ORIGINAL ARTICLE

Total-evidence phylogeny of the owlflies (Neuroptera, Ascalaphidae) supports a new higher-level classification

Joshua R. Jones

Department of Biology, Utah Valley University, Orem, UT, USA

Correspondence
Joshua R. Jones, Department of Biology, Utah Valley University, 800 W University Parkway, Orem, UT 84058, USA.
Email: doc.jonesresearch@gmail.com

Abstract

The first large-scale, total-evidence phylogeny of the owlflies (Neuroptera, Ascalaphidae) is presented. A combined morphological and molecular dataset was analysed under several analytical regimes for 76 exemplars of Myrmeleontiformia (Psychopsidae, Nymphidae, Nemopteridae, Myrmeleontidae, Ascalaphidae), including 57 of Ascalaphidae. At the subordinal level, the families were recovered in all analyses in the form Psychopsidae + (Nymphidae + (Nemopteridae + (Myrmeleontidae + Ascalaphidae)). In the DNA-only maximum-likelihood analysis, Ascalaphidae were recovered as paraphyletic with respect to the Myrmeleontidae and the tribe Ululodini. In both the parsimony and Bayesian total-evidence analyses, however, the latter with strong support, traditional Ascalaphidae were recovered as monophyletic, and in the latter, Stilbopteryginae were placed as the immediate sister group. The long-standing subfamilies Haplogleniinae and Ascalaphinae were not recovered as monophyletic in any analysis, nor were several of the included tribes of non-ululodine Ascalaphinae. The Ululodini were monophyletic and well supported in all analyses, as were the New World Haplogleniinae and, separately, the African/Malagasy Haplogleniinae. The remaining Ascalaphidae, collectively, were also consistently cohesive, but included a genus that until now has been placed in the Haplogleniinae, *Protidricerus*. *Protidricerus* was discovered to express a well-developed pleurostoma, a feature previously only encountered in divided-eye owlflies. The feature traditionally used to differentiate the Haplogleniinae and Ascalaphinae, the entire or divided eye, can no longer be regarded as a spot-diagnostic synapomorphy to separate these groups within the family. A new subfamilial classification based on these results is proposed and includes the following five subfamilies: Albardiinae, Ululodinae, Haplogleniinae, Melambrotinae and Ascalaphinae. In addition, the monophyletic containing group (Myrmeleontidae + (Palparidae + (Stilbopterygidae + Ascalaphidae))) is elevated to the rank of superfamily, as Myrmeleontoidea, in order to accommodate much-needed taxonomic and nomenclatural restructuring anticipated to occur within the Ascalaphidae in the future. A list of genera included in each subfamily of Ascalaphidae is provided.

KEYWORDS

morphology, Myrmeleontiformia, Myrmeleontoidea, Myrmeleontidae, subfamily, tribe

1 | INTRODUCTION

Ascalaphidae, or owlflies, are highly specialized, obligate aerial predators of flying insects. They are peculiar in both form and function, with nearly every aspect of their adult behaviour and anatomy, including their eyes, antennae, mouthparts, thoraxes, legs, wings and terminalia optimized for a completely aerial existence. Owlflies occur in temperate and tropical regions worldwide and generally resemble small-to-medium-sized dragonflies—particularly when in flight—in the shape of the body and wings and in the inclination of the thorax and legs (Figure 1a–e). Indeed, their ecology is largely convergent with that of modern Anisoptera. However, owlflies emerged onto the evolutionary stage much more recently: Odonata arose nearly 300 mya in the Permian (Rehn, 2003), whereas Ascalaphidae emerged in the Cretaceous ~130–150 mya (Michel, Clamens, Béthoux, Kergoat, & Condamine, 2017), presumably from a stilbopterygine-like ancestor (Jones, 2014, and the present paper). Adults of most owlfly species are nocturnal or crepuscular, and active for only a very brief period in each 24-hr cycle, as short as 10–15 min in some species. Their now highly successful radiation may have been spurred along its remarkable trajectory via exploitation of the narrow temporal window open between the activity intervals of diurnal dragonflies and nocturnal bats (Penny, 1982). Notably, some conspicuous, day-flying genera do occur, particularly in Eurasia (Figure 1e), and a few of the common European species have been well studied (Archaux et al., 2011; Belušič, Pirih, & Stavenga, 2013; von der Dunk, 2012; Fetz, 1999; Meglič, Škorjanc, & Zupančič, 2007; Müller, Schlegel, & Krüsi, 2012; Senčič, 2006; Weissmair, 2004). As larvae, owlflies are dorsoventrally flattened, disc-shaped, sit-and-wait predators (Figure 1f–h) that capture passing arthropods in their sharp-tipped jaws, and immobilize them with paralytic venom (Henry, 1977) before carefully sucking out their internal fluids. Immatures of most species are well camouflaged and free living in the soil/litter-open air interface, or on the surfaces of rocks, bark, and leaves, and are rarely encountered in the wild. Subimaginal instars of fewer than 20 species have been confidently allied to adults and taxonomically described, most of them European (Badano & Pantaleoni, 2014).

Owlflies are members of the order Neuroptera, or lacewings. They are usually easily distinguished from other lacewings by their chimeric assemblage of physical characteristics: large size; enormous, nearly holoptic eyes; long, butterfly-like knobbed antennae; robust thoraxes; dragonfly-like wings; and often very setose bodies. Their distinctive morphology has been recognized for some time. Fabricius (1775) was the first to unambiguously separate them from butterflies and dragonflies, placing *Myrmeleon barbarum* Linnaeus in his new Neuroptera (sensu latu) genus *Ascalaphus*, which he differentiated from *Hemerobius* Linnaeus, 1758 and *Myrmeleon* Linneaus, 1767. Prior to this paper, over 435 valid described species have been placed in approximately 100 genera, 15 tribes and three subfamilies. Their true species-level diversity is certainly much greater, however. Due to their ephemeral comportment and often cryptic patterning, owlflies are generally collected only rarely or in small numbers. This is particularly true of (a) obscurely coloured, (b) rapid, night-flying species that (c) are only weakly attracted, if at all, to ultraviolet and mercury vapour light sources, attributes that appear to apply to a considerable portion of the known species. For these reasons, as well as extensive, only partly resolved taxonomic and nomenclatural complexities, most owlflies species have but scant representation in natural history collections, and are only poorly studied and characterized. It may be deduced, therefore, that numerous species remain to be discovered and described.

The Ascalaphidae have long been inferred to belong to an assemblage of families (Psychopsidae, Nymphidae, Nemopteridae, Myrmeleontidae and Ascalaphidae) within the superorder Neuropterida sharing several apomorphies and variously called Myrmeleonoidea (e.g., Withycombe, 1925; but see Canard, Aspöck, & Mansell, 1992, where the Greek stem was shown to be incorrectly formed), Myrmeleontoidea (Henry, 1978c; Mansell, 1992; Machado et al., 2018; New 1991 [minus Psychopsidae]; Stange, 1994, 2004; Tillyard, 1926; Winterton et al., 2018) and Myrmeleontiformia (e.g., Aspöck, Plant, & Nemeschkal, 2001; Badano, Aspöck, Aspöck, & Cerretti, 2017; Badano, Aspöck, Aspöck, & Haring, 2017; Jones 2014; MacLeod, 1964; Michel et al., 2017; Song, Li, Zhai, Bozdoğan, & Yin, 2019; Winterton, Hardy, & Wiegmann, 2010). In every relational study conducted on these distinctive families, be it comparative anatomy or phylogenetic inference, Ascalaphidae have been placed together with Myrmeleontidae as a monophyletic assemblage (Aspöck et al., 2001; Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Gao, Cai, Yu, Storey, & Zhang, 2018; Henry, 1978c; Jones, 2014; Kimmins, 1940; Lan, Chen, Li, & You, 2016; Machado et al., 2018; Mansell, 1992; Michel et al., 2017; New, 1982; Riek, 1976; Song et al., 2019; Song, Lin, & Zhao, 2018; Stange, 1994; Wang et al., 2017; Winterton et al., 2010, 2018; Zhang & Yang, 2017). Thus far, estimation of their sister group relationship (referred to as the Ascalaphidae–Myrmeleontidae complex, or AMC, during analyses performed in the present study) has inconsistently been recovered as (i) a pairing of independent, parallel lineages; (ii, iii, iv) in some manner of nested arrangement; and (v) as grossly paraphyletic relative to one another (see next paragraph). Despite the lack of consensus regarding their relationships, their close affinity has been recognized for over a century based on several shared adult and larval characteristics (Henry, 1978c; New, 1982; Riek, 1976; Stange, 1994; van der Weele, 1909), and over several recent decades, it has been supported by an increasing

FIGURE 1 Representative Ascalaphidae. (a–e) Adults. (a) *Ascaloptynx appendiculata* (Fabricius), USA. (b) *Deleproctophylla australis* (Fabricius), Croatia. (c) *Ululodes* sp., Belize. *Tmesibasis lacerata* (Hagen), South Africa. (e) *Libelloides macaronius* (Scopoli), Slovenia. (f–h) Unidentified larvae. (f) Ascalaphinae, Singapore. (g) Melambrotinae, Mozambique. (h) Ascalaphinae, Singapore. Image credits: (c, f–h) Nicky Bay©2018; (d) Piotr Naskrecki©2018. All others Joshua R. Jones
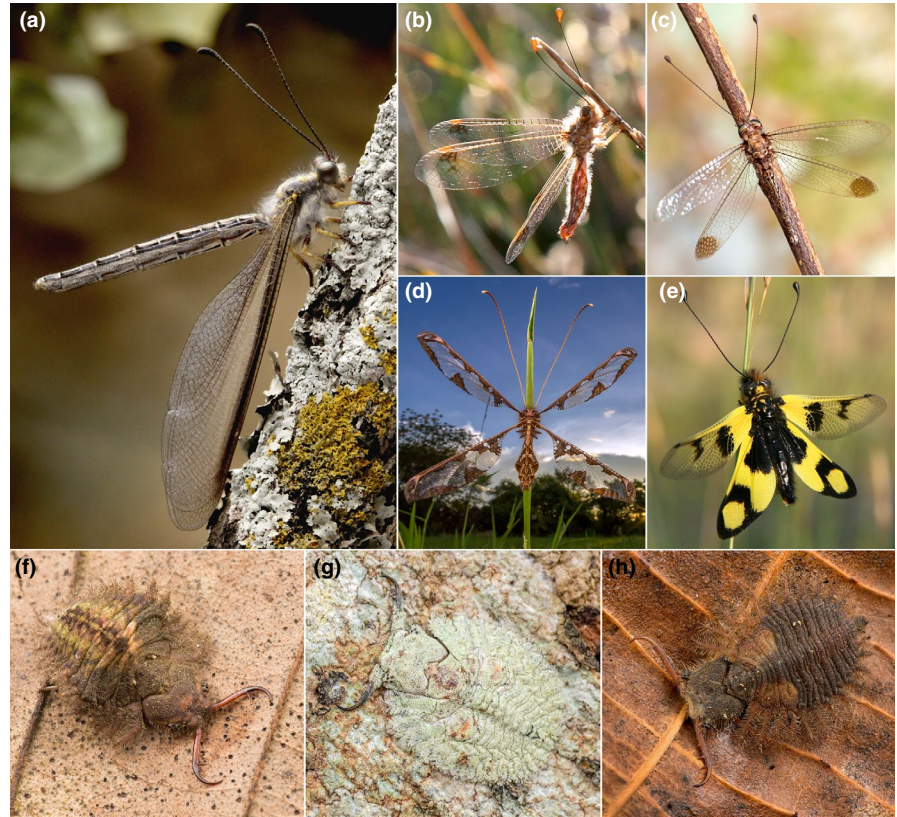
amount of phylogenetic data (Aspöck et al., 2001; Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Gao et al., 2018; Henry, 1978c; Jones, 2014; Lan et al., 2016; Machado et al., 2018; Michel et al., 2017; Riek, 1976; Song et al., 2019, 2018; Stange, 1994; Wang et al., 2017; Winterton et al., 2010, 2018; Zhang & Yang, 2017).

