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Evolution, systematics and historical biogeography of Palparini and Palparidiini antlions (Neuroptera: Myrmeleontidae): Old origin and in situ diversification in Southern Africa

Noémie M.-C. Hévin[1,2] | Gael. J. Kergoat[1] | Anne-Laure Clamens[1] | Bruno Le Ru[3,4] | Mervyn W. Mansell[5] | Bruno Michel[6]

[1]CBGP, INRAE, IRD, CIRAD, Institut Agro, Université de Montpellier, Montpellier, France

[2]Université de Poitiers, Poitiers, France

[3]IRD, CNRS, UMR Évolution, Génomes, Comportement et Écologie, Université Paris-Saclay, Gif-sur-Yvette, France

[4]Unité de Recherche UMR 247, African Insect Science for Food and Health (icipe), Nairobi, Kenya

[5]Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

[6]CBGP, CIRAD, Institut Agro, INRAE, IRD, Montpellier University, Montpellier, France

Correspondence
Noémie M.-C. Hévin, CBGP, INRAE, IRD, CIRAD, Institut Agro, Université de Montpellier, Montpellier, France.
Email: noemiehevin33@gmail.com

Bruno Michel, CBGP, CIRAD, Institut Agro, INRAE, IRD, Montpellier University, Montpellier, France.
Email: bruno.michel@cirad.fr

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Abstract

Palparine and palparidiine antlions constitute an emblematic clade of large and occasionally colourful insects that are only distributed in the western portion of the Eastern hemisphere, with about half of the known species diversity occurring exclusively in Southern Africa. Little is known about their evolutionary history, and the boundaries and relationships of most genera are still unresolved. In this study, we analyse a molecular dataset consisting of seven loci (five mitochondrial and two nuclear genes) for 144 antlion species and provide the first phylogenetic hypothesis for a representative sampling of Palparini and Palparidiini (62 Palparini species, representing 15 of the 17 known genera, and all three known Palparidiini species). In addition, we reconstruct their timing of diversification and historical biogeography. The resulting tree indicates that several extant palparine genera are polyphyletic or paraphyletic and provides interesting leads that ought to be helpful for future taxonomic revisions; it also enables us to re-evaluate the taxonomic utility and relevancy of a number of morphological characters that were previously used to define some genera. Molecular dating analyses indicate that the most recent common ancestor of both groups originated about 92 million years ago (Ma) in the Late Cretaceous. Finally, the results of historical biogeography analyses provide strong support for an origin in Southern Africa, which further acted as both a cradle of diversification and a springboard for successive waves of northern dispersals.

KEYWORDS
Afrotropics, antlions, historical biogeography, out of Africa, paleoendemism, Southern Africa, systematics

INTRODUCTION

Antlions (Neuroptera: Myrmeleontidae) are an iconic group currently consisting of *ca*. 1700 species (Engel, Winterton, & Breitkreuz, 2018), primarily found in arid or semi-arid environments worldwide (Mansell, 1996; Stange, 2004). They are members of the once more diverse superfamily Myrmeleontoidea (Badano, Engel, Basso, Wang, & Cerretti, 2018), which nowadays consists—in its traditional sense—of antlions, owlflies (Ascalaphidae), split-footed lacewings (Nymphidae) and spoonwings (Nemopteridae) (Engel et al., 2018). Antlions are morphologically quite homogeneous and several cladistic studies based on

Noémie M.-C. Hévin and Gael J. Kergoat contributed equally to this work.

Mervyn W. Mansell and Bruno Michel jointly supervised this work.

morphological characters support their monophyly (e.g., see Badano, Aspöck, Aspöck, & Cerretti, 2017; Badano et al., 2018 for larval characters). Recent molecular studies either support the hypothesis that the family is monophyletic (e.g., Michel, Clamens, Bethoux, Kergoat, & Condamine, 2017; Vasilikopoulos et al., 2020) or recover its paraphyly due to the placement of owlfly lineages (e.g., Jones, 2019; Machado et al., 2019; Wang et al., 2017; Winterton et al., 2018). Under the traditional classification system of Stange (2004), antlions are divided into three subfamilies (Myrmeleontinae, Palparinae and Stilbopteryginae) and 15 tribes. This classification was recently questioned, leading to the introduction of several alternative classification systems, such as the novel classification of Machado et al. (2019) where owlflies are incorporated into an expanded concept of Myrmeleontidae. Another new classification system is the one proposed by Jones (2019), where two antlion subfamilies are elevated to familial rank. The last one is the classification system proposed by Badano, Aspöck, Aspöck, and Haring (2017), where Stilbopteryginae are incorporated under Palparinae. These three new classification systems are contradictory and involve numerous changes at the family, subfamily and tribal levels. In this context, the status of the Palparinae subfamily, which includes (sensu Stange, 2004) the Dimarini, Palparidiini, Palparini and Pseudimarini tribes, is of particular interest. Noticeably, in the revised classification system of Machado et al. (2019), Palparinae are being relegated to tribal status (Palparini), within the subfamily Ascalaphinae. However, Dimarini remain a tribe (also within Ascalaphinae), and Palparidiini are merged under Palparini (along with Maulini sensu Stange, 2004). This merging is supported by the fact that Palparidiini and Palparini are recovered as sister groups in all molecular and morphological investigations where they have been sampled (Badano et al., 2018; Badano, Aspöck, Aspöck, & Haring, 2017; Machado et al., 2019). By contrast, Jones (2019) elevated the subfamily Palparinae to full family status. However, this decision was not substantiated, with only the family name Palparidae being mentioned in isolation. In Badano, Aspöck, Aspöck and Haring (2017), a new classification system is proposed for Palparinae, with two tribes (Palparini and Stilbopterygini) consisting of four (Dimarina, Echthromyrmecina, Palparidiina and Palparina) and two subtribes (Pseudimarina and Stilbopterygina), respectively; the corresponding changes are based on the analysis of a 29 species morphological dataset (with 51 characters) and the analysis of a 10 species molecular dataset (with three markers). All this taxonomic instability is further exacerbated by the fact that the recent phylogenomic studies using anchored hybrid enrichment data (Machado et al., 2019; Winterton et al., 2018) or transcriptomes (Vasilikopoulos et al., 2020) have yielded conflicting results regarding the monophyly of Myrmeleontidae, both with maximum statistical support. The latter is not unexpected given that phylogenomic analyses are sensitive to sampling and not impervious to systematic errors (see the review of Young & Gillung, 2020); the inference of conflicting topologies with an equally high support is also not unusual in phylogenomics analyses, where support for incorrect relationships is sometimes inflated by the sheer amount of data analysed (Brown & Thomson, 2017; Jeffroy, Brinkmann, Delsuc, & Philippe, 2006). Finally, it is worth underlining that the recent study of Badano et al. (2021), in which a part of the genomic dataset of Winterton et al. (2018) was combined with a morphological dataset, recovered the monophyly of Myrmeleontidae. Therefore, and until a firmer consensus based on additional investigations is available, we decided to exercise caution and adhere to the traditional classification system of Stange (2004).

Palparini antlions include some of the largest and most spectacular species in the order Neuroptera, and indeed, of all insects. They are characterized by their unusually large size and striking wings (wingspans ranging from 45 to 170 mm), and occasionally conspicuous colouration, which render them unmistakable (Figure 1). Palparini consists of 136 species assembled in 17 genera (Table S1) that are mostly distributed throughout the Afrotropical region and extending across the southern Palearctic to the Oriental region, but are absent from the Australasian region and the Western hemisphere (Mansell, 1990; Stange, 2004). Of the 98 species exclusively found in the Afrotropics, 44 are found in 11 genera occurring in Southern Africa (Botswana, Namibia, South Africa, southern Mozambique and Zimbabwe), with 35 species being endemic to the sub-region. Most of the endemicity, 28 species in nine genera, is centred in the Western and Northern Cape Provinces of South Africa and Namibia. Palparini are mostly found in dry or wet savannas, but few species can also be found in semi-arid deserts or woodlands (Mansell & Erasmus, 2002; Michel, 1999; Prost, 1995). Adults generally fly erratically and over short distances.

Palparini are generally nocturnal predators that are attracted by lights; however, this is not always the case and some species are diurnal, such as those in the genera *Pamares* Mansell and *Pamexis* Hagen (Mansell, 1990, 1992b). During daytime, they generally rest with their wings folded; their intricately patterned wings serve as an effective camouflage (e.g., see some of the pictures in Figure 1), usually matching the predominant vegetation of the environment in which they live (Mansell, 1999). The Palparini also have the distinction of having only two species of antlions that mimic lichens (Mansell & Ball, 2016; see the picture of *Pamexis namaqua* in Figure 1). Palparini larvae (Figure 2) are psammophilous and the protection afforded by their deep sand habitats is a key factor that potentially accounts for their large size, with the larvae of some species reaching a length of 35 mm (Mansell, 1999). Because of their size, Palparini larvae are able to subdue a large range of prey (including grasshoppers) and are an important component of the predator guild in the areas they inhabit (Mansell, 1999). Most live in deep sand and migrate to the surface in the late afternoon and evening when sand temperatures cool. All larvae whose ecology is known do not construct pitfall traps and just lay below the surface with their head and spread jaws exposed, waiting to be alerted by vibrations from approaching prey. The six eye facets set on a prominent tubercle play a role in directing the jaw strike towards their prey. Once secured by the tips and intermeshing teeth on the sickle-shaped mandibles, the larva moves backwards to subdue the prey and protect itself from retaliatory injury. Historically, most species of Palparini have been described in the genus *Palpares* Rambur, the type genus of the subfamily Palparinae and tribe Palparini. It has long been postulated that this genus is polyphyletic and several attempts have been made to clarify its taxonomy. Noticeably, Mansell (1992a) arranged this genus (and other palparine genera) into four divisions and a number of species groups, based on morphology.

FIGURE 1 Pictures of Palparini and Palparidiini antlions: (a) *Palparellus spectrum* (Rambur) (picture by Bruno Michel), (b) *Palparidius fascipennis* (Banks) (picture by Hennie de Klerk), (c) *Golafrus oneili* (Péringuey) (picture by Hennie de Klerk), (d) *Palpares normalis* Navás (picture by Stefan Akame), (e) *Palpares libelluloides* (L.) (picture by Bruno Michel), (f) *Pamexis hamtam* Mansell (picture by Mervyn Mansell), (g) *Tomatares citrinus* (Hagen) (picture by Hanna Roland), (h) *Palparellus voeltzkowi* (Kolbe) (picture by Thierry Cardenos).

Following this, the status of several *Palpares* species was also revised through their transfer to other palparine genera (see Mansell, 1996, 2004, 2018; Prost, 2018, 2019). However, as highlighted by the results of Michel et al. (2017), it is our understanding that the genus *Palpares* still requires further taxonomic and phylogenetic studies to accommodate and clarify the status of the disparate lineages that compose it. This is also likely the case for several other palparine genera, which occasionally have been defined based on the examination

FIGURE 2 Pictures of Palparini larvae: (a) *Palpares immensus* McLachlan (picture by Duncan Robertson), (b) *Crambomorphus kalaharicus* Mansell (picture by Rolf G. Oberprieler), (c) *Palpares libelluloides* (L.) (picture by Gernot Kunz), (d) *Golafrus oneili* (Péringuey) (picture by A.T. Schoeman).

of a small number of species (e.g., Insom & Carfì, 1989) and sometimes lack obvious apomorphic features (such as in the genus *Palparellus* Navás; Mansell, 1996).

Palparidiini consist of only three species belonging to the genus *Palparidius* Péringuey (Table S1). Adults are quite large in size (wingspans up to 90 mm); morphologically they share several characters with Dimarini and Palparini (Mansell, 1999; Stange, 2004) but differ by their highly modified male ectoproct. The larvae of two species (*Palparidius capicola* Péringuey and *Palparidius concinnus* Péringuey) are known (Stange, 2004; Tippett, 2022), and present characters that are similar to both Dimarini and Palparini (Stange, 2004). That said, the hypothesis that Palparidiini are more closely related to Palparini is clearly supported by the phylogenomic study of Machado et al. (2019) and by the cladistic study on larval characters of Badano et al. (2018). Extant members of the tribe Palparidiini are endemic to arid and semi-arid environments of Southern Africa. *Palparidius* larvae are psammophilous predators (Mansell, 1999) that likely live in deep sand; although little is known about their ecology, it can be postulated that both adults and larvae behave similarly to Palparini.

At the moment, no molecular studies have investigated in detail the evolutionary history of Palparini and Palparidiini at the generic and species levels. For instance, the phylogenetic study with the highest number of Palparini species to date (Michel et al., 2017) only encompasses 15 palparine species representing six genera. The current study is consequently a contribution to provide more data for molecular analyses investigating the evolutionary history of the clade consisting of Palparini and Palparidiini, for which a wide coverage of genera and species, especially from southern and western Africa and other disparate geographical regions, is now available. This opportunity arises from the extensive coverage of the group as a result of collections over many years in widely disparate areas, particularly in the Afrotropics. In addition, reconstructing the evolutionary history of this group offers the opportunity of exploring its biogeographic history, which presents a particular interest given the paucity of research focusing on the origin and diversification of Afrotropical insect groups. Indeed, despite the fact that insects are by far the most diverse group in the Afrotropics (more than 150,000 described Afrotropical species are known; Miller & Rogo, 2001), only a few studies have tackled the diversification dynamics and biogeographic history of Afrotropical insect lineages (e.g., Aduse-Poku et al., 2021; Haran, Beaudoin-Ollivier, Benoit, & Kergoat, 2021; Hévin et al., 2022; Kergoat et al., 2018; Price, Marshall, Barker, Simon, & Villet, 2019; Rossini et al., 2022). A large fraction of the Palparini diversity (and all three species of Palparidiini) is found in Southern Africa where many species have restricted distribution ranges. A highly diverse insect fauna is known to be endemic or to have radiated in this region (Hernández-Vera, Caldara, Toševski, & Emerson, 2013; Hévin et al., 2022; Kergoat et al., 2015; Matenaar, Fingerle, Heym, Wirtz, & Hochkirch, 2018; Meregalli et al., 2021; Price et al., 2019; Sole, Scholtz, Ball, & Mansell, 2013; Talavera, Kaliszewska, Heath, & Pierce, 2020). It has been proposed that the extraordinary diversity found in Southern Africa is the result of both old and more recent radiations (Linder, 2005; Linder, 2008; Schnitzler et al., 2011; Verboom et al., 2009). Persistence of old paleo-endemic taxa ('museum of diversity' model) may have been facilitated by a relative climatic stability throughout the Cenozoic (Cowling, Procheş, & Partridge, 2009), even though a cooling event leading to a more arid climate occurred in the Miocene (Goldblatt & Manning, 2002). Major mountain ranges such as the Great Escarpment also potentially acted as buffers or refugia, limiting risks of extinctions (Cowling & Lombard, 2002; Schnitzler et al., 2011). Conversely, high levels of environmental heterogeneity, whether climatic, edaphic, topographic or biome-related, probably played a major role in recent radiations of neo-endemic taxa ('cradle of diversity' model) by providing divergent selection pressures (Cowling et al., 2009; Cowling

& Lombard, 2002; Schnitzler et al., 2011). Such patterns have been well-studied in other Afrotropical subregions, where it was found that reliefs acted both as cradles and museums of diversity (Dagallier et al., 2020).

Here, we provide the first comprehensive phylogenetic framework for Palparidiini and Palparini antlions. We further conduct molecular dating and historical biogeography analyses to deepen our understanding of the evolutionary history of the two clades, especially in relation to the diversification of Afrotropical lineages, by looking at their age, origin and colonization dynamic.

MATERIALS AND METHODS

Taxon sampling, DNA extraction and sequencing

For this study, 121 specimens representing 55 Palparini species (with representatives of 14 of the 17 known genera) and all three Palparidiini species were sampled and sequenced successively, except two specimens (see Table S2). The material generally corresponds to specimens collected by the two senior authors, with most specimens collected between 1980 and 2000 (some specimens were also collected more recently in South Africa by M. Mansell and in Botswana and Kenya by B. Le Ru). All specimens were identified by M. Mansell and B. Michel, who are both experts in Palparini taxonomy and systematics (Akoudjin & Michel, 2011; Mansell, 1990, 1992a, 1992b, 1996, 2004; Mansell, 2018; Mansell & Ball, 2016). For each specimen, DNA was extracted from one hind leg using BioBasic EZ-10 96 Well Plate Genomic DNA Miniprep kits (BioBasic Inc., Ontario, Canada). Following Michel et al. (2017), the following gene fragments were prioritized: (i) mitochondrial cytochrome *b* (*cob*), cytochrome oxidase *c* subunit 1 (*cox1*), large ribosomal RNA (*rrnL*), small ribosomal RNA (*rrnS*), and (ii) nuclear 28S ribosomal RNA (*28S*) (primers listed in Table S3). Initially, we used Sanger sequencing (see Michel et al., 2017 for details), but because DNA was often degraded, the majority of PCR failed (especially when targeting the *28S* gene). Therefore, we relied on high-throughput sequencing (amplicon sequencing) to amplify gene fragments for the *cox1*, *rrnL* and *rrnS* genes. Amplicon libraries were constructed for these three genes following Galan et al. (2017); for the *cox1*, two overlapping fragments were also targeted following Shokralla et al. (2015). Compared with the settings of Galan et al. (2017), we made the following changes to lower the proportion of chimeric fragments: for the first PCR step, we changed the number of cycles to 40 and the extension period for the second PCR step, the extension duration was set to 120 s. The final library was paired-end sequenced on an Illumina MiSeq flowcell using a MiSeq Reagent Kit v2 (500 cycles) at the AGAP laboratory (Montpellier, France). Illumina reads were processed using the FROGS pipeline (http://frogs.toulouse.inra.fr/; Escudié et al., 2018) on the Genotoul Galaxy server using demultiplexing, pre-processing, clustering and chimera removal tools. The remaining contaminants were further detected using the BLAST tool (available at: https://blast.ncbi.nlm.nih.gov/Blast.cgi) and removed manually. The two overlapping fragments of *cox1* were merged using Mesquite v3.70 (Maddison & Maddison, 2021). All mitochondrial and nuclear sequences were aligned using MAFFT v7 (Katoh & Standley, 2013) with default option settings and a gap opening penalty of 5.0, and further manually corrected using Mesquite. For all protein-coding genes (*cob* and *cox1*), coding frames and stop codons were also checked with Mesquite to detect potential pseudogenes.

Molecular datasets

Newly generated sequences were combined with extant data available on GenBank, including data (for 50 species) generated by our research group in the study of Michel et al. (2017). A total of seven gene fragments were concatenated in Mesquite: a 706 bp fragment of *cob*, a 639 bp of *cox1*, a 462 bp fragment of cytochrome oxidase *c* subunit 3 (*cox3*), a 555 bp fragment (when aligned) of *rrnL*, a 409 bp fragment (when aligned) of *rrnS*, a 362 bp fragment (when aligned) of nuclear 18S ribosomal RNA (*18S*) and a 707 bp fragment (when aligned) of *28S*. First, a specimen-level dataset was generated, in which multiple specimens of Palparini and Palparidiini were included (118 specimens representing 62 Palparini species and 10 specimens representing three Palparidiini species). Second, we selected for each Palparini or Palparidiini species the specimen with the largest gene coverage and assembled a species-level dataset that includes a comprehensive set of outgroups (79 other species of Myrmeleontidae, five Ascalaphidae, three Nemopteridae and one Psychopsidae; see Table S2).

Phylogenetic analyses

Phylogenetic studies were conducted under maximum likelihood (ML) using IQ-TREE v2.1.3 (Minh et al., 2020). In a preliminary analysis, the specimen-level dataset was used to evaluate potential species paraphyly. We further analysed the species-level dataset, to generate a phylogenetic tree to be used as a reference tree for the dating and historical biogeography analyses. For both datasets, the same phylogenetic procedures were carried out. The concatenated dataset was partitioned into 13 partitions, with one partition established for each non-coding gene fragment (*rrnL*, *rrnS*, *18S* and *28S*) and three partitions (one for each codon position) defined for each coding gene fragment (*cob*, *cox1* and *cox3*). The Bayesian information criterion (BIC) implemented in IQ-TREE was used to choose the best-fit substitution models and partition schemes (Table S4). Best-scoring trees were obtained using heuristic searches implementing 500 random-addition replicates, with the following settings: random-starting tree, thorough hill-climbing nearest neighbour interchange (NNI) search (*−allnni* option), a perturbation strength set to 0.2 (*−pers 0.2* option), partition-resampling strategy (*−−sampling GENE* option) and best partition scheme allowing the merging of partitions (*−m MFP + MERGE* option). Clade support was estimated using 1000 replicates for both SH-like approximate likelihood ratio tests (SH-aLRT; Guindon et al., 2010) and ultrafast bootstraps (uBV; Minh, Nguyen, & von Haeseler, 2013); in

addition, Transfer Bootstrap Expectation (TBE) branch support metrics were calculated with BOOSTER (Lemoine et al., 2018), using 100 bootstrap trees generated with IQ-TREE as input. Nodes supported by SH-aLRT values ≥80%, uBV ≥95% and TBE ≥70% were considered strongly supported (see Guindon et al., 2010, Minh et al., 2013 and Lemoine et al., 2018, respectively). Finally, supplementary analyses were performed to test the impact of missing data in the dataset (see Appendix S1 for details).

Dating analyses

Divergence times were estimated using Bayesian relaxed clocks as implemented in BEAST v1.10.4 (Suchard et al., 2018). Dating analyses relied on three vetted fossil constraints allowing to specify minimum age constraints (see Appendix S2 for additional details). A conservative maximum age of 201.3 Ma (corresponding to the Jurassic/Triassic boundary) was chosen for these three constraints since it is significantly older than the appearance of any myrmeleontoid in the fossil record (Engel et al., 2018; Michel et al., 2017). These three constraints were enforced using uniform distributions; two distinct uncorrelated lognormal clocks were used for the mitochondrial and the nuclear genes, and the tree model was set to a birth-death speciation process (Gernhard, 2008). A fixed topology corresponding to the best-scoring tree from the ML analyses of the species-level dataset was used to limit the risk of over-parameterization. Dating analyses consisted of 50 million generations of Markov chain Monte Carlo (MCMC) with parameters and trees sampled every 5000 generations. A 25% burn-in was further applied, and the maximum credibility tree, median ages and their 95% HPD were produced using TreeAnnotator v1.10.4, which is part of the BEAST software package. Convergence of runs was evaluated graphically and by looking at the effective sample size (ESS) of relevant parameters under Tracer v1.7.2 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018), using the recommended threshold of 200.

Historical Biogeography analyses

Historical biogeography analyses were carried out using parametric methods (Ree & Sanmartín, 2009) with RASP v4.2 (Yu, Blair, & He, 2020). We used the BioGeoBears (Matzke, 2014) implementation, which can run and compare both dispersal-vicariance analysis (DIVA; Ronquist, 1997), Dispersal–Extinction–Cladogenesis (DEC; Ree & Smith, 2008) and Bayesian inference of historical biogeography for discrete area (BayArea; Landis, Matzke, Moore, & Huelsenbeck, 2013) models.

Seven areas were defined, of which five mirror bioregions defined by Linder et al. (2012) for sub-Saharan Africa: [A] India and Pakistan, [B] western Palearctic (Arabian plate, Mediterranean basin and Saharan bioregion), [C] Sudanian–Ethiopian bioregion, [D] Congolian bioregion, [E] Somalian–Zambezian bioregion, [F] Southern African bioregion and [G] Madagascar. To better reflect extant distribution patterns, a maximum number of two areas was allowed (disjunct areas were also excluded). A time-stratified model was then defined ('reference model'), implementing a matrix of scaling factors for dispersal rates (DR) between areas (from 0 to 1) to account for the respective positions of the geographic areas through time while also accounting for potential geographical barriers to antlion dispersal (e.g., deserts, forests, high reliefs). A DR of 1.0 was set in the absence of barriers between two adjacent areas; a DR of 0.7 was set in the presence of a small or temporary barrier between two adjacent areas (e.g., cycles of fragmentations/reconnections of rainforests, high reliefs); a DR of 0.5 was set in the presence of a large barrier between two adjacent areas (e.g., deep sea, desert, rainforest); a DR of 0.3 was set to account for potential dispersal between two non-adjacent areas separated by one area; a DR of 0.1 was specified for long-distance dispersals, when two areas are separated by more than one area. Dispersal between Madagascar and other areas other than Eastern Africa was also considered as long-distance dispersal.

To better take into account changes through time three time slices were used. The first time slice ('TSI') runs from 120 to 56 Ma. At that time India was initially connected to Madagascar (until 90 Ma) and progressively drifted towards Eurasia (Blakey, 2008); to account for that, a DR of 0.5 was specified between areas A and G, and between areas A and B. Several barriers between West and East Africa have been hypothesized to have existed during the Late Cretaceous and the Paleocene, first in the form of a large intercontinental desert during the Late Cretaceous (Carvalho, de Gasparini, Salgado, de Vasconcellos, & da Silva Marinho, 2010; DeConto, Hay, Thompson, & Bergengren, 1999), followed by the rise of a large pan-African rainforest during the Paleocene (Morley, 2000, 2007). To account for these, a DR of 0.5 was set between areas C, D, E and F. A second time slice ('TSII') runs from 56 to 23 Ma. This timeframe corresponds to the Eocene and Oligocene. At that time India was still connected to Madagascar via a chain of islands and was no longer separated from Eurasia by an ocean, colliding with it ca. 45 Ma (Blakey, 2008); thus, a DR of 0.5 was set between areas A and G, and a DR of 0.7 was set between A and B. This period is also marked by the Eocene–Oligocene transition (EOT, 33 Ma; Zachos, Pagani, Sloan, Thomas, & Billups, 2001; Zachos, Dickens, & Zeebe, 2008) characterized by a global cooling leading to the first fragmentation of the pan-African rainforest (Couvreur et al., 2021; Morley, 2000). Therefore, a DR of 0.7 was set between areas C, D, E and F. This period is also marked by intense volcanic activity in Ethiopia during the Oligocene (Coulié et al., 2003; Couvreur et al., 2021), which likely acted as a barrier to dispersal; thus a DR of 0.7 was set between areas B and E. A third time slice ('TSIII') runs from 23 Ma to the present. At that time India was no longer connected to Madagascar, and to account for this, the DR between A and G was set to 0.1. Until the beginning of the Miocene ca. 23 Ma, cycles of rainforest fragmentation and reconnection brought on by changes from humid and hot environments to dry and cold conditions occurred (Couvreur et al., 2021; Morley, 2000). Also, this time slice corresponds to a period of major uplifts in the Afrotropics, and particularly in Eastern Africa (Guillocheau et al., 2018; Sepulchre et al., 2006). To take that into account, the DR between areas C, D, E and F was set to 0.5. The apparition of three deserts also probably acted as barriers: Namib

desert 16 Ma (DR of 0.5 between areas D and F), Saharan desert 7 Ma and Arabian deserts 3.5 Ma (DR of 0.7 between areas B and C, and DR of 0.5 between B and E). Finally, for comparison purposes, we also defined a model without any constraints (DR of 1.0 between all areas) nor time slices ('null model').

Analyses were carried out for each of these models both with and without the founder-event speciation parameter (+j) sensu Matzke (2014). Models were selected based on the Akaike information criterion corrected for sample size (AICc_wt), following Yu et al. (2020). As a guide tree, we used the dated phylogeny estimated with BEAST; this tree was modified in Mesquite ('*prune clade*' tool) by removing all species not belonging to the Palparini and Palparidiini tribes.

RESULTS

Phylogenetic analyses

The results of the ML analysis of the specimen-level dataset are presented in Figure S1. In the corresponding tree (likelihood score of −38310.305), all species for which multiple specimens were included are recovered monophyletic. Overall, the inferred relationships for Palparini and Palparidiini are similar to those inferred through the analysis of the species-level dataset (see below). The analyses carried out to test the impact of missing data yield branch support values that are generally lower and also result in the misplacement of several lineages (see Appendix S1 for details).

The best-scoring tree from ML analysis of the species-level dataset has a likelihood score of −67640.115 (see Figure 3 and Figure S2 for detailed SH-aLRT, TBE and uBV values). The Myrmeleontidae are recovered monophyletic with a moderate to high support (SH-aLRT of 97.4%, TBE of 50.2% and uBV of 73%). Palparinae are recovered paraphyletic due to the placement of the sole representative of Pseudimarini (*Pseudimares aphrodite* Aspöck & Aspöck), sister to *Stilbopteryx costalis* Newman (Stilbopteryginae) with moderate support (SH-aLRT values ≥80% and uBV ≥95%, but TBE of 62%). Myrmeleontinae are also recovered paraphyletic due to the placement of Acanthaclisini, which are found sister to (Stilbopteryginae + Palparinae). Within the subfamily Myrmeleontinae, when considering the tribes for which we have more than one species, all are recovered monophyletic with at least one high support among the three support estimates (SH-aLRT values ≥80%, TBE values >70% and/or uBV ≥95%), except for Myrmecaelurini that consists of two distinct clades. Within the subfamily Palparinae, the tribes Palparini and Palparidiini are recovered monophyletic with high support (SH-aLRT values ≥80%, TBE values >70% and uBV ≥95%). Within the tribe Palparini, seven genera are recovered monophyletic (*Annulares* Mansell, *Crambomorphus* McLachlan, *Lachlathetes* Navás, *Pamares*, *Pamexis*, *Parapalpares* Insom & Carfi and *Tomatares* Hagen) with high support (SH-aLRT values ≥80%, TBE values >70% and uBV ≥ 95%, except for *Parapalpares* and *Tomatares* that have TBE <70% and uBV <95%, respectively). For the remaining genera, two are recovered polyphyletic (*Palparellus* and *Palpares*), two are monotypic (*Indopalpares* Insom & Carfi and *Pseudopalpares* Insom & Carfi) and the last four (*Golafrus* Navás, *Goniocerus* Insom & Carfi, *Nosa* Navás and *Stenares* Hagen) are only represented by one species, so it is not possible to assess whether they are monophyletic or not. In the case of the polyphyletic genus *Palpares*, 12 distinct lineages are recovered.

Dating analyses

The post-burn-in parameters of the BEAST analyses show ESS ≥ 200 for all relevant parameters. Myrmeleontidae are estimated to have originated ca. 108.88 Ma (95% HPD: 152.66–86.1 Ma). The median age of the most recent common ancestor (MRCA) of Palparinae and Stilbopteryginae is estimated at ca. 98.52 Ma (95% HPD: 138.33–76.44 Ma). The MRCA of the Palparini and Palparidiini tribes is estimated to have originated during the Late Cretaceous ca. 92.26 Ma (95% HPD: 130.57–71.63 Ma) (see Figure 4 and Figure S3). Palparini originated ca. 84.4 Ma (95% HPD: 119.15–65.24 Ma) whereas the Palparidiini tribe (based on the MRCA of the three extant species) originated ca. 39.12 Ma (95% HPD: 60.54–24.66 Ma).

Historical Biogeography analyses

Likelihood ratio tests indicate that +j models provide the best fit across all analyses. The reference model fitted the data better than the null model (lnL = −116.7 vs lnL = −122; Table S5). According to the AICc_w model selection, the DEC+j and DIVALIKE+j models are the best-fit models for both the reference (AICw = 0.58 and AICw = 0.39, respectively; see Figures S4.1 and S4.2 and Table S5) and the null (AICw = 0.56 and AICw = 0.43, respectively; see Figures S4.3 and S4.4 and Table S5) models. The results of the DEC+j and DIVALIKE+j analyses are highly congruent for both models (only two most likely states differ for the reference model, and three for the null model). When examining the results of the reference model (see Figure 4 and Figure S4.1 for DEC+j and Figure S4.2 for DIVALIKE+j), an origin in Southern Africa (F) is inferred for the MRCA of Palparini and Palparidiini (relative probability of 57% recovered with DEC+j, and of 92% with DIVALIKE+j). Overall, the inferred biogeographical pattern is quite dynamic, with 41 dispersal, 34 vicariance and one extinction events reconstructed with DEC+j, and 42 dispersal, 35 vicariance and no extinction reconstructed with DIVALIKE +j. Until 75 Ma (first part of the TSI), all ancestral areas are exclusively found in Southern Africa. Later on, several dispersal events occurred between Southern Africa and the Somalian–Zambezian, Sudanian–Ethiopian and Madagascar bioregions. The TSII is characterized by a high number of dispersal events (27 recovered with DEC+j and 28 with DIVALIKE+j), which resulted in the colonization of all of the Afrotropics as well as numerous non-Afrotropical regions. The colonization of India could be accounted for by two distinct dispersal routes, either from the western Palearctic (B) or Madagascar (G). Since 23 Ma (TSIII), only a few dispersal events are inferred (four recovered with either DEC+j or DIVALIKE+j), whereas several in situ speciation

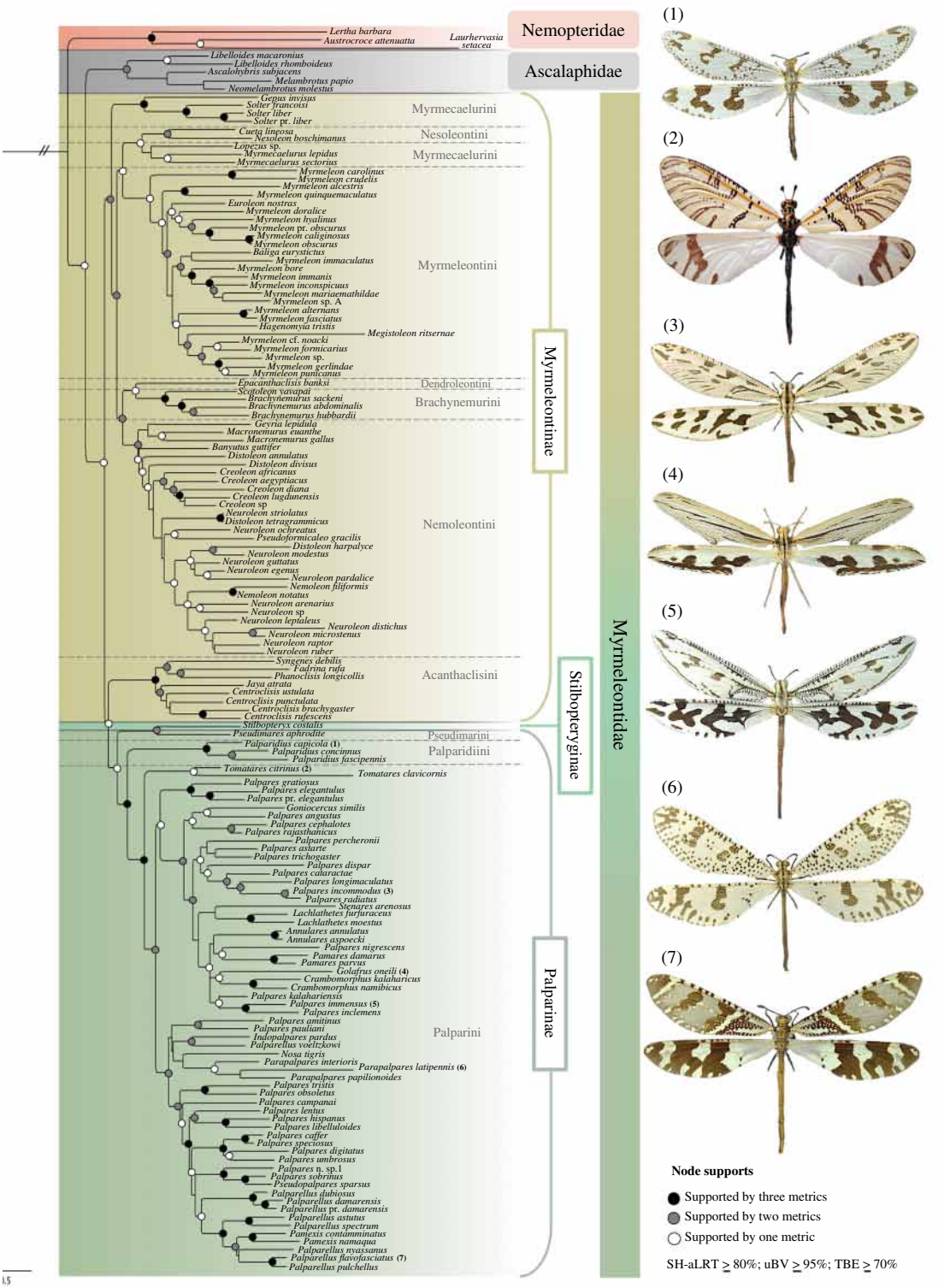

FIGURE 3 Maximum Likelihood tree resulting from the analysis of the species-level dataset. Node support values are indicated using black circles when supported by three metrics (SH-aLRT ≥80%, uBV ≥95% and TBE ≥70%), by grey circles when supported by two metrics, by white circles when supported by one metric; the absence of a circle indicates that the node is not statistically well-supported (see Figure S2 for exact support values). Information on taxonomic ranks sensu Stange (2004) is provided and highlighted using specific colour schemes. On the right, adult representatives of several Palparinae species are illustrated: (1) *Palparidius capicola* Péringuey, (2) *Tomatares citrinus* (Hagen), (3) *Palpares incommodus* (Walker), (4) *Golafrus oneili* (Péringuey), (5) *Palpares immensus* McLachlan, (6) *Parapalpares latipennis* (Rambur), (7) *Palparellus flavofasciatus* (McLachlan) (all pictures by Bruno Michel).

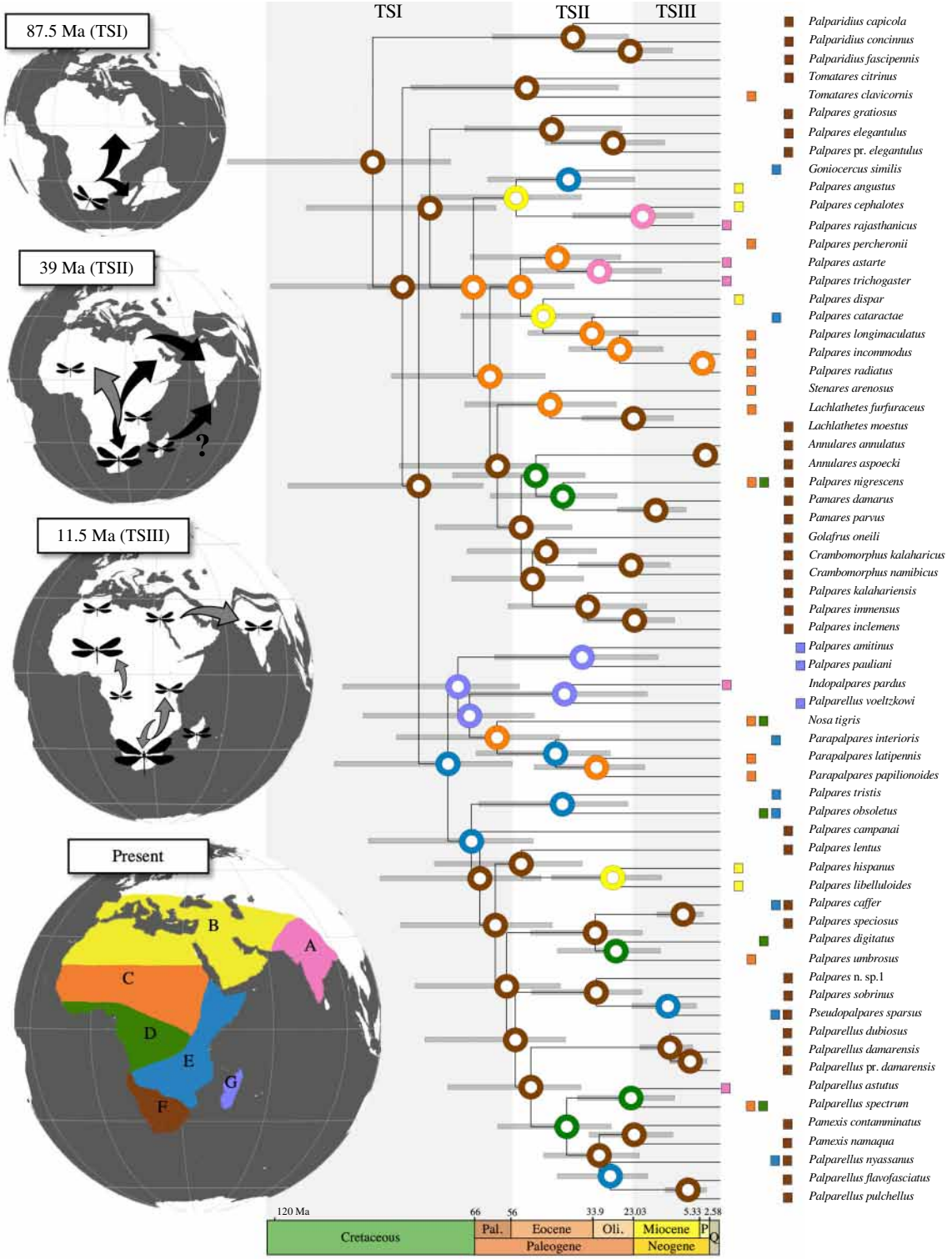

FIGURE 4 Dated phylogeny and historical biogeography of Palparidiini and Palparini antlions. Horizontal bars on nodes represent 95% HPD of age estimates. Ancestral area reconstructions correspond to the result of a RASP analysis with the best-fit model (DEC+j model); coloured circles are used to highlight the most likely states using the coding of areas presented at the bottom of the picture. The main dispersal events are shown on the paleomaps on the left, with black arrows when the time-slice hosts the first dispersal to a bioregion and grey arrows when dispersal to the bioregion has already taken place in a previous time-slice. The size of the antlions on the maps approximately reflects the number of species in the bioregion. The paleogeographic reconstructions are made using the open source software GPlate 2.3.0 (https://www.gplates.org/) with open source data from the EarthByte Alternative Plate Reconstructions made by Merdith et al. (2021).

events are found within almost all considered areas. Southern Africa was where the majority of the Palparini and Palparidiini diversification took place (24 speciation events within this area are inferred with the DEC+j, 23 with the DIVALIKE+j). The biogeographic analyses also never inferred reverse colonization events from India, and just two from the western Palearctic to sub-Saharan Africa.

DISCUSSION

Phylogenetic relationships and systematics

First, we want to stress that this study was not designed to investigate the relative placements of owlfly and antlion lineages, hence the fact that we recovered a monophyletic antlion family does not constitute a finding of particular interest; it was also anticipated given that our sampling outside of the Palparini and Palparidiini is largely based on the sampling of Michel et al. (2017). The supplementary analyses carried out to test for the impact of missing data indicate that removing gene fragments to lower the amount of missing data is detrimental to phylogenetic accuracy and robustness (see Appendix S1). The latter confirms the value of including specimens with a low gene coverage, as this is generally beneficial in terms of support and phylogenetic accuracy (Crête-Lafrenière, Weir, & Bernatchez, 2012; Wiens, 2005; Wiens & Tiu, 2012).

Within Myrmeleontidae, for which we have a substantial sampling (144 species representing 11 of the 15 known tribes sensu Stange, 2004), several results are worth discussing. For instance, it is interesting to address the respective placement of Pseudimarini (represented by *Pseudimares aphrodite*) and Stilbopteryginae (represented by *Stilbopteryx costalis*). Similar to the findings of the study of Badano, Aspöck, Aspöck, and Haring (2017), these lineages form a generally well-supported clade (SH-aLRT of 80%, TBE of 62% and uBV of 99%), sister to a clade grouping Palparini and Palparidiini. This close relationship of Stilbopteryginae with Palparinae was not evidenced in the study of Michel et al. (2017), where *Stilbopteryx costalis* was found sister to all remaining antlions (only with moderate support; uBV of 85%). Like Badano, Aspöck, Aspöck and Haring (2017), we can hypothesize that their limited sampling for Palparinae (which included just 15 Palparini and no representatives of other palparine tribes) led to an artefactual placement of *Stilbopteryx costalis*. Interestingly, the phylogenomic study of Vasilikopoulos et al. (2020) also revealed a close relationship between *Pseudimares aphrodite* and another Palparinae (*Palpares libelluloides* (L.)). By contrast, the phylogenomic studies of Winterton et al. (2018) and Machado et al. (2019) did not find a close relationship between Palparinae and Stilbopteryginae, and instead retrieved Stilbopteryginae sister to a clade of owlflies. Morphology-wise, the cladistic analysis of Badano, Aspöck, Aspöck, and Haring (2017) produced results that are similar to ours, with *Pseudimares aphrodite* and *Stilbopteryx costalis* sister to other Palparinae lineages; their grouping of Stilbopteryginae with *Pseudimares* is based on two homoplasious characters, namely large globose eyes (also present in Ascalaphidae) and a long forewing vein (cubitus posterior) running independently from vein 1A (also present in Palparini) (see Badano, Aspöck, Aspöck, & Haring, 2017). It seems challenging to draw conclusions about the positions of Pseudimarini and Stilbopteryginae based on all of these results. In any case, our results are in line with those of Badano, Aspöck, Aspöck, and Haring (2017). To answer this question definitively, a phylogenomic investigation based on a large sample of Palparinae and members of several Ascalaphidae and Myrmeleontidae lineages will likely be required. The paraphyly of Myrmeleontinae sensu Stange (2004) is due to the placement of members of the tribe Acanthaclisini. This result supports the views of Oswald and Penny (1991) and New (1985, 2003), who do not recognize the acanthaclisines as a myrmeleontine tribe, and instead consider them as a subfamily of their own. Furthermore, this lineage is well-defined by the morphological characters of the larvae and adults and clearly constitutes a homogeneous clade (Hölzel, 1972; Insom & Carfì, 1992; Markl, 1954; Stange & Miller, 1985, 1990). Although it is tempting to propose a formal recognition of acanthaclisines as a subfamily, it is important to underline that the study of Machado et al. (2019) does not support this assumption. Instead, they retrieved acanthaclisines sister to (Myrmecaelurini + Nesoleontini), which is also consistent with the conclusion of Stange (1994) on the basis of morphology. Regarding the paraphyly of Myrmecaelurini, our results are not novel and mirror those of Michel et al. (2017) and support the hypothesis of a distinct tribe Gepini, which was proposed by Markl (1954) for the genera *Gepus* Navás, *Furgella* Markl and *Solter* Navás to which Hölzel (1969) added the genus *Gepella* Hölzel. At this stage, it seems difficult to improve this issue, especially since recent phylogenomic studies are of no use here, as they either have very limited sampling (two species in Machado et al., 2019 and one species in Vasilikopoulos et al., 2020) or no samples at all for the Myrmecaelurini.

With regard to our two focal groups, the Palparini and Palparidiini, their sister relationship is firmly established by the results of our analyses (SH-aLRT values of 83.4%, TBE of 91.8% and uBV of 98%). The latter confirms both morphological evidence (e.g., see Badano, Aspöck, Aspöck, & Haring, 2017) and the findings of Machado et al. (2019), who sampled one species of Palparidiini and 10 species (from four distinct genera) of Palparini for their phylogenomic analyses; it is worth noting that the species/genera included in both studies have essentially the same placement. Within Palparini, our results are only partially in agreement with the four divisions proposed by Mansell (1992a) on the basis of morphological similarity. For instance, the grouping of the *speciosus* group and *Nosa* (division B) is not supported by our results. Similarly, both division C (*Crambomorphus*, *elegantulus* group, *immensus* group, *inclemens* group) and division D (*libelluloides* group [*pro parte*] and *Stenares*) are not retrieved in our phylogenetic analyses. Our findings, however, support Mansell's (1992a) hypothesis regarding the polyphyly of the division A, which consists of the following unrelated lineages: *annulatus* group (now *Annulares*), *Golafrus*, *Lachlathetes*, *nyassanus* group (now *Palparellus*), *Pamares*, *Pamexis*, *sparsus* group (which now includes the monotypic genus *Pseudopalpares*), *Tomatares* and *tristis* group.

The high level of polyphyly evidenced for the species-rich genus *Palpares* (69 valid species; see Table S1) is not unexpected, as it

reflects the complex nomenclatural history of Palparinae (e.g., see Mansell, 1990), where the majority of species were first described in *Palpares* or assigned to this genus after having been initially described in *Myrmeleon* (Mansell, 1990; Stange, 2004; see also Table S1). As a result of the definition of new genera, many species of *Palpares* were also secondarily transferred. However, since several of these new genera were based on the study of a limited number of species (e.g., the work of Insom & Carfì, 1989, who described five new genera while only examining 12 palparine species), this inflated the polyphyly of the genus *Palpares*, while also creating paraphyletic genera due to the non-inclusion of several species. When examining the phylogenetic relationships of the *Palpares* species sampled in our study, some of them could have been predicted based on morphological similarities; for example, a group proposed by Akoudjin and Michel (2011), composed of *P. kalahariensis* Stitz, *P. longimaculatus* Akoudjin & Michel, *P. incommodus* (Walker) and *P. radiatus* Rambur, is retrieved here except for *P. kalahariensis*. Several *Palpares* species that are morphologically closely related were also recovered sister in our analyses; it is the case for instance for *P. caffer* (Burmeister) and *P. speciosus* (L.) (see Banks, 1913; Mansell & Erasmus, 2002), or for *P. digitatus* Gerstaecker and *P. umbrosus* Kolbe (see Banks, 1913; Prost, 1995; Michel, 1999). Here, it remains to be seen whether some of the inferred *Palpares* lineages are supported by apomorphic characters (such as the shape of distal palpomere of labium) that could justify further definition of new genera.

With 12 species, *Palparellus* is the second most speciose genera of Palparini. Mansell (1996) hypothesized that "*Palparellus*, as constituted here, may be a paraphyletic assemblage, as no autapomorphy has yet been found to confirm the monophyly of the genus". Our phylogenetic analyses, which revealed four separate *Palparellus* lineages, support this hypothesis. The first one only consists of *Palparellus voeltzkowi* (Kolbe), a very distinctive and spectacular species endemic to Madagascar; it is retrieved in a clade encompassing *Indopalpares*, *Nosa* and *Parapalpares*, and two *Palpares* species from Madagascar. The remaining three lineages are rendered paraphyletic due to *Pamexis* representatives, which are embedded within them. Interestingly, the study of Machado et al. (2019)—where 10 Palparini species were sampled—retrieved a *Palparellus* sister to a *Pamexis*, hence providing some support for a close relationship between these two genera. That said, this result was not expected because *Pamexis* were originally thought to be the sister group of *Pamares*, as they are morphologically quite similar; the fact that they both have reduced eyes was considered to be a synapomorphy (Mansell, 1990), but it could also be an evolutionary convergence in relation with the diurnal activity of adults. The remaining *Palparellus* lineages can be identified based on male genitalia (shape of the gonarcal bulla) and similarity in wing patterns (see Mansell, 1996 for details) and correspond to the following groups: (i) a first clade grouping *P. damarensis* (McLachlan), *P. dubiosus* (Péringuey), *P. pulchellus* (Esben-Petersen), *P. ulrike* Mansell and a potential new species (labelled *P.* pr. *damarensis* in our study), (ii) a second clade grouping *P. astutus* (Walker), *P. rothschildi* (Van der Weele) and *P. spectrum* (Rambur) and (iii) a third clade grouping *P. festivus* (Gerstaecker), *P. flavofasciatus* (McLachlan), *P. nyassanus* (Navás) and *P. ovampoanus* (Péringuey). These three clades could potentially be assigned to specific genera; this would involve restricting the genus *Palparellus* to the clade including the type species *P. spectrum*, and defining two new genera in the future for members of the remaining two clades.

Lastly, our analyses confirm the recent transfer of *Nosa tristis* (sensu Whittington, 2002) back to the genus *Palpares* by Prost (2019) who performed a comprehensive morphological revision of the genus *Nosa*. They also support the assignation of *P. papilionoides* to the genus *Parapalpares* by Insom and Carfì (1989).

Biogeographic history

Mansell (1992a, 1996) postulated that Palparinae and Stilbopteryginae had a Gondwanan origin, based on extant patterns of distribution for representatives of Palparinae tribes (Oriental and South American distribution for Dimarini, Palearctic distribution for Pseudimarini, Southern African distribution for Palparidiini, Afrotropical, Palearctic and Oriental distribution for Palparini) and Stilbopteryginae (relict lineage endemic to Australia). This hypothesis is comforted by the results of our dating analyses, which recover an old age for the MRCA of Stilbopteryginae and Palparinae ca. 98.52 Ma (95% HPD: 138.33–76.44 Ma). Historical biogeography analyses also support the origin of the MRCA and Palparini and Palparidiini in Southern Africa during the Late Cretaceous (ca. 92 Ma), a region that was heavily impacted by the breakup of Gondwana. Although several dispersal routes are known at that time, the comprehensive review of Sanmartín and Ronquist (2004) found that vicariance events are significantly more frequent than expected by chance in insects, which is consistent with a southern Gondwana pattern. It may thus be hypothesized that Palparinae and Stilbopteryginae diverged there through vicariance events.

For Palparini and Palparidiini, the results of the historical biogeography analyses have to be interpreted with some level of caution because not all nodes are equally supported by the branch support metrics. Following the origin of the MRCA of Palparini and Palparidiini during the Late Cretaceous, speciation occurred exclusively in Southern Africa during 20 Myr and no dispersal event was inferred at that time. The latter suggests that the intercontinental desert belt above Southern Africa inferred based on paleoclimate reconstructions (DeConto et al., 1999) for the Campanian (83.6–72.1 Ma) acted as an effective barrier to dispersal (please note that the same pattern was also inferred with the 'null' model). The presence of a potential rainforest belt further north of this desert also potentially acted as an additional barrier, but it is hard to back up this claim because the African paleobiomes of the Late Cretaceous are not well documented (Jacobs, 2004). The first inferred dispersal events towards eastern and northern Africa occurred for Palparini following the beginning of the Maastrichtian, supporting the hypothesis that open habitats were present at that time in Eastern Africa. It has been hypothesized that a large pan-African rainforest was established during the Paleocene (Morley, 2000, 2007), but interestingly there is little direct fossil evidence to support the existence of a rainforest biome in East Africa

(Jacobs, 2004; Linder, 2017). It has been also suggested in the review of Couvreur et al. (2021) that the Zambezian bioregion was too far south, given that Africa was located about 10° south of its current location, to enable the growth of rainforest vegetation under local climatic conditions. Lastly, the inferred colonization of Madagascar by overseas dispersal, which occurred in the Paleocene, is also of particular interest as it echoes patterns observed for other insect groups such as in Sericini beetles (Eberle, Fabrizi, Lago, & Ahrens, 2017).

The Paleocene ended with a hyperthermal period characterized by global warming (Paleocene–Eocene Thermal Maximum, PETM; ca. 56 Ma; Turner, 2018), followed by the longest and warmest interval of the Cenozoic (Early Eocene Climatic Optimum, EECO; ca. 53–51 Ma; Zachos et al., 2008). In Africa, reconstruction of paleoclimates based on palynofloras indicates that Southern Africa was characterized by arid or temperate climates that were largely unaffected by the PETM (Korasidis, Wing, Shields, & Kiehl, 2022). At higher paleolatitudes, between the PETM and the EECO, the climate was generally warm and humid; therefore, this period was conducive to the maintenance and development of a large rainforest belt (see Jaramillo et al., 2010 for an analogy with the Neotropical region). However, multiple lines of evidence indicate that in East Africa the climate was marked by hot and arid conditions, both before and after the PETM (Carmichael et al., 2017; Handley et al., 2012; Handley, Pearson, McMillan, & Pancost, 2008; Korasidis et al., 2022). During the Middle Eocene, the plant fossil record also indicates the presence of open arid woodland formation in Eastern Africa (Jacobs & Herendeen, 2004; Linder, 2017). We can therefore assume that southern and Eastern Africa have long been suitable environments for palparine antlions. During the Eocene–Oligocene transition (EOT), a major climate shift from a greenhouse to an icehouse climate occurred (Zachos et al., 2001, 2008). These cooler temperatures were associated with more arid conditions, leading to the fragmentation of the Afrotropical rainforest and making way for more open habitats (Bouchenak-Khelladi, Muasya, & Linder, 2014; Bouchenak-Khelladi, Verboom, Savolainen, & Hodkinson, 2010; Pound & Salzmann, 2017), which potentially acted as corridors for dispersal (e.g., see Kamiński, Smith, Kanda, Iwan, & Kergoat, 2022 for a group of xerophilic beetles). All these environmental changes potentially facilitated the spread of groups adapted to open habitats such as Palparini. Indeed, during the Eocene and Oligocene, many dispersal events are reconstructed for the Palparini, with no less than 27 dispersal events inferred by the DEC+j model. This period is also marked by the first dispersals 'out of Africa' for the Palparini, which colonized part of the western Palearctic as well as India and Pakistan on this occasion. Of particular interest is the colonization of India, for which our historical biogeography analyses support the hypothesis that there could have been two distinct routes: one through Madagascar and the other through the western Palearctic. The inferred colonization route through Madagascar is not unexpected because of the well-known existence of a chain of stepping-stone islands that acted as a land bridge between Asia/India and Madagascar–Africa during the Cenozoic (Warren, Strasberg, Bruggemann, Prys-Jones, & Thébaud, 2010). Biogeographic reconstructions in many groups recover this dispersal route (Sanmartín & Ronquist, 2004), including in insects (e.g., Condamine, Sperling, & Kergoat, 2013; Toussaint, Fikáček, & Short, 2016).

During the Miocene, major environmental changes in tropical Africa likely had a significant impact on the evolutionary history of Palparini and Palparidiini. Following the Middle Miocene Climatic Optimum (MMCO; 17–15 Ma), a drop in global temperatures was associated with a decrease in atmospheric CO_2 (Zachos et al., 2001). These changes in climatic conditions favoured more arid and open habitats and led to a major biome shift, in the form of the gradual spread of C_4 grasslands (Edwards et al., 2010), which became dominant in the Late Miocene–Middle Pliocene (8–2.6 Ma; deMenocal, 2004; Bobe, 2006). Interestingly, despite the expansion of open habitats in Africa, our biogeographic reconstructions do not find many dispersal events between the areas we defined but rather supported in situ speciation. The latter suggests that barriers to dispersal have had a fairly significant effect on the biogeographic history of the group. One of these obstacles is certainly the appearance of several major deserts, since the Neogene is also marked by the apparition of the Namib (ca. 17–16 Ma; Senut, Pickford, & Ségalen, 2009), Saharan (ca. 9–7 Ma; Senut et al., 2009) and Arabian (ca. 3 Ma; Vaks et al., 2013) deserts. Although a handful of palparine species are able to live in or on the fringes of desert environments (Mansell, 1990; Prost, 1995), most cannot cope with overly arid conditions. Another potential obstacle is linked to the uplifts that took place during the Miocene, such as those of the East African Dome, Katanga Dome and Angola Dome (Guillocheau et al., 2018). Although the adults of some species are sometimes caught at high elevations (up to 2000 m), most palparine and palparidiine species only thrive at lower elevations where they can find the sandy areas that are required for the development of their larvae. Because of the latter, it is also difficult to determine whether these reliefs potentially acted as climatic refugia for Palparini during cycles of rainforest fragmentation and reconnection over the past 7 Myr, as it has been shown for different groups adapted to closed or open habitats (Bryja et al., 2017; Huntley & Voelker, 2017; Menegon et al., 2014; Mulvaney, Cherry, & Matthee, 2022; Portillo et al., 2018; Tolley et al., 2011).

Most speciation events were inferred in Southern Africa (25 with the DEC+j model and 24 with the DIVALIKE+j model), which echoes the potential role of Southern Africa as a source of diversity for old lineages ('museum of diversity' model). Palparini can therefore be considered as a paleo-endemic group that diverged long ago while being range-restricted (Dagallier et al., 2020). For this group, it may be hypothesized that the relatively stable climates experienced in Southern Africa during the Cenozoic (Cowling et al., 2009)—especially in the Cape Floristic Region (Schnitzler et al., 2011)—limited extinction risks (Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009; Harrison & Noss, 2017). Another factor accounting for the high rates of endemism in Southern Africa is the high variety of vegetation and soil types (Mansell & Erasmus, 2002). It is especially the case in the western part of the subregion where more diverse biomes are found ('Desert', 'Fynbos', 'Nama-Karoo', 'Succulent Karoo' and 'Savanna' sensu Mucina & Rutherford, 2006). Indeed, through the use of georeferenced models, Mansell and

Erasmus (2002) highlighted that most species in Southern Africa were associated with particular edaphic conditions and biomes; each palparine species distributed there typically has a closely related sister species occurring in a different biome, and they are rarely sympatric. The strong relationship between palparines and their environment is also well illustrated by the fact that species co-distributed in the same biome generally have comparable wing patterns even when belonging to distinct genera (e.g., *Pamexis karoo* Mansell, *Pamexis luteus* (Thunberg), *Palparellus pulchellus* and *Palpares speciosus* in Fynbos and Nama-Karoo biomes; Mansell & Erasmus, 2002). Outside of Southern Africa, it can be assumed that similar speciation mechanisms were at play, involving ecological specialization to specific environments. For instance, although the sister species *Palpares incommodus* and *P. radiatus* are both present in the Sudanian–Ethiopian bioregion, each of them is restricted to either a wet or a dry habitat (Prost & Popov, 2021).

CONCLUSION

The results of the phylogenetic analyses performed in this study represent a significant advance in the understanding of Palparini and Palparidiini relationships, and they can already be used to help reassess the status of several genera and species groups. However, as pointed out by Machado et al. (2019), a denser and more robust phylogenetic framework will probably be needed to revise all Palparini genera and gradually redistribute all species into genera that correspond to a set of mutually monophyletic groups. Overall, our results suggest that Southern Africa acted as both a cradle of diversification and a source of repeated episodes of northern dispersals. Although limitations of our dataset exist with regard to branch support, the biogeographic history recovered for Palparini seems credible as it matches 'out-of-Southern Africa' patterns previously documented in several insect lineages adapted to open habitats (e.g., Eberle et al., 2017; Kamiński et al., 2022). Of particular interest in the case of palparine antlions is the fact that their old age contrasts with the younger ages found for other insect groups. With the availability of a large number of environments suitable for Palparini, differing in climate, topography, soil type and vegetation, we can postulate that ecological speciation has probably been the main driver accounting for the high levels of in situ diversification inferred in Southern Africa.

AUTHOR CONTRIBUTIONS

NOÉMIE M.-C. HÉVIN: Conceptualization; methodology; validation; formal analysis; investigation; resources; writing – original draft; writing – review and editing; visualization. **GAEL. J. KERGOAT:** Conceptualization; methodology; validation; formal analysis; resources; data curation; writing – original draft; writing – review and editing; visualization; funding acquisition. **ANNE-LAURE CLAMENS:** Investigation; resources; data curation; writing – review and editing. **BRUNO LE RU:** Investigation; resources; writing – review and editing. **MERVYN W. MANSELL:** Conceptualization; investigation; resources; data curation; writing – original draft; writing – review and editing. **BRUNO MICHEL:** Conceptualization; investigation; resources; data curation; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.21904746. Newly generated sequences were deposited in GenBank, and are registered with the following accession numbers: OQ581997–OQ582070 (*cob*), OQ603605–OQ603608 (*18S*), OQ606012–OQ606168 (cox1), OQ624960–OQ625111 (*rrnL*), OQ625113–OQ625252 (*rrnS*) and OQ625254–OQ625279 (*28S*) (see Table S2 for details).

ORCID

Noémie M.-C. Hévin https://orcid.org/0000-0003-1730-0010
Gael. J. Kergoat https://orcid.org/0000-0002-8284-6215
Anne-Laure Clamens https://orcid.org/0000-0002-7226-4991
Bruno Le Ru https://orcid.org/0000-0002-4208-3727
Bruno Michel https://orcid.org/0000-0003-4085-8100

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SUPPORTING INFORMATION

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

Appendix S1. Supplementary analyses to test for the impact of missing data.

Appendix S2. Details on fossil calibrations.

Figure S1. Best-fit ML tree resulting from the analysis of the specimens-level dataset. Support values are presented on nodes as follows: SH-aLRT/uBV. Clades consistent with those retrieved by the ML analysis of the species-level dataset are represented in blue.

Figure S2. Best-fit ML tree resulting from the analysis of the species-level dataset.

Figure S3. Dated phylogeny resulting from the BEAST analyses relying on a primary calibration approach based on three fossils: (A) †*Roesleriana exotica*, (B) †*Pristinofossor rictus*, (C) †*Porrerus dominicanus*. Median ages are provided on nodes; horizontal bars represent 95% HPD of age estimates.

Figure S4. Results of RASP analyses.

Table S1. Palparidiini and Palparini species list along with additional information on taxonomy and distributional information. Distributional information for almost all species is based on the comprehensive catalogue of Stange (2004) but other studies are also listed when relevant.

Table S2. Taxon sampling, including the species for which we relied on GenBank data. GenBank accession numbers for seven gene fragments are provided on the right (newly generated data is highlighted using bold fonts).

Table S3. List of primers.

Table S4. Best partition schemes and models for the analyses of the species-level (left) and specimen level (right) datasets.

Table S5. Model scores from all historical biogeography analyses with the best-fit models (based on AICc_wt) of each analysis highlighted with bold fonts.

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