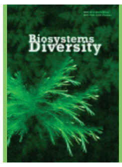

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Phylogenetic and biogeographic reconstruction of Lamiini *sensu lato* (Coleoptera, Cerambycidae) reveals South Gondwanan origin and Panthalasso-Tethyan dispersal pathways

A. M. Zamoroka

Vasyl Stefanyk Precarpathian National University, Ivano-Frankivsk, Ukraine

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Vasyl Stefanyk Precarpathian National University, Department of Biology and Ecology, Shevchenko st., 56, Ivano-Frankivsk, 76018, Ukraine. E-mail: andrew.zamoroka@pnu.edu.ua

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In this study I conduct the phylogenetic and biogeographical analysis of Lamiini *sensu novo* (Coleoptera, Cerambycidae, Lamiinae), confirming it as a monophyletic group that is broader than previously assumed and supporting the redefinition of it as a unified tribe – Lamiini *sensu novo*. The group consist of eight major clades (TAENI, DORCA, ACALO, BATOC, PSACO, ANOLPL, MONOC, LAMIA) and integrates together several traditionally recognized tribes (Dorcaschematini, Batocerini, Petrognathini, Rhodopini, Monochamini, Dorcadionini, Phrissomini). Most of them, including Monochamini, Petrognathini, Dorcadionini, and Phrissomini are polyphyletic, representing multiple lineages with intricate evolutionary history. Phylogeographic analysis suggests a South Gondwanan origin of Lamiini *s. l.*, with its ancestral lineage (LaCA) emerging in the Antarctica–South America suture zone before global expansion through three key migration routes: northeast Pantalassic, Trans-Tethyan, and southwest Pantalassic. Continental drift and climate oscillations influenced this process. Initial diversification (~70–60 Ma) led to vicariant taxa due to continental isolation, with basal clades (TAENI, DORCA, ACALO) distributed across South America, North America, and Australia. Extinction events, including the K–T boundary (~66 Ma) and Cenozoic glaciations, further shaped diversification. The rise of the BATOC and PSACO clades marked the early diversification of crown-group Lamiini *s. l.* within the island continent of Greater India and the multiple archipelagos of the Trans-Tethyan Arc (~60–50 Ma). The collision of Greater India with Asia (~50–45 Ma) facilitated faunal exchanges, aiding dispersal into Africa and Southeast Asia and driving ANOPL diversification (45–35 Ma). The ACALO clade underwent secondary diversification during the initial collision of Australia and Eurasia (~25–20 Ma), coinciding with the uplift of New Guinea in the Miocene. The LAMIA clade likely originated in East Asia (~25–20 Ma). During the Miocene Climatic Optimum, it expanded into Africa via the Gomphotherium Land Bridge (~16 Ma) and colonized Europe. Later cooling and aridification (~5–11 Ma) drove further diversification, particularly in Eurasian steppes. The MONOC clade also originated in East Asia, adapting to montane coniferous forests during the Miocene cooling. It spread across Eurasia during the Miocene glaciations (~20 Ma, ~14 Ma) and entered North America via Beringia. Expansion into Mesoamerica, northern South America, and the Caribbean likely occurred during the Pleistocene glaciations (~0.01–2 Ma) when climate and fluctuating sea levels enabled dispersal. In summary, the findings refine Lamiini *s. l.* phylogeny and highlight the impact of geological and climatic events on its evolution. This study clarifies taxonomic ambiguities and provides a framework for future research on diversification and biogeographic patterns.

Keywords: longhorn beetles; molecular phylogeny; phylogeography; evolutionary history; speciation; cladistics; taxonomy.

Introduction

The tribe Lamiini is among the most prominent yet least understood groups within the subfamily Lamiinae. On the one hand, it includes the monotypic genus *Lamia* Fabricius, 1775, from which both the tribe's name and the name of the entire subfamily Lamiinae are derived. On the other hand, defining the scope and taxonomic boundaries of Lamiini presents a significant challenge. This issue was comprehensively addressed by Gorring (2019) in his dissertation, where he outlined the approximate taxonomic limits of the tribe. It is important to note that, although the formal description of Lamiini is commonly attributed to Latreille (1825), his publication actually introduced the name for the subfamily Lamiinae, rather than the tribe itself. The establishment of Lamiini as a tribe should instead be credited to Mulsant (1839), who provided both its description and diagnosis. Moreover, Mulsant (1839) was the first to delineate the tribe's boundaries, initially including three genera: *Lamia*, *Morimus* Brullé, 1832, and *Monochamus* Dejean, 1821. With the discovery of new genera on a global scale, the boundaries of Lamiini have been repeatedly revised, often based on subjective interpretations by individual researchers. This inconsistency has impeded the establishment of a natural classification for the tribe (Gorring, 2019).

The development and widespread implementation of modern molecular phylogenetic methods have provided a new and highly effective tool for improving the systematics of the longhorn beetles, based on the principle of monophyly (Nie et al., 2020; Souza et al., 2020; Zamoroka, 2022; Zamoroka et al., 2022). The phylogenetic understanding of Lamiini began to take shape only six years ago, starting with the dissertation of Gorring (2019), in which he was among the first to define the tribe's boundaries using molecular methods. Specifically, he merged the former tribes Batocerini, Gnomini, Acridocephalini, and Monochamini with Lamiini sensu Sama, 2008 (Gorring, 2019). Thus, the new taxonomic boundaries of the tribe have gained broad recognition. Therefore, hereinafter it is defined the tribe as Lamiini *sensu lato* (Lamiini *s. l.*). One year later, Souza et al. (2020) further expanded the boundaries of Lamiini *s. l.*, incorporating the former tribes Gnomini and Rhodopinini. However, they retained Batocerini as a separate tribe, considering it the sister clade to Lamiini. The placement of Batocerini has since become a topic of considerable debate, with various studies either including it within Lamiini *s. l.* (Gorring, 2019; Nie et al., 2020; Bai et al., 2022; Pu et al., 2022; Soydabaş-Ayoub & Uçkan, 2023) or treating it as a sister group (Souza et al., 2020; Ashman et al., 2021; Ren et al., 2021; Zhang et al., 2021; Li et al., 2023).

Another controversial group is the tribe Dorcaschematini, which is typically regarded as the sister group to Lamiini *s. l.* (Nie et al., 2020; Souza et al., 2020; Pu et al., 2022) or as part of it (Bai et al., 2022). Overall, significant progress has been made in recent years in understanding Lamiini *s. l.* and establishing its natural phylogenetic framework. Despite this progress, the origin of the tribe remains entirely unclear, particularly given that South American and Australian genera occupy basal positions within Lamiini *s. l.* (Gorring, 2019; Souza et al., 2020; Ashman et al., 2021). This unusual combination of biogeographic patterns and the basal placement of these phylogenetic clades holds the key to resolving questions regarding the origin and expansion of Lamiini *s. l.*

In this study, I proposed and substantiated the hypothesis of a South Gondwanan origin of Lamiini *s. l.*, based on the most comprehensive phylogenetic analysis to date, encompassing 129 taxa across five genes (12S + 16S + COI + 18S + 28S). The results allowed for the identification of the evolutionary lineages of Lamiini *s. l.* and traced them back to the boundary between Antarctica and South America, which is most likely the center of origin for this tribe. Moreover, my findings revealed the intratribal relationships among genera within Lamiini *s. l.*, providing new insights for the further refinement of the tribe's taxonomy.

Materials and methods

The study is based on a phylogenetic analysis of 129 species from the tribe Lamiini *s. l.* (Table 1) and an additional 46 species from the subfamilies Lamiinae, Lepturinae, Cerambycinae, and Prioninae, which collectively formed the outgroup. The species list presented (Table 1) provides the most comprehensive representation of currently available sequence data for various gene sets. In this study, I utilized a dataset comprising sequences from five genes, including three mitochondrial genes (12S rRNA, 16S rRNA, and COI) and two nuclear genes (18S rRNA and 28S rRNA).

Table 1
GenBank accession numbers for gene sequences analyzed in this study on Lamiini *s. l.*

Species	Voucher number	Species	Voucher number
Acalolepta degener	HM034786; AB533614; HM062981; HM046537	*Eodorcadion humerale*	LECHK101-23
Acalolepta fraudatrix	AB533612; AB533643	*Eodorcadion intermedium*	LECHK039-20; LECHK040-20; LECHK041-20; LECHK099-23; VVGPL3537-19; VVGPL3538-19
Acalolepta sejuncta	LC617386	*Eodorcadion oryx*	LECHK027-20
Acalolepta sublusca	AB533613; FJ559003; AB533644	*Hayashiechthistatus inexpectus*	AB278551
Annamanum griseolum	AB533618; AB533649	*Hebestola nebulosa*	MZ057868; MZ061987
Annamanum lunulatum	NC_046851; MN356095	*Herophila fairmairei*	MH613738; MH613737; MH613736
Anoplophora beryllina	MK689202; AB439142; AB439143	*Herophila tristis*	MH613735; MH613734; JX969627
Anoplophora chinensis	MN882586; KF142013; KF141949; KC413801; MN886184	*Iberodorcadion fuliginator*	MH613733
Anoplophora davidis	FJ559022; AB439155	*Iberodorcadion perezi*	OK050449; OK050448; OK048672; OK048671
Anoplophora glabripennis	OP096420; KF142012; KF142011; KF141948; KF141947; HM046528; KF142077; KF142076	*Ithocritus ruber*	MT812980
Anoplophora horsfieldi	MN248534	*Lamia textor*	MN885970; KJ961885; KM445206; MH613743; KJ965883; KJ966718; MN886181
Anoplophora lurida	KF737700; KF737763; AB439141; KF737826; KF142014; KF141950; KF142079	*Lamiomimus gottschei*	KF737701; KF737764; KY683678; KF141953; KF142017; HM046546; HM046546
Anoplophora macularia	AB500919; AB500920; AB500921; AB500922; AB500924; AB439205; AB439204; AB439192; FJ559061; GU270010	*Macrochenus guerinii*	MK689201
Apriona germarii	MW858151; KF142034; KF141970; KF142099	*Macrochenus tigrinus*	MW984319
Apriona japonica	AB533627; LC617384; AB533658	*Mesechthistatus binodosus*	AB278316; AB278315; AB278314; AB278313; AB278312; MW984071
Apriona swainsoni	NC_033872	*Mesechthistatus furciferus*	AB278407; AB278406; AB278405; AB278402; MW983407
Apriona yayeyamai	AB533628; AB533659	*Microgoes oculatus*	MZ057929; MZ062003
Aristobia reticulator	NC_042151	*Monochamus adamitus*	MZ057848; MZ061968
Batocera horsfieldi	KF737694; KF737757; MT812973; DQ224240; KF737820; KF142033; KF141969; KF142098	*Monochamus sutor*	AY258059; KJ963506; KJ964578; KM442023; KM448148; KY357695; KJ964578; KJ964900; KJ965030; KJ967412; KM286021; KM442023; KC692745
Batocera lineolata	MW629558; MN886194	*Monochamus homoeus*	MZ057891
Blepephaeus multinotatus	MW983260	*Monochamus l euconotus*	MZ057880; MZ061998
Blepephaeus succinctor	NC_044697	*Monochamus maruokai*	AB533607; AB533638
Cerosterna pulchellator	MW982254	*Monochamus masaoi*	AB533606; AB533637
Cerosterna scabrator	MZ686949	*Monochamus nitens*	AB533604; MZ057900; MZ057899; AB533635; MZ062007; MZ062006
Chyptodes dejeani	MW983904	*Monochamus saltuarius*	AY258060; AY258061; AB533600; AB533631; KX961659; KY683636; KY683643; AY260842; AY260841; KC692745
Dolichoprosopus sameshimai	AB439150; AB439149; AB439148; AB439147; AB439146	*Monochamus spectabilis*	MZ057878; MZ061996
Dolichoprosopus yokoyamai	AB533610; AB439144; AB439145; AB811723; AB533641; AB811777	*Monochamus subfasciatus*	MN851123; AB533605; LC617385; MZ057889; AB533636; MN905221; MN850923; MN851213; MZ062001
Dorcadion aethiops	OK050369; OK050368; OK050372; OK050373; OK050374; OK048664	*Monochamus grandis*	AB533602; MZ057898; MZ062005
Dorcadion alexandris	OQ955575	*Monochamus x-fulvum*	MZ057892

Species	Voucher number	Species	Voucher number
Dorcadion anatolicum	ON931418	*Morimus inaequalis*	MK689206; MW590270
Dorcadion axillare	OK050393; OK050394; OK050377; OK050378; OK050384; OK048670; OK048669; OK048668; OK048667; OK048666	*Morimus asper*	MZ569365; MZ569364; MZ569363; MZ569362; MZ569361; MZ569430; MZ569429; MZ569428; MZ569427; MZ569426
Dorcadion boluense	MK542396.2; MK542393.2; MK542395.2; MK542394.2; MK542392.2; MK542390.2	*Morimus lethalis*	OL457549
Dorcadion cinerarium	OK050406; OK050405; OK050404	*Neodorcadion bilineatum*	OK050403; OK050401; OK050399; MW984135; MH613740
Dorcadion crux	ON931419	*Neodorcadion exornatum*	MH613741; MH613742; OK050418
Dorcadion decipiens	OK050407	*Neoptychodes trilineatus*	MN886022; MN886131; MZ057854; MZ061974; MN886221
Dorcadion equestre	MH613745; OK050417; OK050415; OK050413; OK050409	*Olenecamptus bilobus*	NC_051945
Dorcadion etruscum	OK050515; OK048663	*Olenecamptus cretaceus*	KF737696; KF737759; KF737822
Dorcadion fulvum	MN885974; MN886086; OK050434; OK050433; OK050432; OK050423; MN886185	*Olenecamptus clarus*	KF737695; KF737758; KF737821; KF142031; KF141966; KF142096
Dorcadion gashtarovi	OK050447; OK050446; OK050445; OK050444; OK050443	*Olenecamptus subobliteratus*	KY796054
Dorcadion holosericeum	OK050452; OK050451; OK050450	*Oxylamia fulvaster*	MZ057894
Dorcadion kozanii	OK050518	*Parechthistatus gibber*	AB278466; AB278465; AB278464; AB278550; AB278549; MW981922
Dorcadion lineatocolle	OK050453; OK048674	*Peblephaeus decoloratus*	FJ559054
Dorcadion litigiosum	OK050455; OK050456	*Peblephaeus okinawanus*	AB533626; AB533657
Dorcadion lugubre	OK050459; OK050458; OK050457; OK048679; OK048678; OK048675	*Peblephaeus ziczac*	FJ559046
Dorcadion micans	ON930588	*Petrognatha gigas*	MN885983; MW983900; MW983029; MN886094; MN886193
Dorcadion mniszechi	OK050460	*Pharsalia subgemmata*	MK689212; MZ057890; OL457547; MZ062004
Dorcadion murrayi	OK050473; OK050472; OK050471; OK050470; OK050469; OK048654; OK048653; OK048652	*Plagiohammus spinipennis*	MW983679
Dorcadion obenbergeri	MH613746	*Plectrodera scalator*	KU255617; MW982125; KU255708
Dorcadion pedestre	OK050479; OK050478; OK050477; OK050475; OK050476; OK048662	*Plectrura spinicauda*	KU875953
Dorcadion phrygicum	MK542411.2; MK542403.2	*Psacothea hilaris*	FJ424074; KF142010; KF141946; KF142075
Dorcadion pilosipenne	OK050480	*Pseudoechthistatus chiangshunani*	NC_066480
Dorcadion pusillum	OK050498; OK050496; OK050494; OK050491; OK050481; OK048661; OK048659; OK048657; OK048656; OK048655	*Pseudoechthistatus hei*	ON641973
Dorcadion scabricolle	ON930032; MK542412.2; MK542399.2; MK542398.2; MK542401.2	*Pseudonemophas versteegii*	AB448738; MW897794; MW982703
Dorcadion scopolii	OK050502; OK050501; OK050500; OK050499	*Ptychodes politus*	MN344578; MN344280
Dorcadion septemlineatum	ON926500; MK542410.2; MK542406.2; MK542408.2; MK542407.2	*Rhodopina subuniformis*	MN885981; MN886093; FJ559064; MN886192
Dorcadion tauricum	OK050517; OK050516; OK050512; OK050511; OK050510	*Sarothrocera lowii*	OL457548
Dorcadion thessalicum	MH613744	*Taeniotes amazonum*	MN885927; MN886036; MN886144
Dorcadion tuleskovi	OK050513; OK050514	*Taeniotes scalatus*	KY212203; MN345939; MN345457
Dorcadion yilmazi	MK542404.2; MK542402.2; MK542400.2	*Trenetica lacrymans*	MW983118
Dorcaschema alternatum	KU255630; KU255706; OK646461	*Uraecha angusta*	KF737704; KF737767; KF737830
Dorcaschema cinereum	KU255629; KU255707	*Uraecha bimaculata*	AB533616; AB533647; MW982431; MW982464
Eodorcadion consentaneum	LECHK098-23	*Uraecha oshimana*	AB533617; AB533648
Eodorcadion dorcas	OQ955568	*Uraecha perplexa*	KF901311; KF901310; KF901309
Eodorcadion exaratum	LECHK103-23; LECHK104-23; LECHK105-23; LECHK106-23	*Xenohammus bimaculatus*	KF737768; KF737831; KF142024; KF141960; KF142089
Eodorcadion gorbunovi	VVGPL3542-19; VVGPL3546-19		

Sequences available in open-access databases were downloaded from GenBank, and an additional COI dataset for Eodorcadion Breuning, 1946 published by Karpiński et al. (2023) was also incorporated. The nucleotide sequences of each gene were initially processed to generate consensus sequences (where possible), which significantly reduced statistical noise caused by random mutations across different populations. Additionally, this approach facilitated the assembly of individual fragments into complete gene sequences. For example, in the case of COI, where feasible, the standard barcode fragment was supplemented with the second portion of the gene from the same species, yielding a full-length sequence. For species with available complete mitochondrial genome sequences, only the necessary gene sequences required for this study were extracted. All manipulations with nucleotide sequences, including assembly, alignment, and consensus sequence generation, were performed using Seaview 5.0, applying the MUSCLE alignment algorithm (Gouy et al., 2021). The final aligned matrix was composed of five genes in the sequence 12S + 16S + COI + 18S + 28S, with a total length of 3,822 nucleotides. It is important to note that this study has certain limitations related to variations in sequence length and the presence of gaps in the final matrix for some species. While these factors may have had a minor impact on resolving certain interspecies relationships, they are unlikely to have significantly affected the overall conclusions.

The construction of the phylogenetic tree was conducted utilizing a maximum likelihood approach, as implemented in the PhyML algorithm (Guindon et al., 2010). This analysis employed the general time-reversible (GTR) model to describe sequence evolution. Branch support was evaluated using the approximate likelihood-ratio test (aLRT), which involves comparing the log-likelihood ratios between the current tree and its most probable alternative topology (Anisimova & Gascuel, 2006; Guindon et al., 2010). Optimization of tree topology was achieved through a combination of nearest-neighbor interchange (NNI) and subtree pruning and regrafting (SPR) algorithms. Furthermore, to refine tree topology and estimate branch lengths accurately, the neighbor-joining algorithm BioNJ was utilized as an initial step in this process (Gascuel, 1997).

Results

Phylogeny of Lamiini sensu lato. The phylogenetic analysis confirms that Lamiini *s. l.* is a monophyletic group that is significantly broader than previously assumed. The clade comprises eight major subclades (Fig. 1): TAENI, DORCA, ACALO, BATOC, PSACO, ANOLPL, MONOC, LAMIA. The key findings of the study reveal several important evolutionary patterns within Lamiini s. l., including: 1) Monochamini is polyphyletic; 2) Dorcaschematini, Batocerini, Petrognathini, and Rhodopini are not separate tribes but rather integral components of Lamiini *s. l.*; 3) Petrognathini is polyphyletic, indicating a complex evolutionary history; 4) Dorcadionini, Lamiini *s. str.*, and Phrissomini form a well-supported monophyletic clade (LAMIA), which is deeply nested within Lamiini *s. l.* These results provide a more comprehensive framework for understanding the phylogenetic structure of Lamiini *s. l.*, highlighting the need for further taxonomic refinement and a reassessment of traditional tribe boundaries.

The analysis strongly supports the polyphyly of Monochamini *s. l.*, with its representatives distributed across multiple distinct evolutionary lineages, each occupying different positions within the Lamiini *s. l.* phylogenetic tree. In particular, the "Taeniotitae" group and *Acalolepta* Pascoe, 1858 occupy basal positions within Lamiini *s. l.*, forming two separate clades: TAENI and ACALO, respectively. The genera *Annamanum* Pic, 1925, *Uraecha* Thomson, 1864, *Peblephaeus* Kusama & Takakuwa, 1984, and *Blepephaeus* Pascoe, 1866, collectively forming the UrAmPe subclade, are closely related to Batocerini, clustering within the BATOC clade. The genus *Monochamus* Dejean, 1821 is polyphyletic, with its African representatives (OxyMo subclade) being closely related to *Anoplophora* Hope, 1839 (Anop subclade), together forming the ANOPL clade. In contrast, Eurasian and American *Monochamus* species form a separate MONOC clade, which is also polyphyletic, suggesting the need for taxonomic revision. Given these findings, the African *Monochamus* should be elevated from subgeneric to full generic status (i.e. *Meliochamus* Dillon & Dillon, 1959 **gen. stat. nov.**, *Laertochamus* Dillon & Dillon, 1959 **gen. stat. nov.**, *Neochamus* Dillon & Dillon, 1961 **gen. stat. nov.**, *Anthores* Pascoe, 1868, *Opepharus* Pascoe, 1868 **gen. stat. nov.** et cet.). These taxonomic changes reflect the deep evolutionary divergence among *Monochamus* lineages and provide a more natural classification aligned with their phylogenetic relationships.

My analysis confirms that Petrognathini is entirely polyphyletic, with its representatives scattered across distinct evolutionary clades within Lamiini *s. l.* Specifically, the three examined species – *Ithocritus ruber* (Hope, 1839), *Petrognatha gigas* (Fabricius, 1792), and *Threnetica lacrymans* (Thomson, 1864) – demonstrate phylogenetic affinities with different major clades of Lamiini *s. l.* rather than forming a cohesive monophyletic group. *Ithocritus ruber* unexpectedly clusters within the ACALO clade, suggesting a close evolutionary relationship with the genus *Acalolepta*. *Petrognatha gigas* is placed within the BATOC clade, exhibiting affinities with the genus *Apriona* Chevrolat, 1852, which challenges its traditional classification within Petrognathini. *Threnetica lacrymans* falls within the PSACO clade, positioned alongside the genera *Sarothrocera* White, 1846 and *Cerosterna* Dejean, 1835. These findings strongly indicate that Petrognathini, as currently defined, does not represent a natural evolutionary unit. Instead, its members are better reassigned to their respective phylogenetic clades, necessitating a comprehensive taxonomic revision of this historically recognized tribe.

In contrast to the polyphyletic nature of Petrognathini, the analysis confirms that Dorcaschematini, Batocerini, and Rhodopini form well-supported monophyletic clades, designated as DORCA and BATOC in the phylogenetic framework. Interestingly, *Rhodopina* Gressitt, 1951, the representative of Rhodopini, forms a distinct yet deeply nested subclade (Rhod) within BATOC. While it remains highly differentiated, its placement suggests a distant evolutionary affinity with Batocerini and the UrAmPe subclade of Monochamini *s. l.*

My phylogenetic analysis confirms that wingless Lamiini sensu Sama, 2008, including Dorcadionini (e.g., *Dorcadion* Dalman in Schönherr, 1817, *Neodorcadion* Ganglbauer, 1883, *Iberodorcadion* Breuning, 1943 and *Eodorcadion*), Lamiini *s. str.* (e.g., *Lamia* and *Lamiomimus* Kolbe, 1886), and Phrissomini (e.g., *Morimus*, *Herophila* Mulsant, 1863, *Mesechthistatus* Breuning, 1950, *Pseudoechthistatus* Pic, 1917), form a well-supported monophyletic clade designated as LAMIA. However, while LAMIA is monophyletic, its internal structure is complex: 1) Phrissomini and Dorcadionini are polyphyletic; 2) Lamiini *s. str.* is paraphyletic. Notably, Phrissomini is dispersed across three distinct sister subclades: HayMes, PseMoLaEo, and MoHe, indicating considerable evolutionary divergence within the tribe. Similarly, within Dorcadionini, the subclades NeIb (*Neodorcadion* and *Iberodorcadion*) and Dorc (*Dorcadion*) form a monophyletic lineage, suggesting a shared ancestral origin. However, *Eodorcadion* represents a separate evolutionary lineage within PseMoLaEo, further supporting the polyphyly of Dorcadionini. This phylogenetic placement of *Eodorcadion* challenges traditional morphological classifications, indicating that its similarities to other Dorcadionini taxa are likely due to convergent evolution and homoplasy rather than shared ancestry. This suggests a preadaptive evolutionary framework within the common ancestor of LAMIA, leading to the repeated evolution of similar morphological traits in different lineages. Additionally, the analysis reveals that the phylogeny of *Dorcadion* does not align with any of the currently accepted subgeneric classifications. Instead, it closely reflects geographic patterns and likely correlates with the postglacial expansion of *Dorcadion* across Western Asia and Europe. This biogeographic signal highlights the importance of considering historical dispersal events when interpreting the evolutionary history of the group.

As a result of this study, I have demonstrated that Lamiini *s. l.* constitutes a monophyletic group, warranting its recognition as a single, unified tribe – Lamiini **sensu novo**. This expanded concept of Lamiini integrates several previously recognized tribes, including Dorcadionini, Phrissomini, Lamiini *s. str.*, Monochamini, Gnomini, Rhodopini, Petrognathini **syn. nov.**, Batocerini, and Dorcaschematini **syn. nov.**, among others. Phylogenetic analysis reveals that Lamiini **sensu novo** comprises eight major clades, which likely represent distinct subtribes.

However, the intrageneric relationships within these clades remain unresolved, primarily due to the limited number of sequenced species available for analysis. Future studies incorporating a broader taxon sampling and additional genetic markers will be essential to refine the understanding of the evolutionary history of Lamiini **sensu novo** and further clarify its subtribal classification and intergeneric relationships.