Until now, however, virtually no phylogenetic investigation has focused primarily on the Ascalaphidae. Some authors have recognized this and called for such a study (Engel, Winterton, & Breitkreuz, 2018; Henry, 1978a; New, 1984; Penny 1982; Riek, 1968; Tjeder, 1992). Numerous works have included owlflies in estimates of relationships among lacewing families (Figures S1–S8), but taxon sampling of ascalaphids in these studies almost universally has been limited to one or a handful of species, with recent studies on owlflies by Jones (2014—the unpublished dissertation upon which the current work is based) and antlions by Machado et al. (2018) being exceptional. In general, owlflies in these studies have been recovered as a monophyletic taxon, either (a) as sister group to the antlions (Aspöck et al., 2001; Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Henry, 1978c; Michel et al., 2017; Riek, 1976; Song et al., 2018; Stange, 1994) or (b) as nested within a paraphyletic Myrmeleontidae or Myrmeleontinae (Jones, 2014; Lan et al., 2016; Song et al., 2019; Wang et al., 2017; Zhang & Yang, 2017). Contrarily, Winterton et al. (2010) recovered a few of their many trees with (c) a paraphyletic Ascalaphidae (based on two included species) as sister to a

monophyletic *Stilbopteryx* + *Palpares*, both traditionally placed within the Myrmeleontidae. And Gao et al. (2018) placed (d) a monophyletic Myrmeleontinae (five spp.) within a paraphyletic Ascalaphidae (four spp.) in their estimate of the phylogeny of Neuroptera. Most recently, Winterton et al. (2018) and Machado et al. (2018) found evidence for (e) a paraphyletic Ascalaphidae intermingled within a paraphyletic Myrmeleontidae, and closely allied to the Stilbopteryginae and Palparinae.

These studies variously have been based on analyses of morphology (Aspöck et al., 2001; Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Henry, 1978c; Stange, 1994; Winterton et al., 2010); entire mitochondrial (mt) genomes (Gao et al., 2018; Lan et al., 2016; Song et al., 2019, 2018; Wang et al., 2017); partial nuclear (nu) genomes (Machado et al., 2018; Winterton et al., 2018); partial nuclear genome amino acid sequences (Winterton et al., 2018); mt- and nu-DNA markers (Badano, Aspöck, Aspöck, & Haring, 2017; Michel et al., 2017); or combined mt-DNA and nu-DNA markers and morphology (="total evidence": Jones, 2014; Winterton et al., 2010). In a general sense, then, data sampling across these surveys has been broad. Nevertheless, because of extremely limited sampling of owlfly exemplars, and to a lesser degree the narrow bandwidth and/or type of data employed in each study, the results regarding the constitution within the owlflies, and the relationship(s) of their constituent clades to the antlions, have been inconclusive. Some common patterns, however, have

been observed, namely proximate relationships of the owl-flies to the Stilbopteryginae and Palparinae (Henry, 1978c; Stange, 1994; Winterton et al., 2010; Winterton et al., 2018; Badano, Aspöck, Aspöck, & Cerretti, 2017; Badano, Aspöck, Aspöck, & Haring, 2017; Michel et al., 2017; Machado et al., 2018), which have verified to some degree long hypothesized alliances based on morphology, particularly with regard to Stilbopteryginae (e.g., van der Weele, 1909; Tillyard in Hacker, 1913; Riek, 1976; New, 1982), but also Palparinae (Kimmins, 1940).

The recently published paper of Machado et al. (2018) on the phylogeny of the AMC, based on analysis of several hundred nuclear genes of antlions and owlflies, marks a long step forward in better understanding relationships among the two families. Their taxon sampling, which was most balanced and comprehensive for the antlions (ca. 165 spp.), also included 18 owlflies. In their analysis, they recovered a monophyletic AMC, and a well-resolved and strongly supported Myrmeleontinae, but a paraphyletic Ascalaphidae with respect to the Stilbopteryginae, and a sister group relationship between these two groups and Palparinae. There is a fair amount of congruence in their higher-level results with the results of Jones (2014) and those presented herein. However, there are some key differences in the respective tree topologies for the owlflies and their immediate relatives (i.e., Stilbopteryginae), some corresponding weaknesses in how key synapomorphies optimize onto their phylogenies, and some practical taxonomic and nomenclatural problems for the owlflies engendered by their proposed classification. Those issues, as well as solutions based on the results obtained here, are explored in detail in the Discussion, below. Additional elaboration of past hypotheses of the relationships of Ascalaphidae and Myrmeleontidae to each other, and to the other families within the Myrmeleontiformia, is presented in the Appendix S1 and Figures S1–S5.

Until Jones (2014 and the present work) and Machado et al. (2018), the only previous author to have attempted any sort of detailed, tree-based analysis of relationships within the family Ascalaphidae was Henry (1978a, 1978c). Henry (1978a) presented a simple dendrogram (Figure S6) that optimized several characters: (a) evolution and loss of repagula ("barriers": defined as abortive eggs laid below egg masses on twigs in some owlflies), from abortive eggs with trophic functions, to abortive eggs with barrier function, to ant-repelling repagula, and then lost; (b) split eyes; and (c) ovariole number. His phylogeny proposed one clade containing *Ascalobyas* Penny (as *Byas* Rambur), *Ascaloptynx* Banks, *Haploglenius* Burmeister, *Verticillecerus* van der Weele and *Amoea* Lefèbvre; one for *Episperches* Gerstaecker (now *Amoea*) judged as transitional, one for the Ululodini, and one for the Old World split-eyed tribes Suhpalacsini, Acmonotini, Proctarrelabrini, Hybrisini, Encyoposini and Ascalaphini. Thirteen unnamed Old World genera were placed tentatively

at the base of the tree. His subsequent optimization (1978c), also based on larval characters but addressing intrafamilial relationships, grouped ascalaphids into two reciprocally monophyletic clades (Figure S1c): the "Neuropteryginae" (=Haplogleniinae sensu Tjeder, 1992) were united by scale-like setae and consisted of two lineages, one in the Old World and one in the New; and the Ascalaphinae had the ventral scolus series of the abdomen reduced and the abdominal tergum bearing litter, and also were subdivided into two lineages, one Old World and one New World. Other recent works that have addressed the phylogeny of the Neuropterida, Myrmeleontiformia and/or the AMC and have included three or more owlfly species (Badano, Aspöck, Aspöck, & Cerretti, 2017; Gao et al., 2018; Henry, 1978a; Lan et al., 2016; Machado et al., 2018; Michel et al., 2017; Song et al., 2019, 2018; Wang et al., 2017), are reviewed and figured in the Appendix S1 (Figures S6–S8).

Traditionally (sensu Tjeder, 1992), the family Ascalaphidae has comprised three subfamilies: the Albardiinae, with a single species from Brazil; the Haplogleniinae, or "entire-eyed owlflies," with ca. 100 valid species in 23 genera distributed in North and South America, western Asia, Africa and Madagascar; and the Ascalaphinae, or "split-eye owlflies," with ca. 350 described species in 76 genera, found worldwide. According to Tjeder, the Albardiinae are distinguished by their short antennae not reaching the mid-point between the forewing base and the pterostigma, and by the "entire" eye. He diagnosed the Haplogleniinae as having antennae that reach past the mid-point between the forewing base and pterostigma, and that also lack a transverse furrow across the eye. The Ascalaphinae, conversely, he diagnosed by the presence of a transverse, sulcus-like division across the eye. They also express long antennae.

The monophyly of the two large subfamilies has been assumed based on the ostensibly synapomorphic feature of the furrowed compound eye. However, the contrary state, that is the eye being "entire," which has been taken to unite the Haplogleniinae, may be understood as the ancestral state and plesiomorphic. Further, several taxa in both subfamilies express intermediate states of eye division. For example, Tjeder (1992) placed his African genus *Proctolyra* Tjeder in Haplogleniinae because its eyes, though divided, are only weakly so—the furrow is not deep or sulcus-like. However, he acknowledged it possesses other features that suggest it belongs within the Ascalaphinae: well-developed male ectoprocts, seen otherwise only in the Ascalaphinae, and the presence of a pleurostoma. Nevertheless, he interpreted the division of the eye, or lack thereof, to be of such importance as to outweigh those other features in determining taxonomic relationships, and for that reason placed *Proctolyra* in its own tribe, Proctolyrini, interpreting it as a "missing link" between the subfamilies. Similarly, the strange South American genus *Fillus* Navás also has

TABLE 1 Historical treatments of tribes within the Ascalaphidae. Navás (1919) revised the definition of Suhpalacsini[1] and sunk Acmonotini within it (=Suhpalacsini[2]). Tjeder (1972) revised the type concept of genus *Ascalaphus*, moving most of the species out of the genus (and thus out of the tribe Ascalaphini[1]), whose males have the ectoprocts well-developed, to *Libelloides* Schäffer, but without addressing the issue of tribal placements. New (1984) was vague in his treatment of the Australian owlflies with regards to tribal placements, but seemed to tentatively accept placement of all Australian taxa within Suhpalacsini[2] under Navás's (1919) concept. Tjeder (1992) reinterpreted Ascalaphini[2] to include only genera whose males have the ectoprocts undeveloped, which corresponds, in part, with van der Weele's original definition of Suhpalacsini[1] before its modification by Navás (1919). He did not address tribal placement for *Libelloides* species formally placed in Ascalaphini, nor for related genera

	van der Weele (1909)	Navás (1912a)	Navás (1912b)	Navás (1919)	Orfila (1949)	Tjeder (1972)	Penny (1982)	New (1984)	Tjeder (1992)	Most recent status
Haplogleniinae	None	Episperquinos	Episperquinos				Haplogleniini			Haplogleniini
	None	Neuroptinginos	Neuroptinginos		Verticillecerini		Verticillecerini			Verticillecerini
	None								Allocormodini	Allocormodini
	None								Campylophlebiini	Campylophlebiini
	None								Melambrotini	Melambrotini
	None								Proctolyrini	Proctolyrini
	None								Tmesibasini	Tmesibasini
Ascalaphinae	Acmonotini	Acmonotinos	Acmonotinos	Suhpalacsini[2]				Suhpalacsini[2]		Suhpalacsini
	Ascalaphini[1]	Ascalafinos	Ascalafinos			*-Revised concept				none
	Encyoposini	Encioposinos	Encioposinos							Encyoposini
	Hybrisini	Hibrisinos	Hibrisinos							Hybrisini
	Proctarrelabrini	Proctarrelabrinos	Proctarrelabrinos							Proctarrelabrini
	Suhpalacsini[1]	Sufalacsinos	Suhpalacsinos	Suhpalacsini[2]				Suhpalacsini[1]	Ascalaphini[2]	Ascalaphini
	Ululodini	Ululodinos	Ululodinos							Ululodini
									Ululomyiini	Ululomyiini

weakly divided eyes, but was placed in the Ascalaphinae by Navás (1919), chiefly on account of its wing venation, which is similar to Old World species in the tribe Suhpalacsini, but also the presence of the abdominal tergal process of males seen in other Ascalaphinae. Several species of Old and New World Haplogleniinae, for example, in *Tmesibasis* McLachlan and *Ascalobyas*, also express a very slight posteromesal depression suggestive of an incipient and possibly progressive division. The dorsal lobe of the superpositional eye is understood to correspond with ultraviolet wavelength reception (Belušič et al., 2013; Meglič et al., 2007), and it is highly likely that an externally expressed bilobation is preceded evolutionarily by an internal division of the optical nerves and specialization of the dorsal bundles, which, in turn, is driven by predatory behaviour and progressive adaptation towards increased UV light sensitivity. Thus, the observations of externally split eyes in diverse and unrelated lineages of owlflies, as elaborated above, suggest that division of the eye has arisen multiple times within the owlflies, and alone is not reliable as an indicator of phylogeny.

Tribal classification within the Ascalaphidae (Table 1) is also problematic. Though a few of the tribes are based on what seem to be reliable characters, several are diagnosed primarily by features that appear to be combinations of plesiomorphies or homoplasies, are described with insufficient detail to enable a proper tribe-level identification for many species and, geographically speaking, seem implausible. Identification of species to tribe is also confounded by the fact that many of the tribes are determined solely by the expression of male morphology. Suhpalacsini van der Weele, as one example, is diagnosed by the males having more or less undeveloped ectoprocts (an ancestral feature) and sometimes bearing a swelling or process on some part of the abdominal tergum (a derived feature). However, in the South American suhpalacsine genus *Fillus*, an acuminate process arises from fused T1 (tergite) plates, but in the Australian suhpalacsines *Megacmonotus* New and *Pictacsa* New, a stout projection rises from T2; and in many suhpalacsine genera, no projection occurs at all. Further, species of *Ascaloptynx* and *Ptyngidricerus*—haplogleniines not placed in the Suhpalacsini—have a dorsal projection rising from T3. This inconsistency and diversity of expression suggest that the Suhpalacsini may be paraphyletic. Tjeder later (1992b) characterized his redefined tribe Ascalaphini as also comprising males with simple ectoprocts, but with no tergal projections, thus overlapping in definition that of Suhpalacsini. As another example, *Neohaploglenius* Penny, *Verticillecerus* and *Ascaloptynx* have been placed in Verticillecerini Orfila (Penny 1982), separated from other New World Haplogleniinae on the basis of the forewing being proximally narrow and the anal angle being developed into a process. But wing narrowing is common and convergent across the Ascalaphidae

and varies even within clearly monophyletic genera (Ardila Camacho & Jones, 2012; Jones, 2014), and thus by itself is not necessarily a reliable indicator of tribe-level phylogenetic relationships.

This study presents the first large-scale phylogenetic estimate dealing primarily with the family Ascalaphidae and putatively immediate ancestors based on both molecular and morphological data. Presented here are the results of combined analyses of DNA and morphology for nearly 80 species from all five extant families of Myrmeleontiformia, which were used to evaluate monophyly at three primary taxonomic ranks: family, subfamily and tribe. Analytical procedures under three phylogenetic paradigms—parsimony, maximum likelihood and Bayesian inference—were employed to explore relationships. In the light of the results, the evolution of the eye (entire vs. divided) and the pleurostoma, the latter a feature suggested by Tjeder (1992) as possibly useful for diagnosis of the Ascalaphinae are briefly discussed, and revised classifications for the owlflies and antlions are proposed.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling

Seventy-six species from the five families of Myrmeleontiformia (Psychopsidae, Nymphidae, Nemopteridae, Myrmeleontidae, Ascalaphidae) were chosen for analysis (Table S1). Sampling was deepest for Ascalaphidae and Myrmeleontidae. Efforts were made to sample as thoroughly as possible from the Ascalaphidae. Two of three subfamilies were sampled (amplifications of *Albardia* van der Weele from dry pinned specimens and older specimens in 70% EtOH were attempted, but no DNA was recovered). Of Haplogleniinae, 11/24 genera in 5/7 tribes (Allocormodini, Haplogleniini, Melambrotini, Tmesibasini, Verticillecerini) were sampled (amplifications of Campylophlebiini [*Campylophlebia* McLachlan] and Proctolyrini [*Proctolyra*] from dry pinned specimens were attempted, but no DNA was recovered). Of Ascalaphinae, 13/75 genera in 6/7 tribes (Ascalaphini, Hybrisini, Proctarrelabrini, Suhpalacsini [=Acmonotini], Ululodini, Ululomyiini) were sampled (amplifications of Encyoposini were attempted from dry pinned specimens, but no DNA was recovered). In the traditional Myrmeleontidae (sensu Stange, 2004), representation was obtained for each of the subfamilies (Myrmeleontinae, Palparinae, Stilbopteryginae). In the Myrmeleontinae, sampling included the tribes Acanthaclisini, Brachynemurini, Dendroleontini (subtribes Dendroleontina and Periclystina), Myrmeleontini (subtribe Myrmeleontina) and Nemoleontini (subtribe Nemoleontina). In the Psychopsidae, only a single exemplar was successfully amplified. In Nymphidae, four species in two genera were sampled. In Nemopteridae, two species were successfully amplified, but the sequence of the
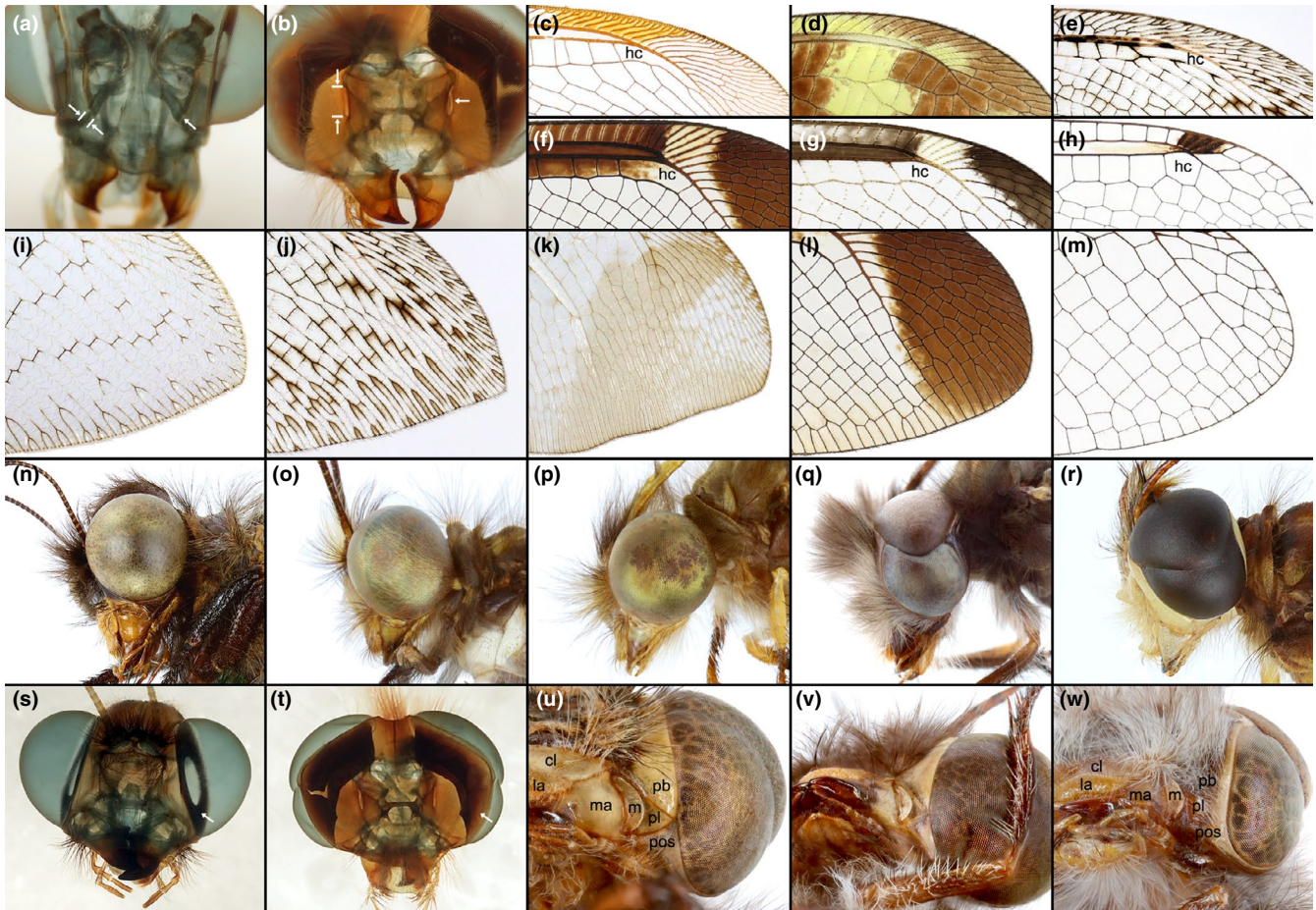
FIGURE 2 Characters of Myrmeleontiformia and Ascalaphidae. A–M, Myrmeleontiformia. (a–b) Anterior tentorial pits (ATP). (a) *Nymphes myrmeleonoides* Leach. (b) *Ululodes macleayanus* (Guilding). The single white arrow marks the ATP aperture, and the brackets indicate its height. In Psychopsidae, Nymphidae and Nemopteridae, the opening of the ATP is round, or laterally compressed, but dorsoventrally short. In Myrmeleontidae and Ascalaphidae, the ATP is laterally compressed and dorsoventrally elongate and slit-like. (c–h) hypostigmatic cells. (c) *Nymphes aperta* New. (d) *Nemoptera bipennis*. (e) *Vella fallax*. (f) *Stilbopteryx costalis* Newman. (g) *Aeropteryx gibba* Riek. (h) *Ululodes mexicanus* McLachlan. The hypostigmal cell is elongate in Psychopsidae, Nymphidae and nearly all Myrmeleontidae. It is short and indistinguishable from adjacent cells in Nemoptera, some species of *Stilbopteryx*, and Ascalaphidae. (i–m) Marginal twigging of longitudinal veins. (i) *Osmylops armatus* (McLachlan). (j) *V. fallax*. (k) *Lachlathetes moestus* (Hagen). (l) *S. costalis*. (m) *A. latipennis*. Twigging is more or less lost in Ascalaphidae; all other Myrmeleontiformia express 10 or more marginal furca along the wing margin, with a gradual reduction seen in the stilbopterygids and *Albardia*. (n–w) *Stilbopteryx* and Ascalaphidae. (n–p) Entire eyes. (n) *Stilbopteryx napoleo* (Lefèbvre). (o) *Balanopteryx locuples* Karsch. (p) *Haploglenius angulatus* (Gerstaecker). (q–r) Divided eyes. (q) *Ululodes floridanus* (Banks). (r) *Ascalaphus sinister* Walker. (s–t) Ocular diaphragms, indicated by a white arrow, in macerated specimens. (s) *S. walkeri*. (t) *U. macleayanus*. In *Stilbopteryx* and examined entire-eyed owlflies, the diaphragm is flat and the foramen circular. In owlflies with a well-developed external division to the eye, the diaphragm is truncated conical, and the foramen oblong. (u–w) Pleurostomata. (u) *Megacmonotus magnus* (McLachlan). (v) *Protidricerus irene* van der Weele. (w) *Ululodes arizonensis* Banks. In *Megacmonotus* and other non-ululodine, divided-eye owlflies, and in the entire-eyed genera *Protidricerus*, *Idricerus*, and *Nicerus*, the pleurostoma is a triangular or quadrate sclerite bounded mesally by the crescent-shaped basilateral membrane of the mandible, laterally by the ventral margin of the eye, anteriorly by the paraocular band, and posteriorly by the postorbital sclerite. It is generally offset by an anterior and posterior sulcus (which may be obscured by setae) and is either tangent to the eye margin, or connected by a short lateral sulcus. In all other entire-eyed owlflies (not figured), the paraocular band is ventrally narrow such that the basilateral membrane of the mandible sits tangent to the eye margin, leaving no space for a pleurostoma. In the ululodines, the pleurostoma is not bounded by sulci, and the paraocular band and postorbital sclerite are contiguous and undivided. cl, clypeus; hc, hypostigmal cell; labrum; m, basilateral membrane of the mandible; ma, mandible; pb, paraocular band; pl, pleurostoma; pos, postorbital sclerites

crocine exhibited anomalous properties during analysis and was removed. Included in taxon sampling for Ascalaphidae were three species whose information was extracted from GenBank. In sum, for the owlflies, roughly 13% of known species-level diversity (57/435), 24% of genus-level diversity (24/100), and 80% of tribe-level diversity (12/15) were sampled. The total sampling, including the outgroup, was 77 species.

As outgroup, *Polystoechotes* Burmeister was selected. In Aspöck and Aspöck (2008), Winterton et al. (2010), Wang et al. (2017) and Gao et al. (2018), a clade containing (Ithonidae + Polystoechotidae) was consistently placed as sister group to the Myrmeleontiformia.

2.2 | Material examined and morphological data generation

Thousands of specimens of ingroup and outgroup material, from over 40 international arthropod research collections, were examined for this study. From these, a matrix of 25 anatomical features, mostly relating to higher-level relationships within the Myrmeleontiformia, was compiled (Table S2). A complete list of ingroup material examined is available from the author. Descriptions of the morphological characters selected and character states determined are provided in the Appendix S1. Some of the characters systems examined are presented in Figure 2.

2.3 | Gene selection, DNA extraction, amplifications and gene sequencing

Because of their utility in previous Neuropterida-targeted phylogenetic studies (Haring & Aspöck, 2004; Winterton et al., 2010), the mitochondrial genes cytochrome oxidase subunit I (COI) and 16S rRNA (16S), and the nuclear genes 18S rRNA (18S), were selected for use in this study. Carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD) was also selected, but extensive efforts at amplification were ultimately only partially successful, and it was removed.

DNA extraction was performed using the Qiagen DNeasy® blood and tissue kit. Amplification primers utilized and thermocycling regimes developed and employed are provided in the Appendix S1 (Tables S3, S4).

Amplification of PCR product was confirmed via gel electrophoresis. DNA yields were verified after initial amplifications with a Thermo Scientific NanoDrop Fluorospectrometer (NanoDrop products). PCR product was cleaned with USB® ExoSAP-IT® PCR Product Cleanup (Affymetrix) following manufacturer's directions.

Sequencing was outsourced to the University of Arizona Genetics Core (UAGC), Tucson, AZ.

2.4 | Alignment

Chromatogram files were edited using Sequencher™ 4.8 (GeneCodes Corp.). Verification of the COI alignment was determined in Sequencher, and a second check was performed in Mesquite (Maddison & Maddison, 2011). Potential saturation at third codon positions in COI was investigated using PAUP* (Swofford, 2002) and was interpreted to be minimal (Figure S9).

Alignment of the ribosomal genes was carried out in MAFFT (Multiple Alignment using Fast Fourier Transform: Katoh, Kuma, Toh, & Miyata, 2005) and GBlocks (Castresana, 2000, 2002) via the CIPRES (Cyberinfrastructure for Phylogenetic Research) portal (Miller, Pfeiffer, & Schwartz, 2010).

2.5 | Model selection

For the COI partition, model fit was explored in Partitionfinder (Lanfear, Calcott, Ho, & Guindon, 2012). Selection of models for the ribosomal genes was performed in JModelTest2 (Darriba, Taboada, Doallo, & Posada, 2012; Guindon & Gascuel, 2003).

2.6 | Phylogenetic analyses

Parsimony analysis was conducted on (a) the morphological partition and (b) the total-evidence dataset containing the morphological partition + all molecular partitions. Both datasets were analysed in TNT (Goloboff, Farris, & Nixon, 2008). The consistency index (C. I.) and retention index (R. I.) were generated using the "stats.run" script found at http://tnt.insectmuseum.org/index.php/Scripts. Bremer supports (Bremer, 1994) were calculated within TNT using the internal utility.

Maximum-likelihood analysis of the molecular datasets was performed in the RAxML-HPC Black Box environment (Stamatakis 2014) at the CIPRES portal using four separate partitioning schemes (Table S5).

Bayesian analysis was performed in MrBayes 3.2.2 (Ronquist & Huelsenbeck, 2003) on XSEDE and was run for 10 million generations. Stationarity occurred after ~535,000 generations (Figure S10), and the first 1 million generations were discarded as burn-in.

2.7 | Figures

Trees diagrams were built in FigTree v1.4.1 (Rambaut, 2014) and manually.

More extensive information for each of the methods sections above, including figures and tables, is provided in the Appendix S1.

3 | RESULTS

3.1 | Morphological data phylogeny

Analysis of the morphological data partition by itself resulted in six equally parsimonious trees.

A strict consensus cladogram of these trees can be seen in Figure S11. This cladogram was largely unresolved, particularly at the subfamily and genus levels. It presented its strongest

signal at the node containing Myrmeleontidae + Ascalaphidae (Bremer support: 3) and placed representatives of the families of Myrmeleontiformia as stem lineages leading up to the Ascalaphidae. The lack of genus- and species-level resolution is to be expected—very few characters were coded in the morphology dataset that addressed relationships within the families.

3.2 | Molecular data: maximum-likelihood phylogeny

Four trees were returned from RAxML analyses of the molecular data, one for each partition scheme. The trees were not identical but were all quite similar to one another, differing primarily in the arrangement of tribes within the Myrmeleontidae, which experienced some internal rearrangements in the various analyses. Figure S12 presents a phylogram of the unpartitioned result (partition "i"—see Table S5). This topology illustrates a trend seen in the results of all analytical approaches, even those including morphological data—a monophyletic AMC, with strong support for some medium- and lower-level groupings within, including species and genus groups and several tribes, but somewhat non-traditional placements and thus taxonomic novelty at higher internal levels. Most notably in this analysis, the tribe Ululodini was placed separately from remaining Ascalaphidae as sister group to a paraphyletic assemblage of myrmeleontid groups + remaining Ascalaphidae, which were collectively placed as monophyletic.

Some of the well-supported mid- and lower-level taxonomic groups in the AMC included the Palparinae (bootstrap: 99), Stilbopteryginae (bootstrap: 100), Ululodini (bootstrap: 100), New World Haplogleniinae (NWH)(bootstrap: 87), African Haplogleniinae (bootstrap: 88), Australian Suhpalacsini (bootstrap: 94), *Protidricerus* van der Weele (bootstrap: 100) and *Libelloides* (bootstrap: 100). These relationships were recovered in every analysis (including parsimony and Bayesian; see Figures S13, S14) with high support and are marked with a common set of symbols (see Figure S12 caption) in each topology presented in the appendices of this paper, in order to more easily track their consistency and draw robust final conclusions.

3.3 | Total-evidence analysis: parsimony phylogeny

Total-evidence analysis in TNT resulted in two equally parsimonious trees with a length of 6,701. One of the trees placed Stilbopteryginae + Palparinae as sister to the African Haplogleniinae, but the other tree (Figure S13) expressed most of the same relationships as the ML and Bayesian topologies. The RI and CI for the latter topology were 0.528 and 0.235, respectively.

The Myrmeleontidae were nearly recovered as monophyletic, with only the Dendroleontini placed separately, on a stem basal to the remaining AMC. This differed from the other analyses (see Figures S12, S14), where the Myrmeleontidae were placed as multiple paraphyletic stem lineages to the Ascalaphidae (and the Dendroleontini exhibited different placements, but united with other Myrmeleontinae). The AMC was supported with a relatively very high Bremer value of 27. Within the Myrmeleontidae, Palparinae (Bremer: 9) and Stilbopteryginae (Bremer: 28) were placed together with a support value of 6. Support values for other basal nodes within the family ranged from 1 to 4.

Although branch lengths of stem lineages along the backbone of the tree were somewhat short and expressed weak support, the analysis was able to recover a monophyletic Ascalaphidae, with the Ululodini placed at the base of the owlfly clade. Support for this relationship, however, was low (Bremer: 1). Bremer support for the Ululodini was 15. The NWH were placed as sister to the remaining Ascalaphidae (as in the ML analysis), but with low support (Bremer: 1). Within this clade, the African Haplogleniinae were placed as sister to the remaining species, but again with low support (Bremer: 1). Monophyly of the NWH had a support value of 4, and support for the African Haplogleniinae was 5. The remaining Ascalaphidae (with *Protidricerus* included) were strongly supported as monophyletic with a Bremer support value of 10. Within this group, the Australian Suhpalacsini and *Libelloides* were both supported as monophyletic, each with Bremer supports of 10.

3.4 | Total-evidence analysis: Bayesian inference phylogeny

Bayesian analysis (Figure S14) resulted in a mostly resolved topology with well-supported clades. The base of the Myrmeleontinae remained unresolved, as were some tribes within the Ascalaphinae, and a few tribe- and genus-group relationships.

The analysis sorted Myrmeleontidae as a paraphyletic grade at the base of the Ascalaphidae. The Stilbopteryginae were placed with high support (pp = 89%) as sister to the owlflies and near the base of the antlions, an hypothesis put forward by van der Weele (1909) and Tillyard in Hacker (1913), and supported by numerous morphological character systems (see Figure 3). They were also placed immediately distad of the Palparinae; a close relationship between the two subfamilies was proposed by Kimmins (1940) and is supported by synapomorphic features on the head (Figure 3). The implications of these higher-level results are treated in greater length in the Discussion.

As in the parsimony tree, the Ascalaphidae were recovered as monophyletic, but with 100% posterior probability (pp) support. Within the Ascalaphidae, the Ululodini
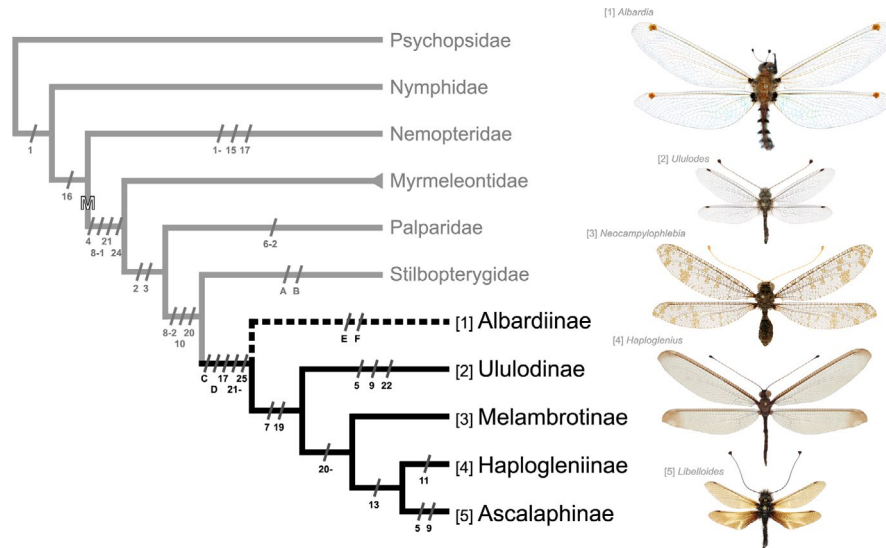
FIGURE 3 Summary tree of subfamilial relationships in the Ascalaphidae and family-level relationships among myrmeleontiformian ancestors corresponding with the new higher-level classifications presented herein. The topology is based on results of the Bayesian analysis (Figure S14). Important character state changes (putative synapomorphies) from the morphology dataset are mapped onto the phylogeny and are indicated by a gain (character number only, or number and state, e.g., 8–2) or loss (e.g., 20-). Synapomorphies determined from characters not included in the morphology matrix/Bayesian analysis are indicated by letters A–F. The M along the stem marks a redefined superfamily Myrmeleontoidea, and the Ascalaphidae are indicated by black lines. The position of *Albardia* (not included in the phylogenetic analyses) is estimated based on the collective character optimizations presented here. Branch lengths for this tree are not estimated. Summary of characters and changes (see Appendix S1 for a full listing): 1, paraocular band developed; 16, recurrent vein lost; 1-, paraocular band reduced; 15, hind wings greatly elongated; 17, hypostigmatic cell reduced, indistinguishable from adjacent cells; 4, anterior tentorial pit opening oblong, slit-like; 8–1, antennal apex clavate; 21, pilulla axillaris developed; 24, larval metathoracic tibia and tarsus fused; 2, extratorular sclerites well-formed; 3, prefrons well-formed; 6–2, labial palpus distal segment swollen apically, extremely elongate; 8–2, antennal apex capitate; 10, pronotum length less than half width, collar-like; 20, HW CuA distinctly curved and MP fork indistinct; A, antennal club asymmetric; B, males with T4 bearing dorsal elevations; C, antennal club symmetrically pyriform; D, posterior margin of third-instar larval head cordate; 17, hypostigmatic cell reduced, indistinguishable from adjacent cells; 21-, pilulla axillaris lost; 25, larvae with well-developed scolus-like processes, total length >5x width at base; E, adult tergites with lateroposterior tufts of setae; F, female S8 posteromedially well-developed, sclerotized; 7, antennomeres of antennal flagellum greatly elongated; 19, marginal furca of longitudinal veins reduced to 7 or fewer; 5, pleurostoma present* (*but without lateral sulcus connecting to ocular margin); 9, eye divided; 22, abdomen segment 8 with spiracle opening of females on pleural membrane; 20-, HW CuA more or less straight with apical portion reduced, and MP fork distinct; 13, pteropleuron patterned with various striping; 11, prothoracic valve of males developed; 5, pleurostoma present* (*with lateral sulcus connecting to ocular margin); 9, eye divided

were placed as sister to all remaining species, with high support (pp = 100%), but separate from other split-eyed species. The African Haplogleniinae were then placed as sister to the remaining ascalaphid species, also with high support (pp = 100%). The NWH were once again monophyletic with high support (pp = 100%), although their inner relationships were somewhat unresolved. In the remaining Ascalaphidae, the entire-eyed *Protidricerus* was placed in a small clade with the split-eyed *Proctarrelabis* Lefèbvre and another species of *Proctarrelabrini* with rather high support (pp = 88%). Together, they form the sister group to the remaining owlflies, which are all split-eyed. Relationships within the large split-eyed owlfly clade differ slightly from the ML topology, mainly in the positions of *Protidricerus*, the small clade (2 spp.) containing *Proctarrelabis*, and the clade (5 spp.) containing *Maezous princeps* (Gerstaecker).

4 | DISCUSSION

4.1 | The arrangement of families within the Myrmeleontiformia

An identical arrangement of families was recovered in every analysis and took the form Psychopsidae + (Nymphidae + (Nemopteridae + (Myrmeleontidae + Ascalaphidae))). This result agrees with numerous studies based on morphological (Stange, 1994; Winterton et al., 2010), molecular (Winterton et al., 2010; Gao et al., 2018; Michel et al., 2017; Song et al., 2019; Wang et al., 2017) and combined data (Winterton et al., 2010). It contradicts, however, most studies based solely on morphology (Aspöck & Aspöck, 2008; Aspöck et al., 2001; Badano, Aspöck, Aspöck, & Cerretti, 2017; Beutel, Friedrich, & Aspöck, 2010; Mansell, 1992; Randolf, Zimmermann, & Aspöck, 2014) and two based on nuclear

genomic data (Machado et al., 2018; Winterton et al., 2018). The contrary studies vary slightly in their placements of constituent taxa, but generally deviate from the solution obtained here in (a) placing Psychopsidae, Nemopteridae and Nymphidae together in one clade, and the AMC in another (Aspöck & Aspöck, 2008); in (b) recovering a non-monophyletic Psychopsidae (Winterton et al., 2010) or Nemopteridae (Beutel et al., 2010); and/or (c) in placing Nymphidae, rather than Nemopteridae, as sister to the AMC (Aspöck et al., 2001; Badano, Aspöck, Aspöck, & Cerretti, 2017; Beutel et al., 2010; Mansell, 1992; Randolf et al., 2014); or (d) in placing Ithonidae within the Myrmeleontiformia as sister group to Psychopsidae (Winterton et al., 2018) or Nymphidae (Machado et al., 2018; Winterton et al., 2018), or along the stem between the Psychopsidae and Nymphidae (Winterton et al., 2018), or in a clade with both Psychopsidae and Nymphidae (Winterton et al., 2018), the latter a result not recovered elsewhere.

The study of Aspöck and Aspöck (2008) was based on optimization of genital sclerites across a hypothetical phylogeny of the Neuropterida and holds important clues to relationships within the Myrmeleontiformia, but the topological arrangement for the suborder they reported was not recovered here, nor has it been recovered in other studies. Because only a single representative of Nemopterinae was included in the final analyses here, the monophyly of Nemopteridae cannot be evaluated. Nor can be evaluated the monophyly of the Myrmeleontiformia relative to Ithonidae, because *Polystoechotes*, an ithonid, served as outgroup in the analyses here, and no other potential outgroups (e.g., Hemerobiidae, Chrysopidae) were included. The matter of the immediate extant sister group to the AMC, however, can be explored and discussed, and such discussion is presented in the Appendix S1. In summary, analyses that include DNA consistently place Nemopteridae as extant sister group to the AMC, as is the case in the present study. A plausible explanation for the anomalous derivations observed in the Nemopteridae is presented in Appendix S1.

4.2 | Monophyly of the AMC

The AMC was recovered as monophyletic in every analysis, with high node support. Several morphological characters also supported this relationship: the anterior tentorial pit opening oblong and slit-like; the antennal apex clavate; the pilulla axillaris developed (secondarily lost in the owlflies); and the larval metathoracic tibia and tarsus fused (chars. 4, 8–1, 21, 24: "Morphological characters," Appendix S1; Table S2; Figure 3). Additional synapomorphies not included here have been proposed by other authors. Mansell (1992) cited, for the larvae: a prominent ocular tubercule, and the tubercule bearing seven stemmata; and for the adults: the male terminalia with parameres situated apicomedially on

the gonarcus. Stange (1994) added, for the larvae: the mandible with 2–3 parallel teeth, and abdominal sternite VIII with submedial teeth; and for the adults: the labial palpus with an oval-shaped pit, the pronotum articulating with the mesothoracic spiracle, and the female posterior gonapophysis plate-like. And Badano, Aspöck, Aspöck, and Cerretti (2017) included for the larvae: the mesothoracic spiracle raised on a conical tubercle, abdominal segment 1 spiracle dorsal and rastra present.

Other traits have been proposed as synapomorphies for the AMC, but may, in fact, be more accurately placed as unifying characters for AMC + Nemopteridae, for example the loss of the oviruptor (Badano, Aspöck, Aspöck, & Cerretti, 2017), and the fusion of the oblique forewing MP with CuA (Mansell, 1992).

4.3 | Relationships within the Myrmeleontidae: monophyly of the Myrmeleontinae

None of the analyses here recovered a monophyletic traditional Myrmeleontidae. At the subfamilial level, however, some trends were consistently observed (Figure S15). Specifically, in all analyses (Figures S12–S14), Palparinae and Stilbopteryginae were each recovered as monophyletic lineages with strong support, though their placements varied. This is perhaps unsurprising, as their taxonomic representation was rather limited. The Myrmeleontinae, however, were paraphyletic in every analysis, although they were nearly recovered as monophyletic in the parsimony and Bayesian phylogenies. In fact, each analysis recovered a slightly different set of higher-level relationships among the members of the subfamily. This inconsistency was likely due to inadequate taxon sampling (only eight myrmeleontines were included), and probably insufficient molecular data. Almost certainly it was not helped by the low sampling of morphological data, as few intrafamilial characters were included in the morphological dataset (see Figure S11).

Understandably, then, relationships were also inconclusive at the level of tribe (Figure S16). The Dendroleontini were anomalously placed separately from the remaining Myrmeleontinae in the parsimony analysis (in Machado et al., 2018 they were placed firmly within the Myrmeleontinae), and the Nemoleontini were polyphyletic in each analysis, the latter result based only on two exemplars. Not enough taxa were included to evaluate the monophyly of the other sampled tribes Acanthaclisini, Brachynemurini and Myrmeleontini. The results presented here are clearly insufficient to resolve tribal relationships among the Myrmeleontinae.

Several recent molecular studies have recovered a paraphyletic Myrmeleontinae (Gao et al., 2018; Lan et al., 2016; Michel et al., 2017; Song et al., 2019; Wang et al., 2017; Winterton et al., 2018; Zhang & Yang, 2017).

Many of these studies included genome-level data, either nuclear (Winterton et al., 2018) or mitochondrial (Gao et al., 2018; Lan et al., 2016; Song et al., 2019; Wang et al., 2017; Zhang & Yang, 2017). Nearly all, however, included only a handful of species, ranging from two to six. Winterton et al. (2018) and Michel et al. (2017) included the most, with 20 and 70 exemplars of Myrmeleontinae, respectively. Notably, the final tree of Winterton et al. (2018) was only paraphyletic with respect to a single taxon, Maulini, and that of Michel et al. (2017) recovered a mostly monophyletic Myrmeleontinae, but placed a monophyletic Acanthaclisini separately, as sister to (Palparinae + remaining Myrmeleontinae). Machado et al. (2018) placed Acanthaclisini deep within the Myrmeleontinae, as sister to Nesoleontini + Myrmecaelurini.

Other recent studies, however, have recovered a monophyletic Myrmeleontinae (Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Haring & Aspöck, 2004; Machado et al., 2018; Song et al., 2018), a number of these with extensive sampling and strong support (Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Machado et al., 2018). Machado et al. (2018), in particular, applied a considerable amount of molecular data and taxa to the question, sampling very deeply (ca. 150 spp.) and including numerous outgroups. This appears to indicate that when a threshold amount of taxa and data are analysed, the monophyly of the subfamily is, indeed, recoverable.

4.4 | Higher-level relationships within the AMC: Ascalaphidae and Stilbopteryginae

In every analysis conducted here, the Ascalaphidae were placed together with a paraphyletic traditional Myrmeleontidae, and in the morphology and Bayesian analyses, the Ascalaphidae were grouped in a clade with the Palparinae and Stilbopteryginae. This latter result, taken as a single broad stroke, agrees with that of Machado et al. (2018) and Winterton et al. (2018). Close examination of the phylogenies here to theirs, however, reveals significant topological differences in the placement of the various clades traditionally placed within the owlflies (sensu Tjeder, 1992), and in how the Stilbopteryginae and Palparinae were placed.

Firstly, as previously noted, in the two analyses here that included morphology and molecular data, the various clades of traditional Ascalaphidae were placed together as a monophyletic unit, with high support for this relationship in the Bayesian phylogeny (100% pp). In the latter, each of the major subclades of Ascalaphidae recovered had high support (100% pp). The monophyly of Ascalaphidae is discussed in detail in the section below ("Monophyly of the Ascalaphidae"). Also in the Bayesian phylogeny, which of the three analyses had the highest support generally, and is here taken as the best

overall estimate of relationships, the Stilbopteryginae were placed as the immediate sister group to the Ascalaphidae, again with high support (89% pp).

Both of these results—a monophyletic Ascalaphidae, and Stilbopteryginae as sister group—differed considerably from those of Machado et al. (2018) and Winterton et al. (2018). Winterton et al. (2018) recovered numerous topologies that differed in the placement of Palparinae, Dimares and Maulini (see Figure S5). Machado et al. (2018) recovered the following relationships in both trees shared in their paper: (Myrmeleontinae) + (Palparinae: *Dimares* + (Palparinae: part + ((*Albardia* + Ascalaphinae: Ululodini) + (Stilbopteryginae + (Haplogleniinae + non-ululodine Ascalaphinae))))) (see also Figure S5). Backed by the strong node support of their results, Machado et al. (2018) proposed a novel classification that treated the entire non-Myrmeleontinae grouping as a redefined Ascalaphinae, simultaneously sinking the family group Ascalaphidae into the Myrmeleontidae, and reducing its name in rank.

While their classification is reasonable based on their results, the newly woven relationships recovered by Machado et al. (2018) for the owlflies and close relatives may be a result of several factors other than the phylogenetic "answer." They may be due chiefly to (a) inadequate taxon sampling, particularly for the Ascalaphidae, but also (b) peculiarities in data analysis (as indicated by the multiplicity of different topologies obtained when the same data were analysed under different regimes in Winterton et al., 2018), and/or (c) a reliance on nuclear genome data alone. The data gathered and analysed by Machado et al. (2018) were extensive and seem to be of the highest quality, and their node support appears robust. But some (e.g., Borkent, 2018) have pointed out the dangers of relying solely on a single data stream for phylogenetic inference, in this case nuclear phylogenomic data, to draw conclusions. Borkent (2018), in particular, argued that (a) reliance on molecular data independent of morphological analysis is not strictly Hennigian (i.e., synapomorphy-based); that (b) support values for nodes have no biological reality, despite being taken as evidence; that (c) the results of molecules-only-based studies are prone to tumultuous inconsistency; and that, (d) for all these reasons, these sorts of studies should be viewed with caution. It is not being argued here that the results of Machado et al. (2018) are unreliable, but rather that they are inconclusive; that is, despite the breadth of the dataset used, their results must be interpreted carefully, and that almost certainly they have not yet arrived at the true sequence of evolutionary events, despite the wishes of at least some of their co-authors (Engel et al., 2018). This seems to be the case especially for the portion of their tree dealing with the Ascalaphidae and close relatives.

Although the results obtained in the current study are based on much less data than those of Machado et al. (2018),

the topology presented here (Figure 3, based on the Bayesian phylogeny) is taken as a better estimate of relationships for the Ascalaphidae and closely allied antlions, for the following reasons.

I   The final topology here of a monophyletic Palparine + (Stilbopteryginae + Ascalaphidae) is congruent with that obtained by Machado et al. (2018).

II   The present study included a much richer taxon sampling for the ingroup.

III   Key higher-level clades were recovered as monophyletic in every analysis (Figs. S12–S14), including all major groups within the owlflies, despite their relationships to one another changing slightly.

IV   These same nodes, generally, exhibited high support in each analysis (posterior probabilities, bootstrap values, decay indices).

V   The result of a monophyletic Ascalaphidae independent of Stilbopteryginae is congruent with previous hypotheses and numerous analyses based on either morphology or molecular data (Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Henry, 1978c; Mansell, 1992; Michel et al., 2017; New, 1982; Stange, 1994, 2004).

VI   The result of Stilbopteryginae as an independent lineage immediately adjacent to Ascalaphidae is congruent with other recent studies based on extensive morphological (Badano, Aspöck, Aspöck, & Cerretti, 2017) and molecular data (Michel et al., 2017).

VII   Examination of the results of the morphology-only cladogram (Figure S11) in the current study reveals that while it supports a monophyletic Ascalaphidae, and a sister group relationship for the Stilbopteryginae, Bremer supports are very low or nil, suggesting that most of the signal for relationships recovered in the combined data analyses comes from the molecular data, and is not being overpowered by the morphological data.

VIII   Although the morphology-based cladistic analysis (Figure S11) had weak support, and exhibited numerous unresolved clades, its sequence of nesting of major groups nevertheless agreed with that of the Bayesian analysis (Figure S14). Thus, it provided mostly positive, and little, if any, negative signal.

IX   The molecular data include, though slight in amount compared to Machado et al. (2018), both nuclear and mitochondrial markers, these representing both ribosomal and protein-coding genes. Thus, they may be taken as a heuristic sampling of both genomes, and all major gene types.

X   A careful examination of character states on the nodes of the Bayesian topology (Figure 3) reveals a more parsimonious optimization, and thus interpretation of them, as synapomorphies.

In summary, the present study provides multiple lines of direct, counter-positional, Hennigian support for the final topology obtained and conclusions drawn.

4.5 | Higher-level relationships within the AMC: Palparinae

The present study recovered a sister group relationship for Palparinae with Stilbopteryginae + Ascalaphidae. The placement of the Palparinae adjacent to the Stilbopteryginae agrees with several past hypotheses and analyses that recovered a similar relationship (Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Stange, 1994). Badano, Aspöck, Aspöck, and Haring (2017), who explored the phylogeny of these taxa in great depth, particularly the Palparinae, found support for a sister group relationship based on separate analyses of both morphological and molecular data.

4.6 | Higher-level relationships within the AMC: Maulini, Dimarini and Pseudimarini

A few genera of potential importance with regard to the monophyly of the Palparinae and Stilbopteryginae were not included in the current study, and so their placements were not tested and could not be verified. These include Maulini, which were placed separately from other Palparinae in Winterton et al. (2018); *Dimares* and *Millerleon*, traditional palparines that were placed outside of other Palparinae in Badano, Aspöck, Aspöck, and Haring (2017), in some of the trees of Winterton et al. (2018), but not others (see discussion in Appendix S1 and Figure S5a–g), and in Machado et al. (2018); and *Pseudimares*, another traditional palparine, which was placed as sister to Stilbopteryginae in Aspöck, Aspöck, and Haring (2015) and Badano, Aspöck, Aspöck, and Haring (2017). All of these results came from analyses of DNA.

Michel et al. (2017) and Badano, Aspöck, Aspöck, and Cerretti (2017), Badano, Aspöck, Aspöck, and Haring (2017) did not include Maulini in their studies. Machado et al. (2018), however, whose matrices represented an expanded dataset from Winterton et al. (2018), placed *Maula* as sister to *Isonemurus* within, but at the base of Palparinae, with strong support (100% pp).

Dimares and *Millerleon* have been recovered previously in a position separate from other Palparinae in an analysis of morphological data, in Stange (1994). His analysis placed them together as sister to the Myrmeleontinae. However, Badano, Aspöck, Aspöck, and Haring (2017), who re-estimated the phylogeny of the Myrmeleontidae also using morphological data, placed *Dimares* again with *Millerleon*, but squarely within a monophyletic Palparinae (except for

Pseudimares—see next paragraph). Michel et al. (2017) did not include Dimarini in their studies.

Pseudimares has been an enigmatic genus since it was first described, but generally it has been treated as a palparine (Stange, 2004, who included it in Palparinae as tribe Pseudimarini). Aspöck et al. (2015), and soon after Badano, Aspöck, Aspöck, and Haring (2017), found both morphological and molecular evidence for a sister group relationship between *Pseudimares* and the Stilbopteryginae.

From these various studies, it appears that Maulini and Dimarini are anomalous taxa, but that their affinities lie within Palparinae, perhaps as basal or stem lineages, a view embraced here. But in the light of the limited number of studies focusing on their phylogenetic affiliations, and the recent disagreements of placement when they have been included, more evidence will be needed to corroborate this conclusion.

The data from Aspöck et al. (2015) and Badano, Aspöck, Aspöck, and Haring (2017), however, seem rather clear: *Pseudimares* appears to belong within the Stilbopteryginae as a stem lineage. Its position, though, should be corroborated as well.

4.7 | Elevation of the AMC to superfamily Myrmeleontoidea, and a new higher-level classification of the same

The current study, which included the largest taxon sampling and analysis to date for the owlflies, and the recent one of Machado et al. (2018), which was nearly comprehensive for the antlions, both recognize within the AMC a well-supported, major clade that includes the Palparinae (130 spp.), the Stilbopteryginae (14 spp.: *Stilbopteryx*, *Aeropteryx*, *Pseudimares*) and the Ascalaphidae (435 spp. +), ca. 580 species in total. The composition of this clade represents a significant departure from most previous hypotheses for the AMC, in placing the Palparinae and Stilbopteryginae together with the Ascalaphidae, rather than grouping them with the Myrmeleontinae (ca. 1,800 species).

Conversely, although the Myrmeleontinae were not recovered as monophyletic in the present suite of analyses, nearly all recent studies with extensive taxon and character sampling (Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Machado et al., 2018) have found support for the monophyly of the subfamily. A strong case can be made that the Stilbopteryginae, redefined to include *Pseudimares*, are monophyletic as well. Further, the Palparinae are also likely monophyletic. And lastly, as demonstrated in the current study (see more discussion in the section below), and in numerous studies previous to this one, the Ascalaphidae are monophyletic.

What we have, then, within the AMC, are four most-closely related, but independent and monophyletic, lineages. It also appears that each lineage within this set will continue to be supported as essentially monophyletic, and more-or-less resilient to perturbations of both taxon and data sampling, even if different placements of the lineages relative to one another within the AMC are found. Any repeated deviations from this conclusion that are consistent in placement and well supported will warrant reassessment of the higher-level classification presented here (e.g., possibly Dimarini).

It is proposed now to raise the AMC to the rank of superfamily, with the epithet Myrmeleontoidea, and to include within it four families: Myrmeleontidae, Palparidae, Stilbopterygidae and Ascalaphidae (Figure 3). See Appendix S1 for a more complete nomenclatural listing and classification. The purpose for the elevation to superfamily will now be explained.

The decision by Machado et al. (2018) to redefine the entire containing group Palparinae + Stilbopteryginae + Ascalaphidae as the Ascalaphinae and to reduce in rank the former owlfly subfamilies to tribes was facilitated by (a) considerable undersampling of the owlflies relative to their true proportion within the AMC (as was the case for the traditional Myrmeleontidae in the current study) and (b) permanently dispensing with the existing tribal structure within the traditional owlflies. Such an approach, however, carries with it negative practical consequences. Chief among these is that more taxonomic and nomenclatural room, not less, is needed within the component lineages of Ascalaphidae (sensu this paper), for the restructuring of tribes and for the possible erection of additional intermediate ranks within the subfamilies.

Rather than a minor suite of tribes with a taxonomically simple internal structure, as implied by the classification of Machado et al. (2018), the Ascalaphidae actually constitute an evolutionarily complex, anatomically diverse, species-rich group, which upon more intensive analysis will yield extensive hierarchical layering. This will be particularly true for the larger subfamilies. Thus, more internal taxonomic ranks will be required, not fewer.

Therefore, although a revision of the existing tribal classification of owlflies is not proposed in this paper, it also is not altogether abandoned and, in fact, within the framework of the novel classification for the owlflies proposed below, it is now well positioned for resuscitation. More taxa and data will be needed to determine the limits of monophyly of the current tribes, but they will benefit highly from additional, finer-grained phylogenetic and taxonomic analyses.

4.8 | Nomenclatural implications of the new classification

Recent use of the term Myrmeleontoidea by Winterton et al. (2018) and Machado et al. (2018) is based on the placement in Winterton et al. (2018) of Ithonidae within the Myrmeleontiformia in a clade with Nymphidae and

Psychopsidae, and the authors' subsequent effort to apply nomenclatural consistency to the major groups recovered in their phylogeny of the entire Neuropterida. In the case of their Myrmeleontoidea, however, the name may be too inclusive. As the largest of the seven superfamilies they characterized, it comprises, by far, the most species, and therefore needs the most room internally for various taxonomic ranks (as evidenced by the unnecessary compression of the Ascalaphidae mentioned above). Engel et al. (2018) cleverly referred to this same group instead as the "Geoneuroptera," because of the apparently relictual affinity of the larvae for sand- and soil-based terrestrial habitats.

At this point, it is unclear if the new placement of Ithonidae will hold up. If it does, then it may prove useful to divide the superfamily of Winterton et al. (2018) into two. The name Myrmeleontoidea then could be applied to the Nemopteridae, Myrmeleontidae, Palparidae, Stilbopterygidae and Ascalaphidae, and a new name, perhaps Ithonoidea, could be provided for the Ithonidae, Psychopsidae and Nymphidae. If there was a need to continue to group these two large clades under one name (at the risk of upsetting the nomenclatural continuity proposed by Winterton et al., 2018), the subordinal terms Myrmeleontiformia or Geoneuroptera could be applied. The use of either name is entirely justifiable, as subordinal epithets are not governed by the Code, but the former has a longer and fuller history.

For now, it makes most sense to continue with usage of the name Myrmeleontiformia for the families Psychopsidae, Nymphidae, Nemopteridae, Myrmeleontidae, Palparidae, Stilbopterygidae and Ascalaphidae, as it is the umbrella term for these taxa in common currency among practicing Neuropterologists (Aspöck et al., 2001; Badano, Aspöck, Aspöck, & Haring, 2017; Badano, Aspöck, Aspöck, & Cerretti, 2017; Lan et al., 2016; MacLeod, 1964; Michel et al., 2017; Song et al., 2019; Wang et al., 2017; Winterton et al., 2010).

4.9 | The matter of common names

One last nomenclatural point will be made, regarding the use of names commonly applied within the AMC. A desire to continue using decades- or even centuries-old common names can tend to inadvertently compel pushback on acceptance of new classifications, no matter how reasonable. New terms are thus suggested here, if they will help with the transition to the new classification herein proposed. Thus "antlions *sensu latu*," or alternatively, "antlions, owlflies, and relatives" may be applied generally to the newly defined Myrmeleontoidea. "Antlions," "antlions *sensu stricto*," or "true antlions" may be applied to the newly refined Myrmeleontidae (=Myrmeleontinae sensu Stange, 2004). The Palparidae may become the "giant antlions," "map-winged antlions," "mapwings," or perhaps some other

reasonable and descriptive name. And the Stilbopterygidae may be termed the "owlfly-like antlions." The Ascalaphidae will retain the moniker "owlflies."

4.10 | Evolutionary implications of the new classification

Assuming the higher-level relationships that define the clade of owlflies and immediate extant ancestors continue to hold up under further scrutiny, they suggest a novel interpretation of morphological characters, states and changes thereof. Rather than an early split of the AMC into antlions on the one hand and owlflies on the other, as has so often been supposed, instead we now see a different sequence of evolution, from a primitive, antlion-like ancestor into two different, but also major, radiations. On the one side, this ancestor bloomed into an immense clade of antlions, the myrmeleontids. On the other side, this same ancestral population led to a palparid-like radiation, with its several peculiarities, and from thence to a stilbopterygid-like one, with its many primitively owlfly-like characteristics, and finally to *Albardia* and the Ascalaphidae, with their full-blown ascalaphid traits (see Figure 3).

4.11 | Monophyly of the Ascalaphidae

The single analysis that yielded a paraphyletic Ascalaphidae (Figure S12) included no morphological data, and it differed only in the placement of the Ululodini. This is an important clue that ululodines have a unique history relative to other owlflies (see additional discussion under "entire vs. divided eye," below), and that molecules alone, in many cases, are insufficient to resolve the monophyly of the family.

In the two analyses that did include morphology, the Ascalaphidae were recovered as monophyletic, with Ululodini placed as the basal lineage, agreeing with hypotheses discussed by Jones (2014) regarding both *Albardia* and the owlfly-like antlion genera *Aeropteryx* Riek and *Stilbopteryx* Newman, and their close relationship to *Ululodes* Smith. In the Bayesian analysis, pp support was 100%. These results provide objective support for the traditional characterization of owlflies as a monophyletic entity based on numerous morphological attributes not found in any member of the traditional Myrmeleontidae. These include the third-instar larvae (not necessarily the first or second) with the posterior margin of head bilobed, and with well-developed scolus-like processes, and in adults the antennae apically pyriform (and not merely "clubbed," as they are often inadequately characterized), the hypostigmatic cell reduced, and the pilula axillaris lost (see chars. C, D, 17, 21-, 25: "Morphological characters," Appendix S1; Table S2; Figure 3). Stilbopterygines are sometimes treated in phylogenetic studies as having the hypostigmatic cell reduced, but actually it is short in some species and long in others, suggesting the state is transitional in the

group. Numerous additional anatomical features that were not coded in the original analysis have since been observed, and should be considered in future analyses of the family, including the narrowed vertex, and the shortening of legs from anterior to posterior thoracic segments, among others. The Ascalaphidae are here taken to be an independent lineage, derived from the stilbopterygines, or a common recent ancestor with the stilbopterygines, as indicated in the Bayesian analysis (Figure S14). In particular, females of *Aeropteryx* are more similar to *Albardia* than are males, or *Stilbopteryx*, especially in wing shape and venation, and in future studies should be examined and characterized carefully. It is important to observe that molecular data for the subfamily Albardiinae were unavailable for the phylogenetic analyses here. Morphological evidence considered post-analysis, however, suggests strongly that it is an independent lineage that belongs within the Ascalaphidae at the base of the family (see New, 1982, Winterton et al., 2018, and Figure 3), proximal to, but not monophyletic with (contrary to Machado et al., 2018), the ululodines. Future analyses of the Ascalaphidae should include both morphological and molecular data for *Albardia*, in order to verify or refute this hypothesis.

4.12 | Ascalaphidae and the entire versus divided eye

At the subfamily level, traditional Ascalaphidae were broadly paraphyletic in all analyses—neither the traditional entire-eyed Haplogleniinae nor the traditional split-eyed Ascalaphinae were recovered as monophyletic (Figure S15; see also Figures S12–S14). The Haplogleniinae, which have long been inferred to represent the most primitive group beside *Albardia*, were placed as three well-supported, non-sister lineages. The largest two are endemic to the Americas and Africa/Madagascar (Figure S17, square and cross, respectively). For these two groups, their collective non-monophyly is not completely surprising, as no shared morphological characters that might be interpreted as synapomorphies to unite them (aside from entire eyes) have been discovered. The third traditionally haplogleniine lineage, represented in the analysis by the genus *Protidricerus*, is a small group that occurs in Asia.

The Ascalaphinae were divided into two main groups. The larger one had *Protidricerus* imbedded within it (suggesting the genus belongs within the Ascalaphinae—see further discussion in following paragraphs) and includes species from Africa, Asia, Australia and Europe. The smaller clade comprises the exclusively New World tribe Ululodini, placed in this analysis at the base of all owlflies. The Ululodini, in many regards, are highly derived. Their eyes are distinctly split, more so than in many other Ascalaphinae. Their bodies are small, compact and aerodynamic. *Ululodes* have distinct abdominal patterns, and several species of *Cordulecerus*

Rambur display wings with highly modified shapes and maculation. In addition, the antennae of *Ascalorphne* Banks are greatly elongated. But the Ululodini also retain several plesiomorphic features. In the hind wings, CuA is first sinuous and then continues down the length of the wing, a venational behaviour seen in the stilbopterygines and Albardiinae, but not in other owlflies, and discussed in Jones (2014); the MP fork also is not a distinctive feature, as it is in other owlflies. Many ululodines also have the wings unreduced basally, although this occurs in other owlflies as well. The key attribute, then, uniting them with other Ascalaphinae, is the split eye. If the external division of the eye represents instead a parallelism, rather than a synapomorphy, a basal placement of Ululodini seems reasonable, especially in the light of the plesiomorphic wing features just mentioned. However, such a consideration leads to the conclusion that the traditional subfamilial classification of the owlflies must be dismantled. The divided eye, which has served as a lynchpin of owlfly taxonomy for nearly a century and a half, must now be removed, re-evaluated and reinterpreted.

4.13 | Ascalaphidae and the pleurostoma

During preparation of the morphology matrix, it was discovered that the pleurostoma is present in the entire-eyed Asian genus *Protidricerus* (Figure 2v). This was quite surprising. Tjeder (1992:60), as a result of his comparative anatomical research on numerous genera of owlflies, reported that the pleurostoma, a small facial sclerite he had recently discovered, occurred in none of the Haplogleniinae and all of the Ascalaphinae (see Figure 2u) that he had examined. Such a statement suggested that the sclerite might represent a unifying feature for the Ascalaphinae. Tjeder noted one exception, however—his new African genus *Proctolyra* (not included in this analysis), which expresses the pleurostoma quite distinctly. Unlike many other ascalaphines, *Proctolyra* have the eyes only very weakly divided, and for this reason, Tjeder decided to place the genus in the Haplogleniinae (in its own tribe). But, along with the pleurostoma, it expresses at least one other distinctly ascalaphine characteristic—the males have exceptionally long and produced ectoprocts. No other haplogleniine expresses strongly produced ectoprocts. Now, it seems, *Proctolyra* are not the only owlflies with an entire (or nearly entire) eye *and* a pleurostoma. *Protidricerus* also have both. *Protidricerus* are medium-sized, dark-grey or blackish, entire-eyed owlflies rather broadly distributed in Central and East Asia. Fewer than a dozen species have been described, and some are only known from a few specimens. The group is underexplored, however, and its true diversity may be much greater.

Subsequently, during examinations of the genera of traditional Haplogleniinae, the pleurostoma was newly discovered to also be present in the central Asian entire-eyed

genera *Idricerus* McLachlan and *Nicerus* Navás, which were not included in the phylogenetic analyses herein. *Idricerus* and *Nicerus* express several other anatomical similarities to *Protidricerus* in wing shape and venation and appear to belong with it as a branch closely allied to Old World divided-eye owlflies. The pleurostoma was not observed in the central Asian haplogleniine *Ptyngidricerus* van der Weele, however, nor in any other genus of Haplogleniinae, nearly all of which genera have now been examined by the author.

The hint of a pleurostoma is also found in some ululodines (Figure 2w), but without well-developed marginal sulci, nor a corresponding lateral sulcus connecting it to the ocular margin, as is usually found in the Old World Ascalaphinae, particularly those with a broad paraocular band. The pleurostoma may be an anatomical by-product of paraocular band widening corresponding with bilobation of the eye, and merits more investigation across the ululodines and Old World Ascalaphinae.

4.14 | Tribal monophyly

In Figure S16, terminal taxa are colour-coded to indicate their tribal placement under traditional definitions. Within the Ascalaphidae, several tribes were recovered as monophyletic and well supported in each analysis. These included the Ululodini, Ululomyiini and Ascalaphini (all pp 100, Figure S14; see also bootstrap and decay values, Figures S12 and S13, respectively). The Proctarrelabrini also were recovered as monophyletic in both the ML and Bayesian analyses, as were the Suhpalacsini in the Bayesian analysis. The Australian component of the Suhpalacsini was well supported as monophyletic in all analyses (pp 100—see also next section). The New World Verticillecerini and Haplogleniini were each broadly paraphyletic with respect to one another, but together they formed a monophyletic clade (pp 100). The Allocormodini and Tmesibasini were placed as sister taxa within the Melambrotini (pp 100). The Hybrisini were paraphyletic in all analyses. *Deleproctophylla* Lefèbvre and *Libelloides*, which formerly were placed in Ascalaphini but which have had no formal tribal placement since Tjeder revised the type concept of *Ascalaphus* Fabricius (1972) and the tribe Ascalaphini (1992) (see Table 1), were not placed together in any analysis.

The phylogeny further yielded numerous well-supported sister species placements, and small cohesive generic groups, but these do not all correspond with current tribal definitions, nor, necessarily, with what was previously known about the morphological characteristics of the genera. For example, members of *Ascalohybris* Sziráki in the current tribe Hybrisini are medium large with distinctive black and yellow striped pterothoracic colour patterning, and are native to South-East Asia. *Deleproctophylla*, which was placed with them, are smaller, mottled brown, black and yellow, and

occur in western Asia and Europe. In general habitus the two genera look quite dissimilar. However, upon close inspection of the male terminalia, the ectoprocts of both are greatly produced and directed posterad (rather than ventrad, as in other genera with elongate ectoprocts), and the ninth sternite is very large. The fact that these genera were placed together presents clues to new groupings, and begs further investigation, and additional phylogenetic analyses with more morphological data.

4.15 | Correlation of monophyly to geography, and biogeographic considerations

Geographic distribution is mapped onto the Bayesian phylogeny in Figure S17. Perhaps not surprisingly, for many clades within the Ascalaphidae, geographic proximity was a better indicator of genetic affinity than the most recent generic and tribal-level classification. For example, the Ululodini, African/Malagasy Haplogleniinae, New World Haplogleniinae and Australian Suhpalacsini are each monophyletic and well supported, and are also geographically cohesive, forming distinctive geographic faunas. This suggests that geography can and should be carefully considered in reconstructing classifications, at least for these groups. It also hints strongly at pre-Gondwana-breakup origins, and subsequent geographic isolation as the continents split, for almost every major (higher-level) clade (see proposed new subfamilial classification, below).

4.16 | Proposed new subfamilial classification

Prior to this study, many authors (Riek, 1968, Henry, 1978a, Penny 1982, New, 1984, Tjeder, 1992) pointed out weaknesses with the traditional classification of Ascalaphidae and called for revisions to the family, particularly its tribes. Evidence presented here confirms that both traditional subfamilial and tribal definitions for the Ascalaphidae are inadequate to correctly place together many member tribes and genera into truly monophyletic groupings. In particular, the characteristics of the eye have been demonstrated as inadequate for diagnosis of subfamilies, as they are currently defined (entire vs. divided).

In the light of the non-monophyly of several of the traditional tribes analysed in this paper, and the pressing need for deeper taxon sampling and additional examination of physical characteristics of many genera prior to making any such determinations, a novel tribal classification will not be proposed here. The existing tribal organization can almost certainly be refurbished, though, and a tribal classification is warranted. But arriving at that point will require more fine-grained sampling of taxa, and analysis of both morphological and molecular data.

The results in this study do, however, provide important new clues to assist in making new subfamilial placements. Specifically, the Ululodini, New World Haplogleniinae and African/Malagasy Haplogleniinae have each been shown to be well-supported monophyletic lineages, and should be regarded as independent taxa in a revised classification. The remaining owlflies (the non-ululodine Ascalaphinae + *Protidricerus*) are likewise monophyletic and are united by the presence of a well-developed and complete pleurostoma bounded by sulci, sometimes with a lateral sulcus that connects to the ocular margin (see diagnoses under "*New classification of the Ascalaphidae*," in the Appendix S1). Still somewhat unclear is the sister group relationship among the New World Haplogleniinae, and African/Malagasy Haplogleniinae, and the full pleurostoma-bearing ascalaphines. In the Bayesian analysis, the New World Haplogleniinae were placed as sister to the full pleurostoma-bearing ascalaphines, with 100% support. One character state that unites the new Haplogleniinae and Ascalaphinae, pterothoracic pleural patterning (char. 13: "Morphological characters," Appendix S1; Table S2; Figure 3), was observed as a possible synapomorphy. Contrarily, however, in the ML and parsimony analyses, it was the African/Malagasy Haplogleniinae placed as sister to the ascalaphines, albeit with only weak support. A summary tree of subfamilial relationships and proposed synapomorphies based on the Bayesian phylogeny is presented in Figure 3.

In line with all of these observations, a revised subfamilial classification is proposed in the Appendix S1 text, under "*New classification of the Ascalaphidae*." A list of genera included in each subfamily is presented in Table S6.

4.17 | Concluding thoughts

Molecules alone (ML analysis) gave several trees, each with slightly different results at the mid- and finer branch levels, suggesting the genes selected do not by themselves provide satisfactorily robust phylogenetic outcomes.

When the molecular data were combined with merely a small set of morphological characters in the parsimony and Bayesian analyses, however, the resulting phylogenies suddenly became considerably more robust, and in many cases achieved great congruence with long-held traditional hypotheses based on morphology alone. In particular, the owlflies were recovered as monophyletic, with strong support given in the Bayesian analysis. In other cases, novel placements were obtained that revealed nuanced and long-hidden relationships and key synapomorphies (e.g., non-monophyly of the traditional subfamilies, and the importance of the pleurostoma). All of this strongly suggests that for the owlflies and immediate sister groups, a total-evidence phylogenetic approach is more effective than use of molecular data or morphology alone. Examination and inclusion of more characters, both molecular *and* morphological, then, are needed to help resolve the internal phylogeny of the owlflies in future analyses.

ORCID

Joshua R. Jones (iD) https://orcid.org/0000-0002-1554-329X

REFERENCES

Archaux, F., