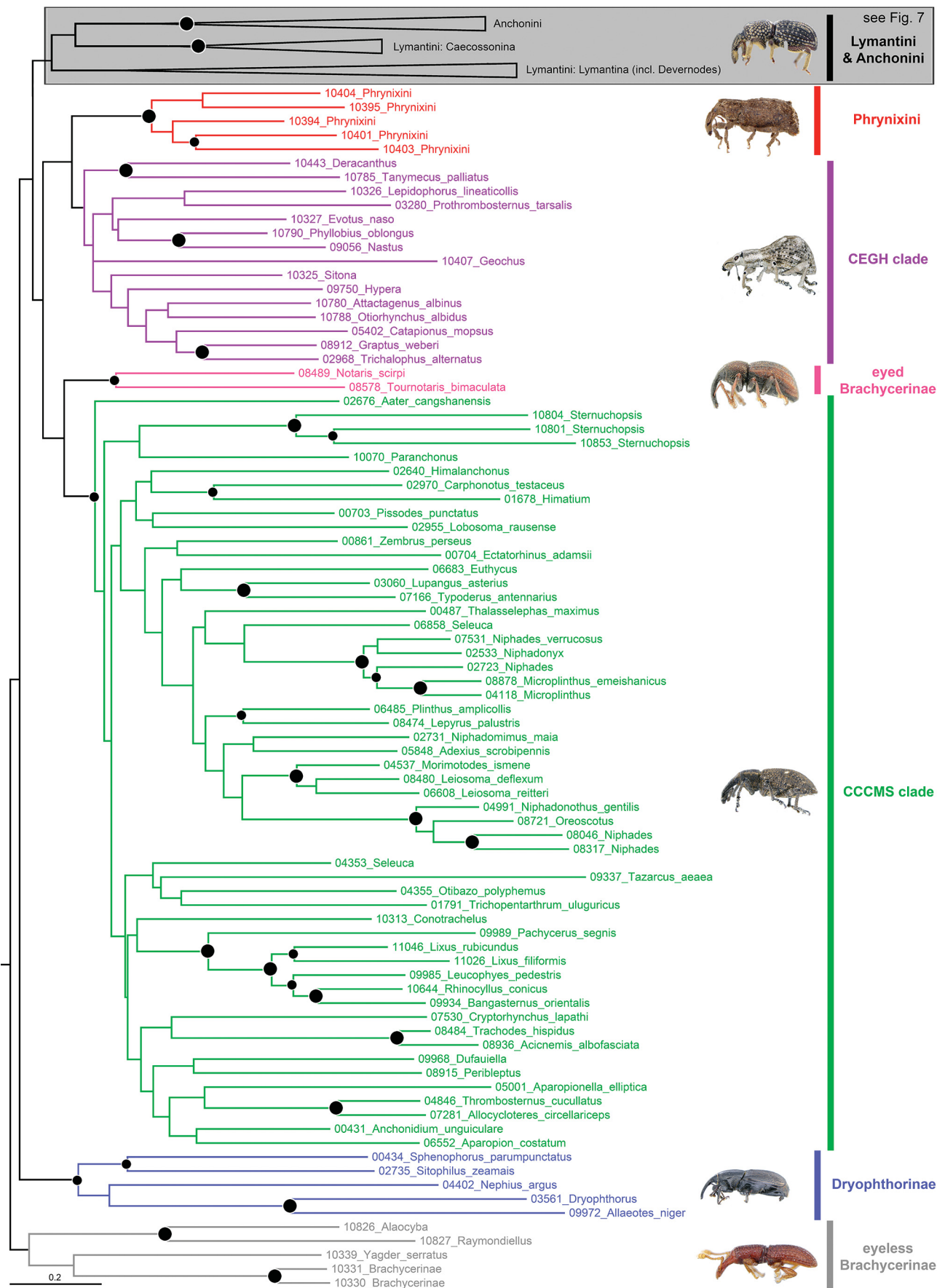


Fig. 6. Maximum likelihood tree of true weevil relationships reconstructed by RAxML from the three-fragment concatenated matrix. Three subclades forming the clade of Anchonini plus Lymanitini are collapsed. Large and small circles denote strongly and moderately supported clades, respectively.

relationships of this weakly supported and weakly resolved clade was Lymantina + (Anchonini + Caecossosina); the latter two taxa each strongly statistically supported clades and together uniquely characterized by a funicle with eight antennomeres. The monophyletic Asian genus *Devernodes* was placed inside the monophyletic subtribe Lymantina; the latter weakly supported if including the genus *Decuanelus* Osella, 1977, or strongly supported, if without it. The Lymantina genera *Dioprophorus* Faust, 1892 and *Theognete* were both recovered as strongly supported. Conversely, the genera *Epibaenus* Kuschel, 1959 and *Lymantes* were recovered as non-monophyletic.

Outside of the Anchonini plus Lymantini clade, the remaining 86 analysed terminals clustered into the following six groups, all weakly resolved among themselves. All five terminals of eyeless Brachycerinae formed a weakly supported cluster, permitting straightforward rooting between them and the rest of the topology. The remaining five clusters/clades were Dryophthorinae (moderately supported), the CCCMS clade (weakly supported and excluding the Anchonini plus Lymantini clade, as well as Phrynixini), eyed Brachycerinae (moderately supported), the CEGH clade (weakly supported) and Phrynixini (strongly supported).

Discussion

Reliability of phylogenetic tree. Excepting a few deviations discussed below, our ML topology (Figs 6, 7) is remarkably consistent with the existing ideas on weevil phylogeny based on a much larger set of DNA data (e.g., SHIN et al. 2017; references therein). Specifically, we recovered the following well-established clades, some of them with moderate or strong statistical support: Dryophthorinae, CEGH clade, CCCMS clade (excluding, however, Phrynixini, Anchonini and Lymantini; see below), Phrynixini and Anchonini. This consistency between our results and those of earlier studies suggest that our topology is a credible source of phylogenetic interpretations (see below).

Non-monophyletic Lymantini form a clade with monophyletic Anchonini. Perhaps the most significant phylogenetic result of our analysis is that the tribe Lymantini, the ingroup of this study, emerged paraphyletic to the tribe Anchonini. Although weakly statistically supported, this result lends credence to the century-old “Anchonina” of CHAMPION (1902, 1903) and appears sound in light of at least four other lines of evidence. Firstly, both tribes have been already linked into a moderately supported clade in our recent Anchonini-focused analysis (GREBENNIKOV & ANDERSON 2021a). There, however, the tribe Lymantini was represented by a single species of the genus *Devernodes*, then a questionable member of the latter tribe (but see below). Secondly, in the same study, we hypothesized that the clade of Anchonini plus Lymantini might have at least one morphological apomorphy, the polished head capsule of these beetles; a supposition corroborated in the present analysis. Thirdly, larvae of Anchonini and Lymantini are remarkably similar (ANDERSON 1952). Fourthly, available biogeographic interpretations for amphi-Atlantic monophyletic Anchonini (GREBENNIKOV & ANDERSON 2021a)

and amphi-Pacific non-monophyletic Lymantini (see below) suggest that their most recent common ancestor (MRCA) likely inhabited the North American continent before the Eocene (see below). If Anchonini and Lymantini indeed share a MRCA, as all available data consistently suggest, its exact age, geographic localization, and the identity of its sister group are three main unknowns yet to be elucidated. Summing up, in the current absence of alternatives, the monophyly of Anchonini and Lymantini is the only existing hypothesis that, although weakly statistically supported, agrees with all available evidence.

The Mesoamerican Lymantini subtribe Caecossosina is sister to amphi-Atlantic Anchonini. The monophyly of the Lymantini subtribe Caecossosina plus the tribe Anchonini is statistically weakly supported, although likely credible. Two independent lines of evidence support this conclusion. Firstly, both analyzed genera of Caecossosina (and by extension its third and the last genus, *Pseudocaecossosus*) likely form a clade supported by at least two morphological characters: lack of eyes and small adult bodies not exceeding 3 mm in length. Secondly, all members of the subtribe Caecossosina differ from those of the subtribe Lymantina by sharing with Anchonini a rare morphological trait: the 8-segmented antennal funicle (Figs 4, 5, 20, 33). Moreover, the MRCA of American Caecossosina and amphi-Atlantic Anchonini, if it has existed, likely inhabited the North American continent (at that time widely separated by the sea from insular South America) not later than the eastwards transatlantic dispersal of Anchonini to West Africa some 9.5–5.2 million years ago (GREBENNIKOV & ANDERSON 2021a; see below). The amphi-Pacific subtribe Lymantina with its MRCA likely living in North America (see below) is herein considered as sister to the Caecossosina plus Anchonini clade. Summing up, in the current absence of alternatives, sister relations of the Lymantini subtribe Caecossosina and the tribe Anchonini is the only existing hypothesis which, although weakly statistically supported, is in agreement with all available evidence.

The Anchonini plus Lymantini clade is outside of the CCCMS clade. The current taxonomic assignment of both Anchonini and Lymantini in the subfamily Molytinae (ALONSO-ZARAZAGA & LYAL 1999, LYAL 2014) implies that both tribes are phylogenetically nested within the CCCMS clade of “higher” weevils (e.g., SHIN et al. 2017). Our results, however, indicate that the clade of Anchonini plus Lymantini is outside of the CCCMS clade; the latter having moderate statistical support (Fig. 6). This result is consistent with our earlier analyses which resolved these tribes outside of the CCCMS clade (e.g., GREBENNIKOV 2018, GREBENNIKOV & ANDERSON 2021a). These analyses, however, used the subset of the herein analyzed dataset and the same analytical methods, which might make them similarly biased. In the present lack of other evidence, two alternatives best explain the observed discrepancy between taxonomy-based expectations and our topologies. One alternative is that the taxonomic interpretation is correct, and its inconsistency with the topology is the result of analytical shortcomings, such as the scarcity

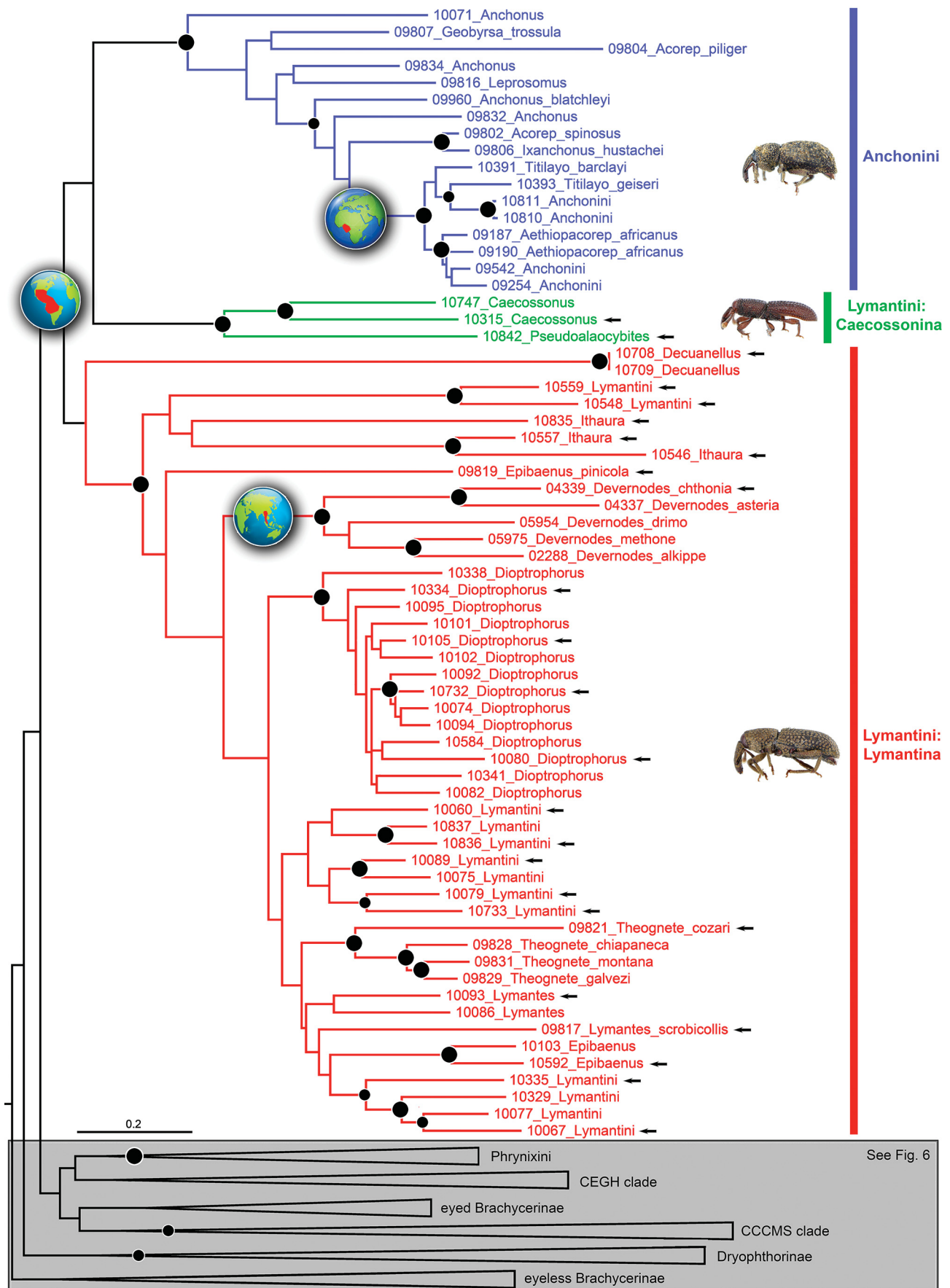


Fig. 7. Maximum likelihood tree of Anthonini and Lymanitini relationships reconstructed by RAxML from the three-fragment concatenated matrix. Clades outside of the Anthonini plus Lymanitini clade are collapsed. Large and small circles denote strongly and moderately supported clades, respectively. Arrows indicate 26 specimens shown in Figs 1, 2, 8–33. Superimposed globes indicate the current distribution.

of the phylogenetic signal extracted from our dataset. Another alternative is that the subfamily Molytinae, which is known to be non-monophyletic (e.g., SHIN et al. 2017), might artificially unite grossly unrelated organisms, some of them perhaps even nested outside the CCCMS clade.

Phrynixini, an obscure Gondwanan tribe, is outside of the CCCMS clade. Similarly, with the Anchonini plus Lymantini clade, all five herein analyzed members of the tribe Phrynixini formed a strongly supported clade placed outside of the CCCMS clade (Fig. 6). Phrynixini is a phylogenetically neglected group of some 35 genera taxonomically assigned to Molytinae (LYAL 2014). PULLEN et al. (2014) did not assign Phrynixini to any subfamily when providing a catalog of Australian weevils but suggested that the tribe belongs to the CEGH clade. GUNTER et al. (2016) included two Australian genera of this tribe in a molecular phylogenetic analysis; these genera resolving in separate clades within the CEGH clade. We corroborate the molecular results of LESCHEN et al. (2022) who recently recovered a monophyletic Phrynixini outside of the CCCMS clade. KUSCHEL (1987) noted that Phrynixini have the “Gondwanan” distribution, being found in New Zealand, Australia, New Caledonia and Chile. If the plate tectonics was the factor behind the Phrynixini distribution, then the age of this clade might be comparable with the time of the Gondwana breakup and, therefore, be at least twice greater than the age of the CCCMS crown group; the later originating about 75 million years ago (SHIN et al. 2017).

High altitude inter-continental dispersal of thermophilic Lymantina across Arctic land bridges. A new, strongly supported and evolutionary significant result of our analysis is the recovery of the recently described Asian genus *Devernodes* nested within the otherwise exclusively American subtribe Lymantina (Fig. 7). This corroborates the earlier morphology-based assumption of *Devernodes* relationships with Lymantini (GREBENNIKOV 2018) made, however, without the benefit of a formal analysis. This result also means that the stenotopic, thermophilic, flightless and presumably low-dispersing monophyletic subtribe Lymantina is found in two widely separated unglaciated warm regions of the World: in Southeastern Asia (the genus *Devernodes*) and the tropical Americas (the rest of the subtribe; Fig. 3). Below we offer a biogeographic interpretation of this distribution.

Sister-relationships between Asian and American extant animals is not an infrequent phenomenon. It is perhaps best known for tapirs (Tapiridae), a clade of large, herbivorous, odd-toed mammals similar in appearance to pigs with a short, prehensile trunk. Malayan tapir, *Tapirus indicus* Desmarest, 1819, inhabits Southeast Asia, while the remaining three or four extant congeners are found between Mexico and Argentina (COZZUOL et al. 2013). Arthropod examples are numerous (e.g., ALLEN 1983) and include, among others, Penichrolucaninae stag beetles (RATCLIFFE 1984) and freshwater water fleas *Leydigopsis* Sars, 1901 (Cladocera: Anomopoda: Chydoridae; VAN DAMME & SINEV 2013). To account for the intercontinental distribution of terrestrial animals, risky and low-probability long-distance transoceanic dispersals are occasionally justifiably

evoked (DE QUEIROZ 2014). Examples include the likely out-of-America Cretaceous single dispersal event of the opilionid family Zalmoxidae, leading to their spectacular radiation in Southeast Asia and Australia (SHARMA & GIRIBET 2012). Another transoceanic example of dispersal involves anchonine weevils, the clade likely rendering Lymantini paraphyletic (Fig. 7). These flightless beetles have been shown to disperse overwater (CRISTÓVÃO & LYAL 2018) in the later Miocene (GREBENNIKOV & ANDERSON 2021a) across the Atlantic from the Americas to West Africa. Might then the overwater dispersal be the likeliest hypothesis for the present-day amphi-Pacific distribution of the East Asian genus *Devernodes* and its American Lymantina relatives?

The answer is likely “no”. Our main analytical limitation is the lack of Lymantina fossils to determine the past distribution of the clade and to date our topology (Fig. 7). Still, the amphi-Pacific distribution of this monophyletic subtribe can be plausibly explained without evoking long-distance chance dispersal. All available data consistently suggest that the current disjunct distribution of Lymantina in both Asia and the Americas is most likely a result of high latitude inter-continental normal ecological dispersal (HEADS 2014). It implies gradual overland dispersal of thermophilic Lymantina across Arctic land bridges during the warmest periods of the Cenozoic, e.g., the Paleocene–Eocene Thermal Maximum some 56 Ma (MCINHERNEY & WING 2011). We assume, therefore, those flightless lymantine weevils have dispersed overland between their current areas of distribution in North America and Asia using the currently submerged North Atlantic and/or the Beringia land bridges (e.g., the De Geer, Thulean, or Beringia; BRIKIATIS 2014). This gradual dispersal likely took place before the Eocene–Oligocene boundary some 33.5 Ma, when the warm global “greenhouse” climate turned to that of an “icehouse” (ELDRETT et al. 2009). This climatic event is considered to have triggered the decline and disappearance of the Boreotropical flora (WOLFE 1975). This was a belt of thermophilic vegetation in the Northern Hemisphere during the Eocene epoch reaching as far north as 80°N in which these weevils may have thrived. Last but not least, the Eocene timing appears consistent with the phylogenetic position of *Devernodes* nested deeply within Lymantina (Fig. 7) and sufficiently long (as opposite to e.g., Pliocene–Pleistocene timing) to account for the sizable morphological distinctness of this Asian genus from the American rest of the subtribe.

Our assumption of climate-mediated vicariance between American and Asian Lymantina is consistent with hypotheses evoked for other similarly distributed clades of terrestrial thermophilic animals, such as lizards (SMITH 2011), or extinct giant ants (ARCHIBALD et al. 2011); for a review on the Eocene flora and vertebrate fauna see EBERLE & GREENWOOD (2012). At that time warm-loving non-volant terrestrial animals such as stem-group tapirs (EBERLE & EBERLE 2015) and camels (RYBCZYNSKI et al. 2013) inhabited what is presently Ellesmere Island, Canada’s northernmost island lying within the Arctic Archipelago. Beetle examples of such vicariance include the giant

Callipogon Audinet-Serville, 1832 longhorns (KIM et al. 2018), *Bolitogyrus* Chevrolat, 1842 rove beetles (BRUNKE et al. 2017) and Megasternini terrestrial water scavenger beetles (ARRIAGA-VARELA et al. 2021). This assumption is also consistent with the likely relictual presence of the genus *Lymantes* in the northwestern USA (Fig. 3). These coastal populations of Lymantina are widely isolated from the more southwards rest of the subtribe's American distribution, occupy areas that were unglaciated and wetter during at least the Last Glacial Maximum (LORA et al. 2019), and likely represent a remnant of the former much wider Lymantina presence in the American North. Directionality of the trans-Arctic Lymantina dispersal remains unknown, although a single overland migration event of the stem *Devernodes* from North America to Asia appears most plausible. We conclude, therefore that the disjunct presence of Lymantina in the Americas and Asia is a result of normal ecological dispersal first creating an uninterrupted Holarctic distribution of this clade, with subsequent climatic cooling obliterating these cold-intolerant beetles between the widely disjunct areas of their recent distribution.

Our hypothesis on the normal overland ecological dispersal of Lymantina across arctic land bridges implies the presence of Lymantina fossils in the presently Lymantina-free temperate and arctic regions along the hypothesized dispersal routes (Fig. 3). Examples of such coveted fossil discoveries for other terrestrial animals include the Eocene *Bolitogyrus* Chevrolat, 1842 rove beetles found in the Baltic region of Europe and from Green River formation in Colorado, USA (BRUNKE et al. 2017) and the early Oligocene bones of legless Dibamidae burrowing blind skinks found in the presently Dibamidae-free Mongolia (ČERNÁNSKÝ 2019). The discovery of such a Lymantina fossil from these intervening Lymantina-free regions would, therefore, considerably strengthen our hypothesis.

North American origin of Lymantina crown group and that of Anchonini plus Lymantini. It is tempting to speculate which of the three continents currently inhabited by the crown group Lymantina, if any, i.e., Asia, North America and South America, has supported the clade's MRCA. Numerical preponderance of recent Lymantina in Mesoamerica, and their corresponding scarcity in Asia are not informative in this respect. Clades of non-volant terrestrial animals with exceptionally well-documented fossil records are known to have their MRCA on one continent, disperse to others, and then become extinct in the continent of their origin. Examples include crown group camels originating in the Eocene of North America, dispersing to Eurasia across the Arctic land bridges (and then to Africa) and also to South America across the newly formed Isthmus of Panama, and becoming extinct in North America (HEINTZMAN et al. 2015). Even though our analysis is inconclusive on this point, a North American origin and subsequent dispersal to Asia appears to be the most parsimonious explanation for Lymantina, particularly in light of the American origin of their sister group, Anchonini (GREBENNIKOV & ANDERSON 2021a) plus Caecossosina (Fig. 7).

Finally, assuming that (1) MRCA of Lymantini inhabited North America likely in Eocene time to permit overland dispersal of the stem *Devernodes* to Asia and (2) assuming existence of the Lymantina + (Caecossosina + Anchonini) clade, on which continent did the MRCA of this clade live? If restricting our choice to either North (including Central America) or South America, as it is most parsimonious options considering all available evidence, North America is by far the likeliest candidate. The choice is pivoted on a consideration that South America, being for most of its geological and biotic history widely separated from other landmasses, is highly unlikely to have any of its native organisms reaching across the sea to North America, to account for the herein hypothesized Lymantina dispersal event between North America and Asia. Formation of the Isthmus of Panama (and corresponding closure of the Central American Seaway separating both Americas), which would be needed to permit the South American origin of the Lymantina + (Caecossosina + Anchonini) clade, is a hotly debated subject (e.g., WOODBURN 2010), with dates varying widely, depending on the evidence used. Either way, geological evidence suggesting the earlier date (the mid-Miocene, MONTES et al. 2015) or biological evidence suggesting a much later date (3 Ma, O'DEA et al. 2016) of the Great American Biotic Interchange (GABI) both greatly postdate the time when members of Lymantina have likely made their way overland from North America to Asia. Thus, if the logic above is sound and the assumptions correct, the crown group of the Anchonini plus Lymantini clade originated in North America. It follows that the Late Miocene eastwards transatlantic overseas dispersal of Anchonini to West Africa (GREBENNIKOV & ANDERSON 2021a) took place from North America, and not from South America; the latter at that time likely still surrounded by the sea and uninhabited by these beetles. It also follows, that the current presence of Anchonini and Lymantini in South America is yet another example the Great American Biotic Interchange, a fascinating phenomenon exceptionally well-documented for vertebrates, while with only a few examples among beetles (e.g., TELLO et al. 2021 on a dung beetle subfossil; ŽYLA et al. 2021 on paederine rove beetles).

Unsatisfying taxonomy of the tribe Lymantini. The taxonomy of Lymantini weevils is unsatisfactory for two reasons. Firstly, if our phylogenetic interpretation of Lymantini is correct, the tribe is paraphyletic with respect to Anchonini (Fig. 7). To address this inconsistency, the younger name Lymantini Lacordaire, 1865 might be synonymized under Anchonini Imhoff, 1856, to return to the concept of "Anchonina" of CHAMPION (1902, 1903). This will result in the larger monophyletic tribe Anchonini containing three monophyletic subtribes: Anchonina, Caecossosina and Lymantina. Alternatively, the Lymantini subtribe Caecossosina might be elevated to the tribe level, to create three monophyletic tribes: Anchonini, Caecossosini and Lymantini. As there are additional tribes in Molytinae other than these three, the latter taxonomic solution will fail to imply that they form a clade and is, therefore, less preferable. Lacking sufficient statistical confidence in the



Fig. 8. Sequenced Lymantini specimen 4339: *Devernodes chthonia* Grebennikov, 2018.



Fig. 9. Sequenced Lymantini specimen 9817: *Lymanthes scrobicollis* Gyllenhal, 1838.



Fig. 10. Sequenced Lymantrini specimen 9819: *Epibaenus pinicola* Kuschel, 1959.



Fig. 11. Sequenced Lymantrini specimen 9821: *Theognete coxari* Anderson, 2010.



Fig. 12. Sequenced Lymantini specimen 9829: *Theognete galvezi* Anderson, 2010.



Fig. 13. Sequenced Lymantini specimen 10060: *Lymantina*.



Fig. 14. Sequenced Lymantini specimen 10067: Lymantina.



Fig. 15. Sequenced Lymantini specimen 10079: Lymantina.



Fig. 16. Sequenced Lymantini specimen 10080: *Dioprophorus* sp.



Fig. 17. Sequenced Lymantini specimen 10089: *Lymantina*.

Fig. 18. Sequenced Lymanitini specimen 10093: *Lymanites* sp.Fig. 19. Sequenced Lymanitini specimen 10105: *Dioprophorus* sp.



Fig. 20. Sequenced Lymantini specimen 10315: *Caecossonus* sp.



Fig. 21. Sequenced Lymantini specimen 10334: *Dioprophorus* sp.

Fig. 22. Sequenced Lymanitini specimen 10335: *Lymanitina*.Fig. 23. Sequenced Lymanitini specimen 10546: *Ithaura* sp.



Fig. 24. Sequenced Lymantini specimen 10548: *Lymantina*.



Fig. 25. Sequenced Lymantini specimen 10557: *Ithaura* sp.



Fig. 26. Sequenced Lymanitini specimen 10559: *Lymanitina*.



Fig. 27. Sequenced Lymanitini specimen 10592: *Epibaenus* sp.



Fig. 28. Sequenced Lymantini specimen 10708: *Decuanellus* sp.



Fig. 29. Sequenced Lymantini specimen 10732: *Dioptraphorus* sp.



Fig. 30. Sequenced Lymantini specimen 10733: Lymantina.

Fig. 31. Sequenced Lymantini specimen 10835: *Ithaura* sp.



Fig. 32. Sequenced Lymantini specimen 10836: Lymantina.



Fig. 33. Sequenced Lymantini specimen 10842: *Pseudoalaocybites* sp.



Fig. 34. Not sequenced Lymanitini specimen of *Gononotus angulicollis* (Suffrian, 1871).



Fig. 35. Not sequenced Lymanitini specimen of *Kuschelaxius discifer* Howden, 1992.

phylogenetic affinities of these beetles precludes us from introducing these taxonomic changes.

Secondly, the subtribe Lymantina likely contains non-monophyletic genera (e.g., *Lymantes* and *Epibaenus*), as well as unnamed species not currently attributable to any genus, monophyletic or not (e.g., all specimens identified as “Lymantina” in Figs 1 and 2). Below we list all 12 valid genera of the tribe Lymantini and provide information on their diversity and distribution.

Tribe Lymantini Lacordaire, 1865

Subtribe Caecossosina Osella, 1980

Caecossonus Gilbert, 1955: four species in Belize, Cuba, Mexico and USA (Florida).

Pseudoalaocybites Osella, 1980: 16 species in Colombia, Cuba, Jamaica, Ecuador and Venezuela (GERMANN 2020).

Pseudocaecossosonus Osella, 1977: monotypic, Cuba (HOWDEN 1992).

Subtribe Lymantina Lacordaire, 1865

Decuanellus Osella, 1977: 12 species inhabiting Caribbean islands between the Bahamas and St. Lucia (COLONNELLI 2010; RUIZ & VAN DAM 2021).

Devernodes Grebennikov, 2018: five species in China (Sichuan), Malaysia and Vietnam (GREBENNIKOV 2018).

Dioprophorus Faust, 1892: seven species in Guatemala and Mexico (O'BRIEN & WIBMER 1982). The Cuban generic record by CHAMPION (1902: 92, followed by O'BRIEN & WIBMER 1982) refers to the type species of the genus *Gononotus*.

Epibaenus Kuschel, 1959: two species in Guatemala and Mexico (KUSCHEL 1959).

Gononotus LeConte, 1876: monotypic, USA (Florida), Mexico, Cuba, Puerto Rico (O'BRIEN & WIBMER 1982). This genus has been recently added to the subtribe (LYAL 2014), not available for our analysis, and its phylogenetic position is the least known.

Ithaura Pascoe, 1871: at least six species in Central America and the northern half of South America (RHEINHEIMER 2006). This is the only genus of the subtribe found in South America, and as far south as Bolivia and central Brazil (Fig. 3).

Kuschelaxius Howden, 1992: two species in the Dominican Republic and Puerto Rico (HOWDEN 1992).

Lymantes Schoenherr, 1838: seven species in the USA and El Salvador (ANDERSON 2016, 2022).

Theognete Champion, 1902: 94 species in Mexico, Honduras, Guatemala and El Salvador (ANDERSON 2010).

Alleged Lymantini fossil from Dominican amber. POINAR & LEGALOV (2021) established a new extinct genus and species, *Bronchotibia adunatus* Poinar & Legalov, 2021, based on a Dominican amber adult weevil inclusion. They decisively attributed this taxon to the subfamily Molytinae and to the tribe Lymantini, and less decisively to the subtribe Lymantina, by listing morphological similarities. These authors pivoted their Lymantini attribution of the fossil on “... eyes ... basally located on rostral part of head ...”; a diagnostic character of non-monophyletic

Lymantini. Illustrations of the fossil, however, do not corroborate this morphological interpretation. As illustrated on their Figure 2, the placement of the eyes is clearly on the head and dissimilar to that in Lymantini. Three additional morphological characters, namely (1) rectangular shape of the well-developed elytral shoulders suggesting presence of hind wings and capacity of active flight, (2) opisthognathous (rather than prognathous) orientation of the rostrum, and (3) strongly bilobed and likely adhesive tarsomeres 3 suggesting plant climbing behaviour are notably unlike anything known among the members of the Anchonini plus Lymantini clade, which are flightless and ground-dwelling beetles. POINAR & LEGALOV (2021) also did not mention the well-established opinion that the subfamily Molytinae is not monophyletic (e.g., SHIN et al. 2017) and, therefore, meaningless in the phylogenetic sense. We, therefore, conclude that attribution to the extinct weevil genus *Bronchotibia* to either Molytinae, Lymantini, or Lymantina is unwarranted and use the criteria of CLARKE et al. (2019: 31) to re-classify this fossil as Curculionidae *incertae sedis*.

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