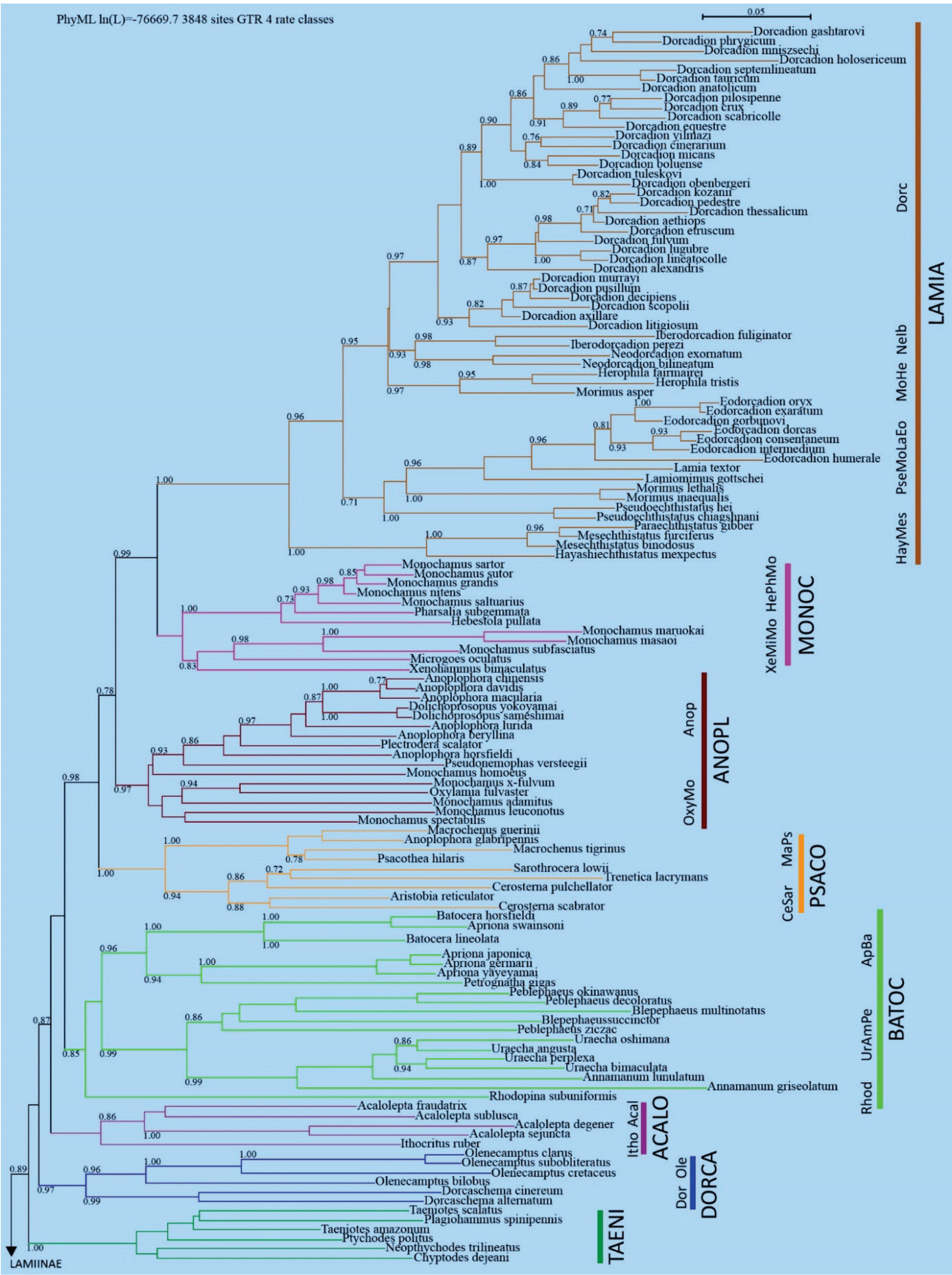

Fig. 1. The Phylogenetic hypothesis of intratribal relationships within Lamiini *s. l.*

Phylogeography of Lamiini sensu lato. Lamiini *s. l.* (~2500+ species) is a pantropical tribe with a limited representation in the Holarctic region (~600+ species). Globally, the diversity of Lamiini *s. l.* increases from west to east. Specifically, the tribe is represented by approximately 90+ species in the Neotropics, around 300+ species in the Afrotropics, and about 1200+ species in the Oriental tropics. Additionally, approximately 350+ species are known from Australasia. Despite this biodiversity gradient along the west–east axis, six major centers of diversification for Lamiini *s. l.* can be identified globally (Fig. 2), including: Indochinese-Malaysian Center (~650+ species); Balkan-Anatolian Center (~300+ species); New Guinean Center (~200+ species); Central African Center (~180+ species); Central Asian Center (~100+ species), and Mesoamerican Center (~70+ species).

The current patterns of global distribution of Lamiini *s. l.* are difficult to explain if the Indochinese-Malaysian Center is assumed to be its center of origin. On one hand, this region exhibits a high level of species diversity, whereas diversity in Africa and the Americas is significantly lower. On the other hand, my phylogenetic analysis indicates that both the Indochinese-Malaysian Center and the Central African Center are composed of evolutionarily young clades (LAMIA, MONOC, ANOPL, PSACO), whereas the Mesoamerican Center and the New Guinean Center harbor evolutionarily older clades (TAENI and ACALO). Finally, another ancient clade, DORCA, has a cosmopolitan distribution. However, it includes a relict subclade, Dor, which is highly localized in North America. All these biogeographic patterns, in synergy with phylogenetic data, suggest that Lamiini *s. l.* likely originated in the Southern Hemisphere.

The TAENI clade comprises approximately 90+ known species distributed across the tropical regions of both Americas. Its center of diversification is located in Mesoamerica, where about 74% of all known species occur. The geographical patterns of TAENI suggest a prolonged (likely island-driven) isolation followed by relatively recent diversification. In South America, despite the vast distribution area (~11.9 million km²), only about 44% of the total species diversity is recorded. This may indicate a relatively recent colonization of South America, likely during the Pliocene (~3 Ma), coinciding with the formation of the land bridge between Meso- and South America. The expansion of TAENI into the West Indies probably occurred even later, during the Pleistocene (2.5–0.012 Ma), a period marked by repeated glaciations and significant fluctuations in sea levels. Notably, TAENI represents the most basal clade within Lamiini *s. l.*, suggesting that it originated in the distant past.

The DORCA clade (~140+ species) has a cosmopolitan distribution, inhabiting all continents except Antarctica and South America. It is divided into two subclades: 1) the Nearctic Dor and 2) the Paleotropical-Australasian Ole. The Dor subclade (4 species) represents the basal lineage within DORCA and diverged from the common ancestor at an early stage of evolution. Today, it exhibits a relictual distribution, characterized by its small range and low species richness. In contrast, the Ole subclade (~140+ species) is widely distributed across the Paleotropics and Australasia, extending from west to east beyond the Wallace Line. Its center of diversification is located in the Indomalayan region.

The ACALO clade (~260+ species) has an Oriental-Australasian distribution, with its center of diversification in New Guinea. It is divided into two subclades: 1) the Oriental Itho and 2) the Australasian Acal. The Itho subclade (4 species) represents part of the former tribe Petrognathini and is restricted to the western part of the Oriental region. In contrast, the Acal subclade is more widely distributed, spanning Australia, Oceania, and Southeast Asia, extending northward into the eastern Palearctic. Notably, the Acal subclade crosses the Wallace Line from east to west.

The BATOC clade (~320+ species) is distributed across the Paleotropics and Oceania, with several weakly defined centers of diversification in southern China, Sumatra, and New Guinea. It comprises three subclades: 1) the Oriental Rhod, 2) the Oriental UrAmPe, and 3) the Paleotropical-Oceanian ApBa. Among these, only the ApBa subclade crosses the Wallace Line from west to east, extending into the Australian region. In the New Guinean center of diversification, ApBa is represented by the endemic genus Rosenbergia Ritsema, 1881 (~40+ species). In equatorial Africa, ApBa includes several species of the genera *Batocera* Laporte de Castelnau, 1840 and *Petrognatha* Leach, 1819, the latter of which was previously classified in the separate tribe Petrognathini. The Rhod subclade (~50+ species) is scattered across Southeast Asia and is likely a relict group. The UrAmPe subclade (~110+ species) is widespread throughout the Oriental region, with its center of diversification in southern China.

The PSACO clade (~50+ species) is distributed throughout the Oriental region, crossing the Wallace Line from west to east but not extending beyond Sulawesi. It consists of two subclades: CeSar and MaPs.

The ANOPL clade (~300+ species) includes species groups distributed across the Paleotropics, the Eastern Palearctic, and Southeastern Nearctic, with two centers of diversification in equatorial Africa and Southern China. It comprises two subclades: 1) the African OxyMo and 2) the Oriental-Nearctic Anopl. The only Nearctic species, *Plectrodera scalator* (Fabricius, 1792), is evidently a relict member of the Anopl subclade.

The MONOC clade (~150+ species) is widespread across Eurasia and North America. In the Oriental region, its species do not cross the Wallace Line, while in the Neotropics, it extends into Northern South America. It consists of two subclades: 1) XeMiMo and 2) HePhMo, both of which are present in both Eurasia and the Americas.

The LAMIA clade (~620+ species) is distributed across Eurasia and Africa and consists of five subclades with distinct biogeographic patterns. The HayMes subclade is centered in the Sino-Japanese region, while the PseMoLaEo subclade spans the Eastern Palearctic and Oriental regions. In the Western Palearctic, three subclades are recognized: MoHe, NeIb, and Dorc, each contributing to the clade's diversification across this region. The African species formerly classified under the tribe Phrissomini likely represent a sixth subclade within the LAMIA clade. Unfortunately, the absence of sequence data for this intriguing and understudied group of Lamiine beetles prevented their inclusion in the phylogenetic analysis.

I hypothesize that all the current centers of diversification within Lamiini *s. l.* are secondary or even tertiary, having emerged following a series of extinctions and subsequent diversifications over the last 50–70 million years. These extinction events may have been caused by events such as the K-T boundary (~66 Ma), the Antarctic glaciation (~34 Ma), the Miocene glaciations (~20 Ma and ~14 Ma), and repeated glaciations during the Pliocene-Pleistocene (~3–0.01 Ma), which were accompanied by large-scale desertification, the expansion of grassland biomes, and the reduction of temperate and tropical forests. It is evident that African and South American Lamiini *s. l.* species are relicts that survived large-scale regional extinction events in the geological past.

The hypothesis of a South Gondwanan origin, Panthalassa-Tethys expansion, and diversification of Lamiini *sensu lato*. The discrepancies between the geographical patterns of contemporary centers of diversification and the molecular phylogeny of Lamiini *s. l.* may be reconciled through the hypothesis of the origin of this mega-diverse group of the longhorn beetles in the southern part of Gondwana. Firstly, the most basal clade, TAENI, is the most geographically isolated from the rest of Lamiini *s. l.* and is distributed across South America, Mesoamerica, and the West Indies. Secondly, the DORCA clade, which is phylogenetically close to TAENI and also occupies a basal position, exhibits significant geographical disjunction between North America on one side and the Paleotropics on the other. Finally, the third basal clade, ACALO, encompasses the Australasia region with a current center of diversification in New Guinea. In general, the three most basal groups of Lamiini *s. l.* are distributed across the most distant continents, two of which were once part of the ancient Gondwanan landmass.

My hypothesis suggests that the common ancestor of all Lamiini *s. l.* (LaCA) likely originated in the contact zone between Antarctica and South America. This event is thought to have occurred during the time period between the final separation of Africa and India from South Gondwana (~100 Ma) on one hand, and the formation of the Trans-Tethyan Arc (~90 Ma) on the other. The emergence of LaCA is likely to be dated to the late Cretaceous period, around 90 Ma. The most probable biome for LaCA would have been the southern megathermal forests, which, during the late Cretaceous, extended as far as 60° S latitude (Morley, 2003). The integrity of South Gondwana persisted until the Oligocene (~30 Ma), which facilitated the migration of biota between South America, Antarctica, and Australia (Morley, 2003; Rodríguez et al., 2015; Eagles, 2016), including the basal clades of Lamiini *s. l.*

The hypothesis posits several key stages (for further details, see the discussion) of expansion and diversification of Lamiini *s. l.* (Fig. 3), which led to the establishment of its present diversity and distributional patterns:

Stage 1: Out of Antarctica (~90–80 Ma): The dispersal of LaCA across South Gondwana with early penetration into North America and Western Burma (the Trans-Tethyan Arc).

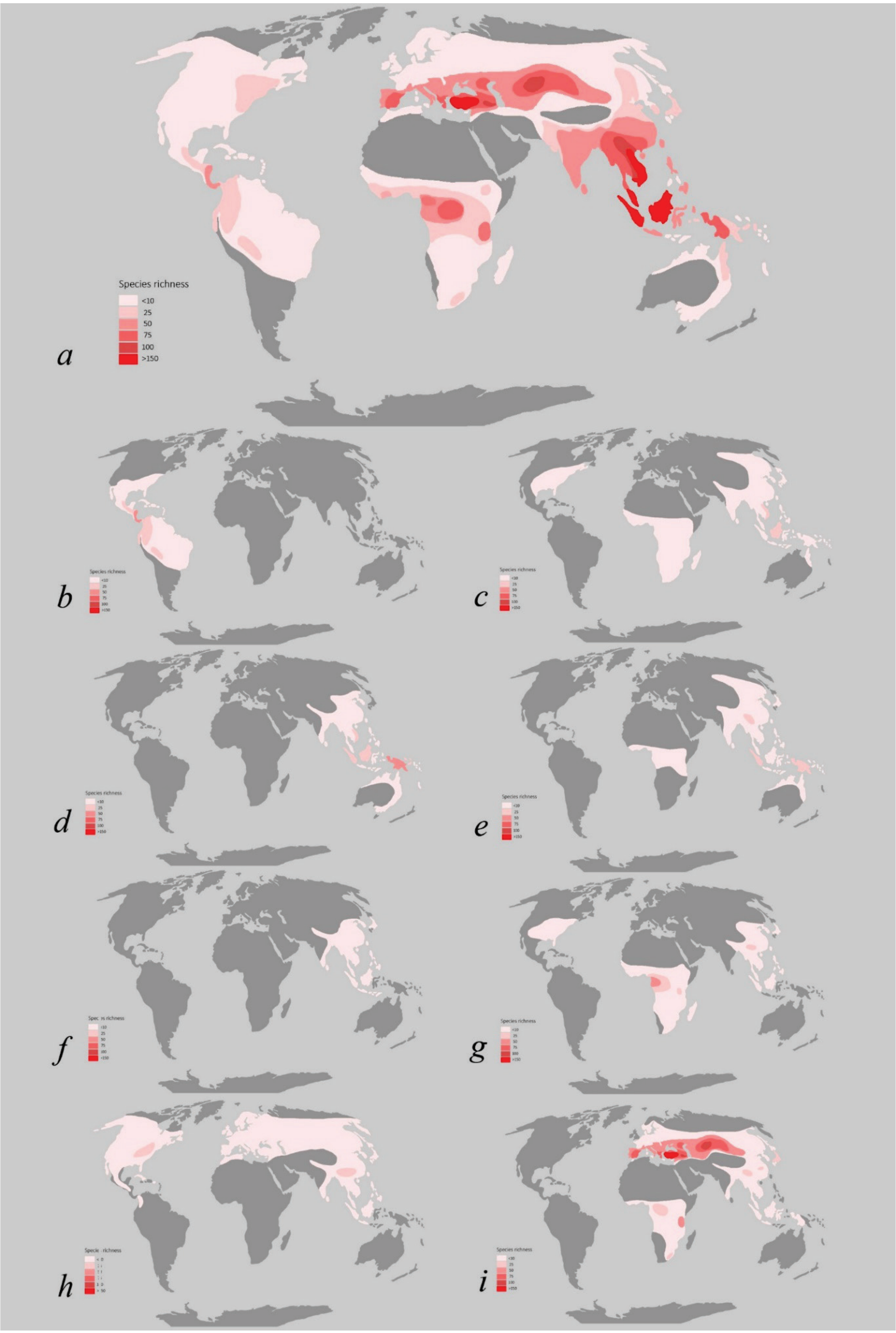

Fig. 2. Global biogeographical patterns of Lamiini *s. l.* (*a*), illustrating the distribution and diversification centers of its major lineages, including TAENI (*b*), DORCA (*c*), ACALO (*d*), BATOC (*e*), PSACO (*f*), ANOPL (*g*), MONOC (*h*), and LAMIA (*i*)

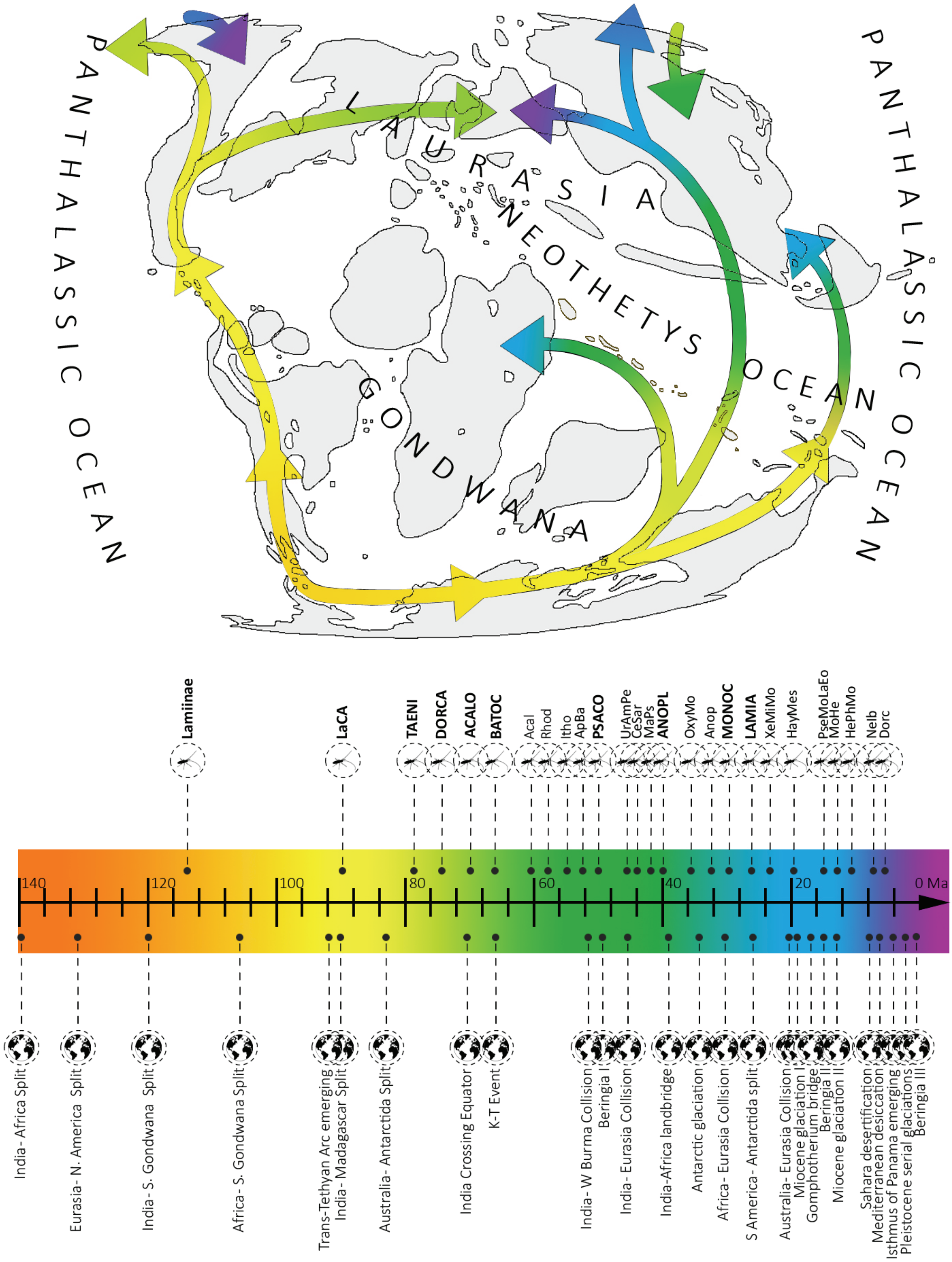

Fig. 3. Conceptual model illustrating the South Gondwanan origin of Lamiini *s. l.* and its Panthalasso-Tethyan dispersal pathways, highlighting key migration routes and historical biogeographical patterns

Stage 2: On the way to India (~70–60 Ma): Diversification of the basal clades TAENI, DORCA, and ACALO; penetration of DORCA into East Asia by northeast Panthalassic route; emergence of the ancestor of the crown clades of Lamiini *s. l.* and its expansion into Greater India and throughout the Trans-Tethyan Arc.

Stage 3: Long journey to Asia (~60–50 Ma): Diversification of the crown clades of Lamiini *s. l.* and the emergence of BATOC and PSACO within Tethyan archipelagos.

Stage 4: Meeting a new continent (~50–40 Ma): Indo-Asian faunal exchange through the overlap of DORCA from Asia with BATOC and PSACO from Greater India and the Trans-Tethyan Arc; emergence of the clade ANOPL and the diversification of crown clades of Lamiini *s. l.*

Stage 5: Conquest of Africa (~40–20 Ma): Expansion of Lamiini *s. l.* (DORCA, BATOC, ANOPL) into Africa; extinction of Antarctic clade(s) of Lamiini *s. l.* (Antarctic glaciation); emergence of the clades MONOC and LAMIA in East Asia.

Stage 6: The discovery of America (~20–10 Ma): Diversification of the crown clades of Lamiini *s. l.*; expansion of MONOC and ANOPL into North Eurasia and North America; expansion of LAMIA into Eurasia and Africa; faunal overlap of Lamiini *s. l.* between Australia and Asia.

Stage 7: Destination "nowadays" (~10–0 Ma): Series of Pliocene-Holocene global extinctions and the establishment of the modern fauna of Lamiini *s. l.*

Proposed hypothesis provides an explanation for the extraordinary diversity of Lamiini *s. l.* in Southeast Asia. This is the result of the convergence of different phylogenetic clades of Lamiini *s. l.*, which occurred through three distinct migratory routes (northeast Pantalassic, Trans-Tethyan, and southwest Pantalassic). These routes were superimposed on a series of prominent Cenozoic geological events (the Indo-Asian collision, Himalayan uplift, the Australo-Asian collision, and glacial cycles with significant fluctuations in sea level), which led to pulsating diversification and further expansion of Lamiini *s. l.*

The members of the clade DORCA were the first to reach Southwest Asia (subclade Ole), spreading there via the northeast Pantalassic route from North America into Asia (~70–60 Ma). The clades BATOC and PSACO reached Southeast Asia through the Trans-Tethyan migration route via India around ~50–40 Ma. Finally, the clade ACALO arrived in this region via the southwest Pantalassic route around ~20–10 Ma. The mixing of faunas, on the one hand, increased the taxonomic diversity of Lamiini *s. l.* in the region, while, on the other hand, it inevitably led to the intensification of ecological competition, local extinctions, and specialization of ecological niches, followed by further diversification and speciation.

The contribution of geological processes to the diversification of Lamiini *s. l.* in Southeast Asia has been immense. Specifically, active mountain building with the fragmentation of the continent into separate mountain clusters, numerous archipelagos, and significant fluctuations in sea level, in their full synergy, ensured the "pulsations" of intense speciation through periods of isolation and the opening of migration routes for further expansion. These processes in the region continue today, with a significant influence from human activity.

Discussion

My phylogenetic analysis of Lamiini *s. l.* using five genes (12S mt rRNA, 16S mt rRNA, COI, 18S n rRNA, and 28S n rRNA) is the most comprehensive to date, including 129 species from 51 genera. This comprehensive dataset has, on one hand, significantly clarified the internal relationships among different clades, but on the other hand, it has highlighted problematic issues in classification and intergeneric relationships that remain unresolved. A key finding of the study is the confirmation of the monophyly of Lamiini *s. l.*, as suggested by several studies with much smaller taxa samples and using different genetic markers and evolutionary models (Nie et al., 2020; Souza et al., 2020; Ren et al., 2021; Pu et al., 2022). My research demonstrated that Lamiini *s. l.* consists of at least eight distinct evolutionary clades: TAENI, DORCA, ACALO, BATOC, PSACO, ANOPL, MONOC, and LAMIA, which are successively nested on the phylogenetic tree. The first three are the most isolated from the others and represent basal clades, while the last five form the crown group of the Lamiini *s. l.* phylogenetic tree. In the small number of published phylogenetic studies of Lamiini in particular, and Lamiinae in general, a similar topology of phylogenetic trees of this tribe is repeated, with minor variations. However, this topology is highly dependent on the number and selection of species included in the analysis. In almost all studies, the crown group identified by me is supported (Nie et al., 2020; Bai et al., 2022; Pu et al., 2022; Soydabaş-Ayoub & Uçkan, 2023). The most variable results are observed with the basal clades, as well as the position of Batocerini. In many studies, Batocerini is defined as a sister group to Lamiini (Souza et al., 2020; Ashman et al., 2021; Ren et al., 2021; Zhang et al., 2021; Li et al., 2023), while several other studies place Batocerini within Lamiini (Gorring, 2019; Nie et al., 2020; Bai et al., 2022; Pu et al., 2022; Soydabaş-Ayoub & Uçkan, 2023). The phylogenetic position of Batocerini was addressed by Gorring (2019) in his dissertation, proposing that this group should be considered a part of the Lamiini tribe. The results of the current study align with Gorring's conclusions (2019), so I emphasize that Batocerini is indeed part of Lamiini. However, my findings differ from previous studies in that I consider Batocerini as part of the crown group of Lamiini, at least as sister to four other clades (PSACO, ANOPL, MONOC, and LAMIA), whereas other studies place Batocerini as a basal group within Lamiini (Ashman et al., 2021; Zhang et al., 2021; Pu et al., 2022). It is clear that this issue lies within the number of taxa included in the analysis. As the number of taxa increases, so does the quality of resolving phylogenetic relationships.

There are very few studies that include species from the TAENI, DORCA, and ACALO clades in their analyses. Only two studies have incorporated the TAENI clade, and in both cases – as in this study – it occupies a basal position (Gorring, 2019; Souza et al., 2020). The DORCA clade has been placed either as a sister group to Lamiini (Nie et al., 2020; Souza et al., 2020; Pu et al., 2022) or as one of the basal clades (Bai et al., 2022). However, all these studies have only included the genus *Olenecamptus* Chevrolat, 1835, without considering *Dorcaschema* Haldeman, 1847. In the current analysis, I included both genera and confirmed that the clade is monophyletic and basal within Lamiini. Finally, the ACALO clade has been rarely represented in phylogenetic studies (Gorring, 2019; Ashman et al., 2021), where it typically occupies a basal position, which is consistent with my results.

The topology of reconstructed phylogenetic tree for Lamiini *s. l.* reveals strong evolutionary signals that highlight key aspects of the tribe's historical development. Notably, the set of basal clades (e.g., TAENI, DORCA, and ACALO) exhibits highly specific phylogeographic patterns. This is reflected in the fact that the most ancient and least diverse clades – likely due to their relict status – are found on the most geographically isolated continents (South America, North America, and Australia). In contrast, the crown clades are the most diverse and predominantly inhabit the Paleotropics and Palearctic regions, with only limited representation in the Nearctic. These patterns allow me to trace the recent distribution of Lamiini *s. l.* back to the time of the supercontinent Southern Gondwana, which connected South America, Antarctica, and Australia. Based on these findings, I propose a hypothesis of Southern Gondwanan origin for Lamiini *s. l.* Specifically, I suggest that the last common ancestor of Lamiini *s. l.* (LaCA) originated in the region corresponding to present-day Southern South America and Western Antarctica. From this point, the tribe began its expansion across Southern Gondwana and subsequently into Laurentia (North America).

The timing of the origin of Lamiini *s. l.* remains a subject of debate, with a wide range of estimated dates spanning from 117 Ma (Nie et al., 2020) to 52 Ma (Soydabaş-Ayoub & Uçkan, 2023). Despite the widespread application of molecular clock methods by various researchers (Nie et al., 2020; Ashman et al., 2022; Jin et al., 2022; Soydabaş-Ayoub & Uçkan, 2023), the age estimates (Table 2) for the emergence of the tribe and its major clades are still far from being definitively resolved.

A major limitation in accurately calibrating the molecular clock of Lamiini *s. l.* is the critical lack of reliable paleontological data. Moreover, the available fossil records are often problematic due to uncertainties in their taxonomic placement and dating accuracy (Table 3). As a result, these data are generally unsuitable for calibrating the molecular clock of Lamiini *s. l.* Consequently, estimates of divergence times for various lineages remain largely theoretical, relying on the assumptions made by individual researchers based on the selected evolutionary models and substitution rates. This situation may change with the discovery of well-preserved and taxonomically validated Lamiini *s. l.* fossils.

It is important to note that the currently known fossil species (Table 3), which have previously been classified within the tribe Lamiini to varying degrees, are primarily represented by partially damaged, compressed stone imprints (Nel et al., 2024). The only exception is *Dorcaschema succineum* from Baltic amber (Vitali, 2009).

Table 2

Generalized data on the approximate age (Ma) of the emergence of Lamiini *s. l.* and its key clades, corresponding to the phylogenetic division into clades adopted in this study

Clades	Soydabaş-Ayoub & Uçkan (2023)	Gorring & Farrel (2023)	Ashman et al. (2022)	Nie et al. (2020)	Jin et al. (2022)	Current study
Cerambycidae	~153	–	~129	~151	~150	–
Lamiinae	~105	–	~105	~147	~95	~115
LaCA	~52	–	~63	~117	~58	~90
TAENI	–	–	–	–	–	~78
DORCA	–	–	–	~119	–	~74
ACALO	–	–	~52	–	–	~70
BATOC	~52	–	~63	~54	–	~67
PSACO	–	–	–	~51	–	~50
ANOPL	–	~11	~35	–	–	~40
MONOC	~41	~11	~35	–	–	~30
LAMIA	~26	–	–	–	–	~25

Table 3

Fossil species that have historically been classified within the tribe Lamiini *s. l.*, and are potentially considered for calibrating the molecular clock

Fossil species	Age, Ma	Source	Comment
Prolamioides bituminosus	62–59	Piton & Théobald (1937) placed within Lamiini; Nel et al. (2024) placed within Lamiinae	Not Lamiinae; probably belongs to Prioninae
Prolamioides brunneus	62–59	Piton (1940) placed within Lamiini; Nel et al. (2024) placed within Lamiinae	Not Lamiinae; probably belongs to Prioninae
Monohammus orientalis	62–59	Piton (1940) placed within Lamiini; Nel et al. (2024) placed within Cerambycidae	Not Cerambycidae
Parolamia rudis	34–37	Scudder (1878) placed within Lamiini	Not Lamiini; definitely belongs to Lamiinae, probably Parmenini
Dorcaschema succineum	33–38	Zang (1905) placed within Dorcaschematini; Vitali (2009) placed within Dorcaschematini	Most likely belongs to DORCA clade
Lamia petrificata	23–28	Heyden & Heyden (1866) placed within Lamiini	Not Lamiini; definitely belongs to Lamiinae
Dorcadion bachense	23–28	Handschin (1944) placed within Lamiini	Not Lamiini; definitely belongs to Lamiinae
Dorcadion emeritum	23–28	Heyden (1862) placed within Lamiini	Not Lamiini; definitely belongs to Lamiinae
Lamia antiqua	13–12	Heer (1879) placed within Lamiini	Not *Lamia*; probably related to *Phrissoma*, *Herophila* and *Morimus*; definitely belongs to LAMIA clade
Monochamus willershausensis	2–4	Schmidt (1967) placed within Lamiini Vitali (2024) placed within *Monochamus*	Belongs to *Monochamus*; definitely belongs to MONOC clade
Monochamus gehleri	2–4	Vitali (2024) placed within *Monochamus*	Belongs to *Monochamus*; definitely belongs to MONOC clade

Among all the fossil species mentioned, only "*Lamia*" *antiqua* (clade LAMIA) and *Monochamus willershausensis* (clade MONOC) can be confidently assigned to Lamiini *s. l.* However, their generic placement is likely inconsistent with their original descriptions (Vitali, 2024). Another fossil species belonging to Lamiini *s. l.* is *Monochamus gehleri* (Vitali, 2024). Additionally, I classify "*Dorcaschema*" *succineum* as an extinct representative of the clade DORCA. The remaining species listed in Table 3 are unlikely to belong to Lamiini *s. l.* and instead represent other taxonomic groups, including subfamilies Lamiinae (e.g., "*Lamia*" *petrificata*, "*Dorcadion*" *bachense*, "*Dorcadion*" *emeritum*, *Parolamia rudis*) and Prioninae (e.g., *Prolamioides bituminosus* and *Prolamioides brunneus*), or even entirely different families (e.g., "*Monohammus*" *orientalis*) (Vitali, personal communication). Notably, Nel et al. (2024) placed Prolamioides within Lamiinae and "*Monohammus*" *orientalis* within Cerambycidae without further specification. The latter fossil is poorly preserved and could equally belong to any Polyphaga family, as medium- to large-sized species are common across multiple lineages.

In summary, as of today, only three Lamiini *s. l.* clades identified in the current phylogenetic analysis are known with high confidence from the fossil record, and all of them originate from Europe: DORCA, MONOC, and LAMIA. The fossil record suggests that DORCA existed in Europe as early as the late Eocene (33–38 Ma), whereas LAMIA is known from the middle Miocene (13–12 Ma), and MONOC from the late Pliocene (2–4 Ma). Although fossil data on Lamiini *s. l.* are scarce and geographically restricted, they provide some insight into the colonization history of the tribe, at least in Europe. These findings indicate that DORCA were already widespread in Europe (which at the time consisted of an archipelago in the Tethys Ocean) long before the Eocene and likely arrived from Laurentia (North America) via west to east migration route (see below). In contrast, the MONOC and LAMIA clades colonized Europe after the uplift of the continent and the formation of major mountain ranges such as the Pyrenees, Alps, Carpathians, and Caucasus during the Miocene.

The available paleontological data do not provide a definitive answer regarding the center of origin for LaCA. Therefore, I employed phylogenetic analysis as a tool for "molecular paleontology" to infer the probable region of LaCA's emergence. The findings suggest that LaCA most likely originated in the region between present-day South America and Antarctica, which was part of the former supercontinent Southern Gondwana. The emergence of LaCA must have occurred between two major geological events that drastically reshaped continental configurations during the Cretaceous period: the complete separation of Africa and Greater India from Southern Gondwana (~100 Ma) on the one hand, and the formation of the Trans-Tethyan Arc (~90 Ma) on the other (Ali & Aitchison, 2008; Chatterjee & Scotese, 2010; Westerweel et al., 2019; Meng et al., 2023). Notably, LaCA and its direct descendants were absent from Africa and Greater India. In contrast, the Trans-Tethyan Arc likely served as the only, and very short-lived, bridge for the expansion of LaCA from Australia into Greater India. Additionally, the possibility of transoceanic dispersal between Australia, the Trans-Tethyan Arc, and Greater India should not be ruled out. Such dispersal events have been documented in the literature for other insect taxa (McCulloch et al., 2016; Bourguignon et al., 2018; Liebherr et al., 2024).

With the emergence of LaCA (Fig. 4a), this lineage of the longhorn beetles likely underwent a rapid initial expansion across Southern Gondwana, spreading from South America through Antarctica to Australia (Fig. 4b). This dispersal would have taken place within the southern megathermal forests that dominated the region during the Late Cretaceous (Morley, 2003). A southern dispersal route through Antarctica has been documented for many insect groups that later formed vicariant taxa, including Peloridiidae (Ye et al., 2018), Belidae (Li et al., 2024), Carabidae (Sota et al., 2022; Liebherr et al., 2024), Chrysomelidae (Jolivet & Verma, 2009), and Lucanidae (Kim

& Farrell, 2015). Thus, this scenario of LaCA dispersal appears highly plausible.

Another major expansion route for LaCA involved northward migration along the Proto-Andean Mountains, leading to an early incursion into Laramidia (the western island continent corresponding to present-day western North America). Although South America and Laramidia were separated by a marine basin during the Late Cretaceous, the eastward-moving Caribbean Plate formed an island arc known as the Antillean Arc (Viñola-López et al., 2022). This arc served as a land bridge between the two Americas and is believed to have facilitated the first post-Pangaean exchange of flora and vertebrate fauna (Viñola-López et al., 2022). However, data on invertebrate migration via this route remain scarce. It has been proposed that ancient Rhopalocera (Lepidoptera) dispersed from South America to Laramidia via the Antillean Arc, later colonizing Asia through Beringia (Kawahara et al., 2023). I hypothesize that LaCA followed a similar pathway to reach Laramidia (Fig. 4b).

Finally, a third key region colonized by LaCA – and one that played a crucial role in shaping the future megadiversity of Lamiini *s. l.* – was the archipelagos of the Trans-Tethyan Arc. Some remnants of the Trans-Tethyan Arc are still preserved today, having been incorporated into Eurasia. These geological fragments include the Kohistan, Ladakh, Dras, Argo, Andaman, Burma, and Woyla terranes (Vérard et al., 2017; Metcalfe, 2021; Morley et al., 2021). By the end of the Cretaceous, LaCA must have been present at least in the eastern part of Trans-Tethyan Arc, from where its descendants subsequently colonized India and Asia. An alternative expansion route for LaCA into Greater India may have involved dispersal from Antarctica via the Kerguelen Plateau, followed by migration through the Trans-Tethyan Arc into Asia. This pathway has been proposed for other biological groups (Yuan et al., 2018). Whether LaCA migrated into Greater India via one or both of these routes remains unknown.

The initial diversification of Lamiini *s. l.* (~70–60 Ma) led to the emergence of vicariant taxa, shaped by the geographic isolation of LaCA descendants on different continents. Their subsequent evolution resulted in the formation of several basal clades: TAENI in South America, DORCA in North America, ACALO in Australia, and the ancestor of the crown-group Lamiini *s. l.* in the eastern Trans-Tethyan Arc (Fig. 4c). It is also plausible that an additional Antarctic clade emerged but later went extinct during the Oligocene glaciations. The emergence of the ancestor of the crown-group Lamiini *s. l.* likely occurred just before the Cretaceous–Paleogene (K–Pg) mass extinction (~70–66 Ma). During this period, the most probable scenario involved the rise of the BATOC and PSACO clades. At the same time, the divergence of DORCA took place, driven by the westward expansion of the Ole subclade ancestor into Asia from Laramidia, as well as the eastward migration of the Dor subclade ancestor into Europe via the Appalachian corridor.

The transition from the Mesozoic to the Cenozoic was marked by global ecosystem restructuring and significant biodiversity loss (Labandeira et al., 2016; Cai et al., 2022). These changes were driven by a combination of geological and astronomical factors, including intense volcanic activity (e.g. Deccan Traps) and asteroid impacts (e.g. Chicxulub, Bovtyshka, Shiva) around 66 Ma (Pandey & Agrawal, 2000; Pickersgill et al., 2021; Range et al., 2022; Callegaro et al., 2023; Senel et al., 2023). It is highly likely that these events caused substantial losses in Lamiini *s. l.* diversity, leading to the extinction of many ancient taxa (Fig. 4d). However, no direct paleontological or indirect phylogenetic evidence has yet been identified to confirm this for the group. Notably, the topology of the basal clades Lamiini *s. l.* (TAENI, DORCA, ACALO) in the reconstructed phylogenetic tree suggests a past attenuation of their diversity followed by later diversification. This pattern could indicate extinction and subsequent recovery events. However, the timing of these events is more likely associated with later glaciations – Oligocene glaciations (~30–34 Ma) in the Southern Hemisphere affecting TAENI and ACALO, and Miocene glaciations (~20 and ~14 Ma) in the Northern Hemisphere impacting DORCA.

The Cenozoic diversification of Lamiini s.l. (Fig. 4e) was driven by the collision of Greater India with Asia and the subsequent faunal exchanges between these landmasses, as well as with Africa. The landmasses of Greater India and the Trans-Tethyan Arc functioned as giant "carriers", transporting LaCA descendants (BATOC and PSACO clades) from former Southern Gondwana to Asia (~50–45 Ma). This event catalyzed the diversification of the ANOPL clade in the continental environments of Eurasia.

The expansion of Lamiini *s. l.* from India into Africa occurred approximately 45–35 Ma (Fig. 4f), but the precise dispersal route remains a topic of debate. It may have involved a hypothetical land bridge connecting India to the Oman Mountains, or alternatively, an archipelago of islands that temporarily linked both continents rather than a continuous landmass (Chatterjee & Scotese, 2010; Vérard et al., 2017). The biotic exchange between India and Africa remains an unresolved issue in modern biogeography (Yuan et al., 2018; Parmar & Prasad, 2020). Nevertheless, during this period, the DORC, BATOC, and ANOPL clades successfully dispersed from India into Africa.

The total extinction of biota in Antarctica and dramatic ecosystem changes in the Southern Hemisphere – including the disappearance of southern megathermal forests and the expansion of deserts and grassland biomes globally – were driven by Antarctic glaciation during the Oligocene (~34–30 Ma) (Filippelli, 2005). During this period, the hypothetical Antarctic clade of Lamiini s.l. likely went extinct, and the TAENI and ACALO clades experienced a significant and abrupt reduction in both range and diversity (Fig. 5a). Climatic changes in the Northern Hemisphere were less extreme but resulted in increased seasonality, and in mountainous regions, the climate became more similar to modern conditions (Tripati & Darby, 2018). Around this time (~40–20 Ma), the MONOC clade emerged in Asia, likely as an adaptation to the spread of montane coniferous forests associated with global cooling. The ACALO clade underwent secondary diversification during the initial collision of Australia and Eurasia (~25–20 Ma), coinciding with the uplift of New Guinea in the Miocene (Davies, 2012). Subsequent dispersal of ACALO occurred across numerous archipelagos in Oceania and Indo-Malaysia, following a pattern observed in many other insect groups with Australian origins (Austin et al., 2004; Braby & Pierce, 2006; Toussaint et al., 2014; Letsch et al., 2023; Starkie et al., 2023).

The LAMIA clade is the most evolutionarily recent among all other Lamiini *s. l.* and occupies a terminal position in the phylogenetic tree. The origin of this clade remains largely unclear. However, its phylogeny suggests that the most basal subclade, HayMes, and basal branches within the PseMoLaEo subclade have a Sino-Japanese distribution. This could indicate that the common ancestor of all LAMIA species likely formed in East Asia around 25–20 Ma. However, the trigger for the loss of flight capability in LAMIA remains unexplained. It should be noted that some species within the basal subclades retain developed wings and are capable of short-distance flight (Bi & Lin, 2016). Nonetheless, all basal groups of LAMIA (such as *Hayashiechthistatus* Miyake, 1980, *Mesechthistatus* Breuning, 1950, *Parechthistatus* Breuning, 1942, *Pseudoechthistatus* Pic, 1917, *Morimus*, etc.) are associated with mountainous deciduous forests, which may hold the key to understanding the origin of their flightlessness. It is believed that environmental stability, isolation, and high-altitude or island habitats are key factors leading to the loss of flight ability (Medeiros & Gillespie, 2010; Venn, 2016). It is likely that the last common ancestor of the LAMIA clade formed in an isolated mountainous environment during the active uplift of the Himalayas, Tibetan Plateau, and the formation of adjacent mountain systems. The founding population of the LAMIA ancestor likely exhibited dimorphism in wing length or brachyptery but was not flightless. Flightlessness in this clade should be considered as a result of later evolutionary developments. Subsequent geological activity in the region likely disrupted the initial isolation and allowed the ancestors of LAMIA to expand actively across Eurasia, and later into Africa.

The results of the phylogenetic analysis reveal the presence of two sister subclades, PseMoLaEo and MoHe+NeIb+Dorc, within the LAMIA clade. The PseMoLaEo subclade represents groups distributed across Southeast and Central Asia, while the MoHe+NeIb+Dorc subclade occupies Europe and Southwestern Asia. Accordingly, it is most likely that the expansion of LAMIA in Eurasia occurred via at least two routes: southern and northern. Through the southern route, LAMIA (MoHe+NeIb+Dorc) reached Western Asia, Europe, and Africa, while the northern route (PseMoLaEo) led them into Central and Northern Asia (Fig. 5b). Paleontological evidence suggests that LAMIA were present in Europe during the Middle Miocene, with specimens such as "*Lamia*" *antiqua* (Heer, 1879) providing evidence of their earlier existence.

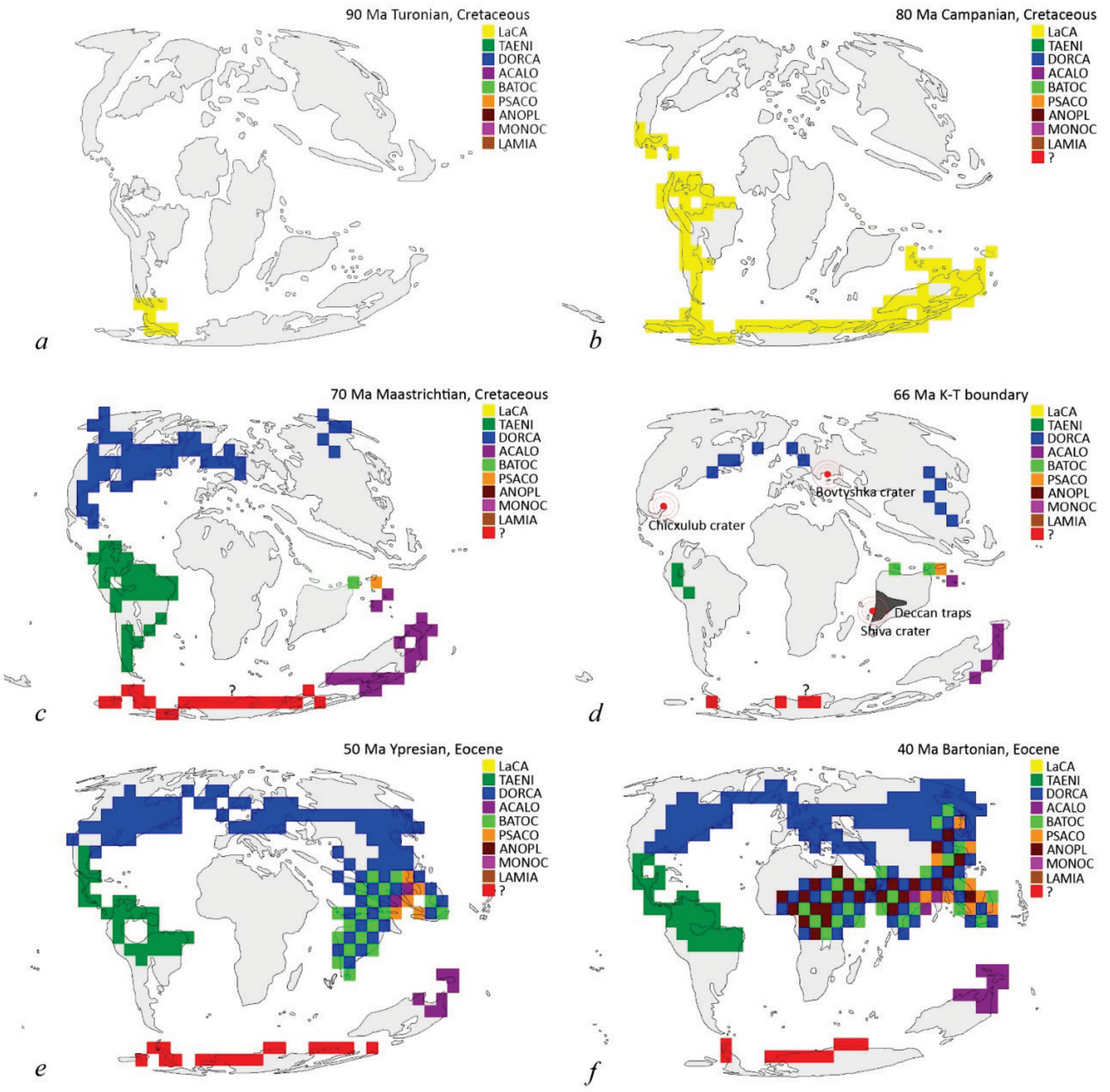

Fig. 4. Schematic representation of the early diversification and global dispersal patterns of Lamiini *s. l.* from the Late Cretaceous to the Paleogene (90–40 Ma)

The early diversification and expansion of LAMIA likely occurred during the Miocene Climatic Optimum, a relatively brief (~2 Ma) interglacial period in the middle Miocene (~15-17 Ma) (Steinthorsdottir et al., 2020). This period was characterized by warm and humid conditions (Herold et al., 2011; Methner et al., 2020), which facilitated the widespread distribution of moist broadleaf forests in the mountain ranges of Eurasia and mixed broadleaf-sclerophyllous forests in North Africa (Doláková et al., 2020; Acosta et al., 2024). I hypothesize that the penetration of LAMIA into Africa occurred via the Gomphothere Bridge (~16 Ma) during the Miocene Climatic Optimum, which correlates well with paleontological evidence, particularly "*Lamia*" *antiqua* in Europe. Unfortunately, I was unable to determine the phylogenetic affiliation of African LAMIA due to the lack of sequences for this intriguing group. The African LAMIA should be related to the MoHe subclade, but this hypothesis still requires further testing and confirmation.

The late diversification and expansion of LAMIA (Fig. 5c) were associated with climatic cooling and increasing xerophylization during the late Miocene (~5–11 Ma). These climatic shifts led to the decline of temperate deciduous forests and the widespread expansion of steppes, semi-deserts, and deserts across vast regions of Eurasia (Utescher et al., 2007; Zhang et al., 2014; Jia & Bartish, 2018; Barbolini et al., 2020; Wen et al., 2023). These environmental changes likely contributed to the Irano-Turanian disjunction in the distribution of LAMIA, a pattern that persists to date. This period also saw the emergence and diversification of non-forest LAMIA lineages, including *Neodorcadion*, *Iberodorcadion*, *Dorcadion*, *Eodorcadion*, and others. It appears very likely that a complete extinction of mid-Miocene LAMIA occurred in Northern Asia, which was associated with the subsequent Miocene cooling (~15 Ma). Consequently, the PseMoLaEo subclade likely lost a significant portion of its diversity. However, available evidence suggests that a small group of this subclade survived, eventually giving rise to the diversification of steppe-adapted *Eodorcadion*. This diversification is estimated to have occurred during the Pliocene (~5–2.5 Ma). The evolutionary history of *Eodorcadion* is complex, involving extensive hybridization, local extinctions, introgression events, and multiple instances of homoplasy (Karpiński et al., 2023). The expansion of *Eodorcadion* northward and westward was likely constrained by Pliocene–Pleistocene glaciations (~5–0.01 Ma).

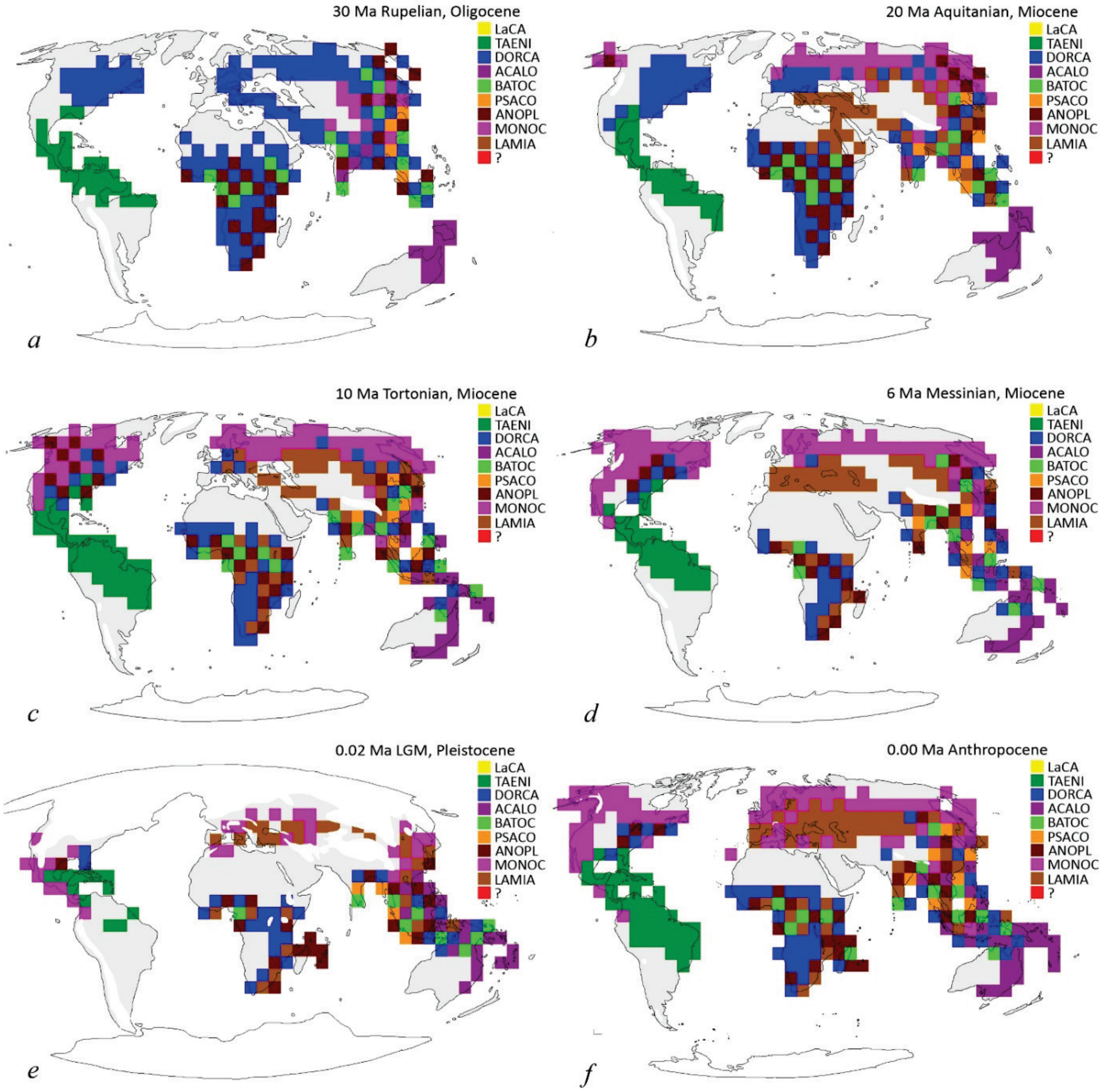

Fig. 5. Schematic representation of the late diversification and global dispersal patterns of Lamiini *s. l.* from the Oligocene to the Anthropocene (30–0 Ma)

Meanwhile, the MoHe+NeIb+Dorc subclade remained isolated in the Balkan-Anatolian region for an extended period, separated from the rest of Europe by the Paratethys and the Mediterranean Sea (Harzhauser et al., 2024a, 2024b). During the late Miocene (~5–11 Ma), increasing xerophylization and forest decline in western Asia facilitated the expansion of steppe and semi-desert ecosystems, triggering the diversification of non-forest LAMIA lineages in this region. The common ancestor of the NeIb and Dorc subclades became widespread in western Asia. Its expansion into Europe likely coincided with the Messinian Salinity Crisis (~6–5.3 Ma), a period when the desiccation of the Mediterranean Sea created a land bridge to Europe (Aufgebauer & McCann, 2011; Krijgsman et al., 2024). This ancestor likely dispersed as far as the Iberian Peninsula, moving across the exposed Mediterranean seabed (Fig. 5d), a dispersal pattern also documented in other insect groups (Kaya et al., 2012; Riccieri et al., 2018; Trájer et al., 2021). The end of the Messinian Salinity Crisis and the reflooding of the Mediterranean Sea led to the isolation of ancestral populations on the Mediterranean peninsulas of Europe. Subsequent diversification within these isolated populations resulted in the formation of distinct genera: *Neodorcadion*, *Iberodorcadion*, *Dorcadion*, and others. The exact center of origin for *Neodorcadion* remains uncertain, but the Balkan Peninsula is the most probable candidate, while Anatolia appears to have been the primary diversification center of *Dorcadion*. These two regions likely experienced multiple faunal exchanges throughout the Pliocene–Pleistocene glaciations, as fluctuations in sea levels periodically re-established land connections between the Balkans and Anatolia (Chobanov et al., 2016; Spassov, 2024; Zamoroka et al., 2024). The modern distribution of *Dorcadion* in Europe took shape during the Holocene (Fig. 5f), following the end of the last glacial period. This distribution pattern is characterized by complex biogeography and numerous instances of inter-species hybridization and reticulate evolution (Zamoroka, 2019; Dascălu et al., 2021; Caba & Dascălu, 2024).

As the LAMIA clade expanded, the MONOC clade simultaneously colonized Northern Eurasia. I propose that MONOC originated in East Asia, evolving as an adaptation to montane coniferous forests in response to global cooling during the Miocene. According to Gorring & Farrell (2023), the emergence of MONOC is estimated at ~11 Ma. However, we suggest that the clade is at least three times older, which aligns well with data from other researchers (Ashman et al., 2022; Soydabaş-Ayoub & Uçkan, 2023). MONOC achieved widespread distribution across Eurasia during the Miocene glaciations (~20 and ~14 Ma). Paleontological evidence (Vitali, 2024) indicates that by the late Pliocene (~2–4 Ma), MONOC species were as common in Europe as they are today. The expansion of MONOC into North America occurred via Beringia, likely through multiple migration events (Gorring & Farrell, 2023). However, the exact timing of these migrations remains a topic of debate. The model proposed by Gorring & Farrell (2023) estimates this event at ~5–7 Ma, which conflicts with geological and biogeographical data suggesting that Beringia-II existed during the Middle Miocene Climatic Optimum (~17.5–14.5 Ma) – a period of active biotic exchange between Eurasia and North America (Jiang et al., 2019). It is likely that MONOC species migrated to North America during this interval, and possibly around the same time, the ancestor of the modern *Plectrodera scalator* (Fabricius, 1792) from the ANOPL clade also reached the continent. Further expansion of MONOC into Mesoamerica, South America, and the Caribbean Basin most likely occurred during the Pleistocene glaciation cycles (~0.01–2 Ma, Fig. 5e), when fluctuating sea levels facilitated dispersal routes.

Conclusions

In summary, the current understanding of the tribe Lamiini *s. l.* has undergone a fundamental transformation compared to historical perspectives, primarily due to the widespread application of molecular methods. Over the past decade, the boundaries of Lamiini *s. l.* have expanded significantly, incorporating several tribes that had long been considered independent. The present study further extends these boundaries by demonstrating that Dorcaschematini **syn. nov.** represents a basal clade within Lamiini *s. l.* Additionally, I have confirmed the monophyly of the tribe, identifying TAENI, DORCA, and ACALO as its most basal and ancient clades. This allowed us to correlate their diversification with modern biogeographic patterns and propose a hypothesis for the South Gondwanan origin of the entire tribe.

However, the study also reveals that the previously recognized tribe Monochamini is non-monophyletic, consisting of at least six distinct clades. Furthermore, Dorcadionini, once considered a single tribe, has been shown to comprise at least two independent clades. I have also confirmed that the former tribe Batocerini belongs within Lamiini *s. l.*

Future phylogenetic studies should incorporate an even broader taxon sampling, particularly focusing on the highly intriguing African representatives of the former tribe Phryssomini. This will contribute to a more comprehensive and precise understanding of the evolutionary relationships within Lamiini s.l. and its affinities with other tribes.

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The author declare that the research was conducted in the absence of any commercial or other relationships that could be construed as a potential conflict of interest.

References

Acosta, R. P., Burls, N. J., Pound, M. J., Bradshaw, C. D., McCoy, J., Gibson, M., O'Keefe, J. M. K., & Feakins, S. J. (2024). Climate conundrum: A wet or dry European and Northern African climate during the Middle Miocene. Geophysical Research Letters, 51(21), e2024GL109499.

Ali, J. R., & Aitchison, J. C. (2008). Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166–35 Ma). Earth-Science Reviews, 88(3–4), 145–166.

Anisimova, M., & Gascuel, O. (2006). Approximate likelihood ratio test for branches: A fast, accurate and powerful alternative. Systematic Biology, 55(4), 539–552.

Ashman, L. G., Shin, S., Zwick, A., Ślipiński, A., & McKenna, D. D. (2021). The first phylogeny of Australasian Lamiinae longhorn beetles (Coleoptera: Cerambycidae) reveals poor tribal classification and a complex biogeographic history. Systematic Entomology, 47(1), 213–230.

Aufgebauer, A., & McCann, T. (2011). Messinian to Pliocene transition in the deep part of the Sorbas Basin, SE Spain: A new description of the depositional environment during the Messinian Salinity Crisis. Neues Jahrbuch Für Geologie Und Paläontologie – Abhandlungen, 259(2), 177–195.

Austin, A. D., Yeates, D. K., Cassis, G., Fletcher, M. J., La Salle, J., Lawrence, J. F., McQuillan, P. B., Mound, L. A., Bickel, D. J., Gullan, P. J., Hales, D. F., & Taylor, G. S. (2004). Insects 'down under' – Diversity, endemism and evolution of the Australian insect fauna: Examples from select orders. Australian Journal of Entomology, 43(3), 216–234.

Bai, Y., Ye, L., Yang, K., & Wang, H. (2022). Complete mitochondrial genome of *Pseudoechthistatus hei* (Coleoptera: Cerambycidae: Lamiinae) and its phylogenetic analysis. Mitochondrial DNA Part B, 7(11), 1997–2001.

Barbolini, N., Woutersen, A., Dupont-Nivet, G., Silvestro, D., Tardif, D., Coster, P. M. C., Meijer, N., Chang, C., Zhang, H.-X., Licht, A., Rydin, C., Koutsodendris, A., Han, F., Rohrmann, A., Liu, X.-J., Zhang, Y., Donnadieu, Y., Fluteau, F., Ladant, J.-B., … Hoorn, C. (2020). Cenozoic evolution of the steppe-desert biome in Central Asia. Science Advances, 6, eabb8227.

Bi, W.-X., & Lin, M.-Y. (2016). A revision of the genus *Pseudoechthistatus* Pic (Coleoptera, Cerambycidae, Lamiinae, Lamiini). ZooKeys, 604, 49–85.

Bourguignon, T., Tang, Q., Ho, S. Y. W., Juna, F., Wang, Z., Arab, D. A., Cameron, S. L., Walker, J., Rentz, D., Evans, T. A., & Lo, N. (2018). Transoceanic dispersal and plate tectonics shaped global cockroach distributions: Evidence from mitochondrial phylogenomics. Molecular Biology and Evolution, 35(4), 970–983.

Braby, M. F., & Pierce, N. E. (2006). Systematics, biogeography and diversification of the Indo-Australian genus *Delia*s Hübner (Lepidoptera: Pieridae): Phylogenetic evidence supports an 'out-of-Australia' origin. Systematic Entomology, 32(1), 2–25.

Caba, F., & Dascălu, M. (2024). Dissecting natural hybridisation in longhorned beetles through an integrative approach: Further proof of reticulate evolution in Dorcadionini (Cerambycidae, Lamiinae). Zoologica Scripta, 53(5), 665–687.

Cai, C., Tihelka, E., Giacomelli, M., Lawrence, J. F., Ślipiński, A., Kundrata, R., Yamamoto, S., Thayer, M. K., Newton, A. F., Leschen, R. A. B., Gimmel, M. L., Lü, L., Engel, M. S., Bouchard, P., Huang, D., Pisani, D., & Donoghue, P. C. J. (2022). Integrated phylogenomics and fossil data illuminate the evolution of beetles. Royal Society Open Science, 9(3), 211771.

Callegaro, S., Baker, D. R., Renne, P. R., Melluso, L., Geraki, K., Whitehouse, M. J., De Min, A., & Marzoli, A. (2023). Recurring volcanic winters during the latest Cretaceous: Sulfur and fluorine budgets of Deccan Traps lavas. Science Advances, 9(40), 8284.

Chatterjee, S., & Scotese, C. (2010). The wandering Indian plate and its changing biogeography during the Late Cretaceous–Early Tertiary period. In: Bandyopahyay, S. (Ed.). New aspects of Mesozoic biodiversity. Springer-Verlag. Pp. 105–126.

Chobanov, D. P., Kaya, S., Grzywacz, B., Warchałowska-Śliwa, E., & Çıplak, B. (2016). The Anatolio-Balkan phylogeographic fault: A snap shot from the genus *Isophya* (Orthoptera, Tettigoniidae). Zoologica Scripta, 46(2), 165–179.

Dascălu, M.-M., Caba, F.-G., & Fusu, L. (2021). DNA barcoding in Dorcadionini (Coleoptera, Cerambycidae) uncovers mitochondrial-morphological discordance and the hybridogenic origin of several subspecies. Organisms Diversity and Evolution, 22(1), 205–229.

Davies, H. L. (2012). The geology of New Guinea – the cordilleran margin of the Australian continent. Episodes, 35(1), 87–102.

Doláková, N., Kováčová, M., & Utescher, T. (2020). Vegetation and climate changes during the Miocene climatic optimum and Miocene climatic transition in the northwestern part of Central Paratethys. Geological Journal, 56(2), 729–743.

Eagles, G. (2016). Tectonic reconstructions of the southernmost Andes and the Scotia Sea during the opening of the Drake Passage. In: Ghiglione, M. C. (Ed.). Geodynamic evolution of the southernmost Andes. Springer. Pp. 75–108.

Filippelli, G. M. (2005). From greenhouse to icehouse: The marine Eocene-Oligocene transition. Palaios, 20(1), 93–96.

Gascuel, O. (1997). BIONJ: An improved version of the NJ algorithm based on a simple model of sequence data. Molecular Biology and Evolution, 14(7), 685–695.

Gorring, P. S. (2019). Gene to genus: Systematics and population dynamics in Lamiini beetles (Coleoptera: Cerambycidae) with focus on *Monochamus* Dejean. Harvard University, Cambridge.

Gorring, P. S., & Farrell, B. D. (2023). Evaluating species boundaries using coalescent delimitation in pine-killing *Monochamus* (Coleoptera: Cerambycidae) sawyer beetles. Molecular Phylogenetics and Evolution, 184, 107777.

Gouy, M., Tannier, E., Comte, N., & Parsons, D. P. (2021). Seaview Version 5: A multiplatform software for multiple sequence alignment, molecular phylogenetic analyses, and tree reconciliation. Methods in Molecular Biology, 2231, 241–260.

Guindon, S., Dufayard, J. F., Lefort, V., Anisimova, M., Hordijk, W., & Gascuel, O. (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Systematic Biology, 59(3), 307–321.

Handschin, E. (1944). Insekten aus den Phosphoriten des Quercy [Insects from the Quercy phosphorites]. Schweizerische Paläontologische Abhandlungen, 64(4), 1–23 (in German).

Harzhauser, M., Landau, B., Mandic, O., & Neubauer, T. A. (2024a). The Central Paratethys Sea – rise and demise of a Miocene European marine biodiversity hotspot. Scientific Reports, 14(1), 16288.

Harzhauser, M., Landau, B., Mandic, O., & Neubauer, T. A. (2024b). The Central Paratethys Sea – Part of the tropical Eastern Atlantic rather than gate into the Indian Ocean. Global and Planetary Change, 243, 104595.

Heer, O. (1879). Die Urwelt der Schweiz [The primeval world of Switzerland]. 2nd ed. F. Schulthess, Zürich (in German).

Herold, N., Huber, M., & Müller, R. D. (2011). Modelling the Miocene climatic optimum, Part 1: Land and atmosphere. Journal of Climate, 24(24), 6353–6372.

Heyden, C. von (1862). Gliederthiere aus der Braunkohle des Niederrheins, der Wetterau und der Röhn [Arthropods from the lignite of the Lower Rhine, the Wetterau and the Rhön]. Palaeontographica, 10, 62–82 (in German).

Heyden, C. von, & Heyden, L. von (1866). Käfer und Polypen aus der Braunkohle des Siebengebirges [Beetles and polyps from the lignite of the Siebengebirge]. Palaeontographica, 15, 131–156 (in German).

Jia, D.-R., & Bartish, I. V. (2018). Climatic changes and orogeneses in the Late Miocene of Eurasia: The main triggers of an expansion at a continental scale? Frontiers in Plant Science, 9, 1400.

Jiang, D., Klaus, S., Zhang, Y.-P., Hillis, D. M., & Li, J.-T. (2019). Asymmetric biotic interchange across the Bering land bridge between Eurasia and North America. National Science Review, 6(4), 739–745.

Jin, M., Shin, S., Ashman, L. G., Leschen, R. A. B., Zwick, A., de Keyzer, R., McKenna, D. D., & Ślipiński, A. (2022). Phylogenomics resolves timing and patterns in the evolution of Australasian Cerambycinae (Coleoptera: Cerambycidae), and reveals new insights into the subfamily-level classification and historical biogeography of longhorn beetles. Molecular Phylogenetics and Evolution, 172, 107486.

Jolivet, P., & Verma, K. K. (2009). Biogeography and biology of the New Caledonian Chrysomelidae (Coleoptera). In: Jolivet, P., Santiago-Blay, J., & Schmitt, M. (Eds.). Research on Chrysomelidae. Brill. Vol. 1. Pp. 211–224.

Karpiński, L., Gorring, P., & Cognato, A. I. (2023). DNA vs. morphology in delineating species boundaries of endemic Mongolian Eodorcadion taxa (Coleoptera: Cerambycidae). Diversity, 15(5), 662.

Kawahara, A. Y., Storer, C., Carvalho, A. P. S., et al. (2023). A global phylogeny of butterflies reveals their evolutionary history, ancestral hosts and biogeographic origins. Nature Ecology and Evolution, 7, 903–913.

Kaya, S., Boztepe, Z., & Çiplak, B. (2012). Phylogeography of *Troglophilus* (Orthoptera: Troglophilinae) based on Anatolian members of the genus: Radiation of an old lineage following the Messinian. Biological Journal of the Linnean Society, 108(2), 335–348.

Kim, S. I., & Farrell, B. D. (2015). Phylogeny of world stag beetles (Coleoptera: Lucanidae) reveals a Gondwanan origin of Darwin's stag beetle. Molecular Phylogenetics and Evolution, 86, 35–48.

Krijgsman, W., Rohling, E. J., Palcu, D. V., Raad, F., Amarathunga, U., Flecker, R., Florindo, F., Roberts, A. P., Sierro, F. J., & Aloisi, G. (2024). Causes and consequences of the Messinian salinity crisis. Nature Reviews Earth and Environment, 5(5), 335–350.

Labandeira, C. C., Rodríguez-Tovar, F. J., & Uchman, A. (2016). The end-Cretaceous extinction and ecosystem change. In: Mángano, M. G., & Buatois, L. A. (Eds.). The trace-fossil record of major evolutionary events. Springer, Dordrecht. Pp. 265–300.

Latreille, P. A. (1825). Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres. J. B. Baillière etc.

Letsch, H., Balke, M., Kusy, D., McKenna, D. D., Pramesa Narakusumo, R., Sagata, K., Toussaint, E. F. A., White, L. T., & Riedel, A. (2023). Beetle evolution illuminates the geological history of the world's most diverse tropical archipelago. Ecography, 2023(12), e06898.

Li, K., Yu, S.-W., Hu, H., Feng, Y.-F., Storey, K. B., Ma, Y., Zhang, J.-Y., & Yu, D.-N. (2023). The phylogenetic relationship of Lamiinae (Coleoptera: Cerambycidae) using mitochondrial genomes. Genes, 15(1), 13.

Li, X., Marvaldi, A. E., Oberprieler, R. G., Clarke, D., Farrell, B. D., Sequeira, A., Ferrer, M. S., O'Brien, C., Salzman, S., Shin, S., Tang, W., & McKenna, D. D. (2024). The evolutionary history of the ancient weevil family Belidae (Coleoptera: Curculionoidea) reveals the marks of Gondwana breakup and major floristic turnovers, including the rise of angiosperms. ELife, 13, RP97552.

Liebherr, J. K., Roig-Juñent, S., & Will, K. W. (2024). Phylogenetic analysis of the circum-Antarctic subfamily Migadopinae (Coleoptera, Carabidae) and assessment of the trans-Tasman *Amarotypus* clade. Deutsche Entomologische Zeitschrift, 71(2), 319–338.

McCulloch, G. A., Wallis, G. P., & Waters, J. M. (2016). A time-calibrated phylogeny of southern hemisphere stoneflies: Testing for Gondwanan origins. Molecular Phylogenetics and Evolution, 96, 150–160.

Medeiros, M. J., & Gillespie, R. G. (2010). Biogeography and the evolution of flightlessness in a radiation of Hawaiian moths (Xyloryctidae: Thyrocopa). Journal of Biogeography, 38(1), 101–111.

Meng, J., Gilder, S. A., Tan, X., Li, X., Li, Y., Luo, H., Suzuki, N., Wang, Z., Chi, Y., Zhang, C., & Wang, C. (2023). Strengthening the argument for a large Greater India. Proceedings of the National Academy of Sciences, 120(33), e2305928120.

Metcalfe, I. (2021). Multiple Tethyan ocean basins and orogenic belts in Asia. Gondwana Research, 100, 87–130.

Methner, K., Campani, M., Fiebig, J., Löffler, N., Kempf, O., & Mulch, A. (2020). Middle Miocene long-term continental temperature change in and out of pace with marine climate records. Scientific Reports, 10(1), 7989.

Morley, C. K., Chantraprasert, S., Kongchum, J., & Chenoll, K. (2021). The West Burma Terrane, a review of recent paleo-latitude data, its geological implications and constraints. Earth-Science Reviews, 220, 103722.

Morley, R. J. (2003). Interplate dispersal paths for megathermal angiosperms. Perspectives in Plant Ecology, Evolution and Systematics, 6(1–2), 5–20.

Mulsant, M. É. (1839). Histoire naturelle des coléoptères de France. Vol. 1. Maison.

Nel, A., Kirejtshuk, A., & Garrouste, R. (2024). A 'giant' Paleocene cerambycid (Coleoptera) from Menat Konservat-Lagerstätte, France. European Journal of Taxonomy, 921, 136–157.

Nie, R., Vogler, A. P., Yang, X., & Lin, M. (2020). Higher-level phylogeny of longhorn beetles (Coleoptera: Chrysomeloidea) inferred from mitochondrial genomes. Systematic Entomology, 46(1), 56–70.

Pandey, O. P., & Agrawal, P. K. (2000). Thermal regime, hydrocarbon maturation and geodynamic events along the western margin of India since late Cretaceous. Journal of Geodynamics, 30(4), 439–459.

Parmar, V., & Prasad, G. V. R. (2020). Vertebrate evolution on the Indian raft – Biogeographic conundrums. Episodes, 43(1), 461–475.

Pickersgill, A. E., Mark, D. F., Lee, M. R., Kelley, S. P., & Jolley, D. W. (2021). The Boltysh impact structure: An early Danian impact event during recovery from the K-Pg mass extinction. Science Advances, 7(25), eabe6530.

Piton, L. (1940). Paléontologie du gisement éocène de Menat (Puy-de-Dôme) (Flore et faune) [Paleontology of the Eocene deposit of Menat (Puy-de-Dôme) (Flora and fauna)]. Imprimeries P. Vallier, Clermont-Ferrand (in French).

Piton, L., & Théobald, N. (1937). Les lignites et schistes bitumineux de Menat (Puy-de-Dôme). II: Les insectes fossiles de Menat [Lignites and oil shales of Menat (Puy-de-Dôme). II: Fossil insects of Menat]. Revue des Sciences Naturelles d'Auvergne, 3(2), 76–88 (in French).

Pu, D.-Q., Liu, H.-L., Wu, X.-L., & Chen, Z.-T. (2022). Complete mitochondrial genomes and phylogenetic positions of two longicorn beetles, *Anoplophora glabripennis* and *Demonax pseudonotabilis* (Coleoptera: Cerambycidae). Genes, 13(10), 1881.

Range, M. M., Arbic, B. K., Johnson, B. C., Moore, T. C., Titov, V., Adcroft, A. J., Ansong, J. K., Hollis, C. J., Ritsema, J., Scotese, C. R., & Wang, H. (2022). The Chicxulub impact produced a powerful global tsunami. AGU Advances, 3(5), e2021AV000627.

Ren, Y., Lu, H., Chen, L., Sabatelli, S., Wang, C., Xie, G., Wang, P., Liu, M., Wang, W., & Audisio, P. (2021). Comparative mitogenomic analysis of two longhorn beetles (Coleoptera: Cerambycidae: Lamiinae) with preliminary investigation into phylogenetic relationships of tribes of Lamiinae. Insects, 12(9), 820.

Riccieri, A., Maura, M., Salvi, D., Bologna, M. A., & Mancini, E. (2017). Messinian salinity crisis and Quaternary glacial events shaped genetic diversification in Siculo-Maghrebian blister beetles (Coleoptera: Meloidae). Biological Journal of the Linnean Society, 122(2), 455–468.

Rodríguez, D., Lanzone, C., Chillo, V., Cuello, P. A., Albanese, S., Ojeda, A. A., & Ojeda, R. A. (2015). Evolution of the Austral-Antarctic flora during the Cretaceous: New insights from a paleobiogeographic perspective. Revista Geológica de Chile, 42(2), 223–248.

Schmidt, G. (1967). Die Bockkäfer (Cerambycidae) von Willershausen [The longhorn beetles (Cerambycidae) of Willershausen]. Bericht der Naturhistorischen Gesellschaft zu Hannover, 111, 113–120 (in German).

Scudder, S. H. (1878). An account of some insects of unusual interest from the Tertiary rocks of Colorado and Wyoming. Bulletin of the United States Geological and Geographical Survey of the Territories, 4(2), 519–543.

Senel, C. B., Kaskes, P., Temel, O., Vellekoop, J., Goderis, S., DePalma, R., Prins, M. A., Claeys, P., & Karatekin, Ö. (2023). Chicxulub impact winter sustained by fine silicate dust. Nature Geoscience, 16(11), 1033–1040.

Sota, T., Takami, Y., Ikeda, H., Liang, H., Karagyan, G., Scholtz, C., & Hori, M. (2022). Global dispersal and diversification in ground beetles of the subfamily Carabinae. Molecular Phylogenetics and Evolution, 167, 107355.

Souza, D. de S., Marinoni, L., Monné, M. L., & Gómez-Zurita, J. (2020). Molecular phylogenetic assessment of the tribal classification of Lamiinae (Coleoptera: Cerambycidae). Molecular Phylogenetics and Evolution, 145, 106736.

Soydabaş-Ayoub, H. K., & Uçkan, F. (2023). Time-scaled phylogenetic analysis of some extant Lamiinae (Coleoptera, Cerambycidae) species of East of Marmara Basin, Türkiye. Biologia, 79(2), 545–555.

Spassov, N. (2024). The final Pliocene and early Pleistocene faunal dispersals from East to Europe and correlation of the Villafranchian biochronology between Eastern and Western Europe. Quaternary, 7(4), 43.

Starkie, M. L., Cameron, S. L., Krosch, M. N., Sweet, A. D., & Clarke, A. R. (2023). Biogeographic influences on the evolution and historical dispersal of the Australo-Pacific Dacini fruit flies (Tephritidae: Dacinae). Zoologica Scripta, 53(1), 87–97.

Steinthorsdottir, M., Coxall, H. K., de Boer, A. M., Huber, M., Barbolini, N., Bradshaw, C. D., Burls, N. J., Feakins, S. J., Gasson, E., Henderiks, J., Holbourn, A. E., Kiel, S., Kohn, M. J., Knorr, G., Kürschner, W. M., Lear, C. H., Liebrand, D., Lunt, D. J., Mörs, T., … Strömberg, C. A. E. (2021). The Miocene: The future of the past. Paleoceanography and Paleoclimatology, 36(4), e2020PA004037.

Toussaint, E. F. A., Hall, R., Monaghan, M. T., Sagata, K., Ibalim, S., Shaverdo, H. V., Vogler, A. P., Pons, J., & Balke, M. (2014). The towering orogeny of New Guinea as a trigger for arthropod megadiversity. Nature Communications, 5(1), 4001.

Trájer, A. J., Sebestyén, V., & Padisák, J. (2021). The impacts of the Messinian Salinity Crisis on the biogeography of three Mediterranean sandfly (Diptera: Psychodidae) species. Geobios, 65, 51–66.

Tripati, A., & Darby, D. (2018). Evidence for ephemeral middle Eocene to early Oligocene Greenland glacial ice and pan-Arctic sea ice. Nature Communications, 9(1), 1038.

Utescher, T., Erdei, B., François, L., & Mosbrugger, V. (2007). Tree diversity in the Miocene forests of Western Eurasia. Palaeogeography, Palaeoclimatology, Palaeoecology, 253(1–2), 226–250.

Venn, S. (2016). To fly or not to fly: Factors influencing the flight capacity of carabid beetles (Coleoptera: Carabidae). European Journal of Entomology, 113, 587–600.

Vérard, C., Stampfli, G., Borel, G., & Hochard, C. (2017). The Indian Promontory: A bridge between plate tectonics and life evolution models. Universal Journal of Geoscience, 5(2), 25–32.

Viñola-López, L. W., Cerda, I. A., Correa-Narvaez, J., Codorniú, L., Borges-Sellén, C. R., Arano-Ruiz, A. F., & Ceballos-Izquierdo, Y. (2022). New fossils shed light on the Late Cretaceous terrestrial community in the Caribbean and the first American Biotic Interchange. Cretaceous Research, 130, 105067.

Vitali, F. (2009). The cerambycids included in Baltic amber: Current knowledge status with the description of new taxa (Coleoptera, Cerambycidae). Denisia, 26(86), 231–242.

Vitali, F. (2024). The fossil Lamiini (Coleoptera: Cerambycidae) from the Pliocene Lake deposits of Willershausen, Germany. Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen. 313(2), 145–151.

Wen, Y., Zhang, L., Holbourn, A. E., Zhu, C., Huntington, K. W., Jin, T., Li, Y., & Wang, C. (2023). CO_2-forced Late Miocene cooling and ecosystem reorganizations in East Asia. Proceedings of the National Academy of Sciences, 120(5), e2214655120.

Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G., Swe, H. H., Thi, M. K., & Aung, D. W. (2019). Burma Terrane part of the Trans-Tethyan Arc during collision with India according to palaeomagnetic data. Nature Geoscience, 12(10), 863–868.

Ye, Z., Damgaard, J., Burckhardt, D., Gibbs, G., Yuan, J., Yang, H., & Bu, W. (2018). Phylogeny and historical biogeography of Gondwanan moss-bugs (Insecta: Hemiptera: Coleorrhyncha: Peloridiidae). Cladistics, 35(2), 135–149.

Yuan, Z.-Y., Zhang, B.-L., Raxworthy, C. J., Weisrock, D. W., Hime, P. M., Jin, J.-Q., Lemmon, E. M., Lemmon, A. R., Holland, S. D., Kortyna, M. L., Zhou, W.-W., Peng, M.-S., Che, J., & Prendini, E. (2018). Natatanuran frogs used the Indian Plate to step-stone disperse and radiate across the Indian Ocean. National Science Review, 6(1), 10–14.

Zamoroka, A. M. (2019). A new subspecies of *Dorcadion fulvum* (Scopoli, 1763) (Coleoptera: Cerambycidae) from Western Ukraine. Polish Journal of Entomology, 88(4), 363–378.

Zamoroka, A. M. (2022). Molecular revision of Rhagiini sensu lato (Coleoptera, Cerambycidae): Paraphyly, intricate evolution and novel taxonomy. Biosystem Diversity, 30(3), 295–309.

Zamoroka, A. M., Ruicănescu, A., & Manci, C.-O. (2024). East and west of the Carpathian Arc: Evidence of postglacial ecological and morphological divergence of *Phytoecia tigrina* metapopulations (Coleoptera, Cerambycidae). Biosystems Diversity, 32(1), 12–29.

Zamoroka, A. M., Trócoli, S., Shparyk, V. Y., & Semaniuk, D. V. (2022). Polyphyly of the genus *Stenurella* (Coleoptera, Cerambycidae): Consensus of morphological and molecular data. Biosystem Diversity, 30(2), 119–136.

Zang, R. (1905). Coleoptera Longicornia aus der Berentschen Bernsteinsammlung [Coleoptera Longicornia from the Berent Amber Collection]. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1905, 232–245 (in German).

Zhang, Z., Ramstein, G., Schuster, M., Li, C., Contoux, C., & Yan, Q. (2014). Aridification of the Sahara Desert caused by Tethys Sea shrinkage during the Late Miocene. Nature, 513(7518), 401–404.

Zhang, Z.-Y., Guan, J.-Y., Cao, Y.-R., Dai, X.-Y., Storey, K. B., Yu, D.-N., & Zhang, J.-Y. (2021). Mitogenome analysis of four Lamiinae species (Coleoptera: Cerambycidae) and gene expression responses by *Monochamus alternatus* when infected with the parasitic nematode, *Bursaphelenchus mucronatus*. Insects, 12(5), 453.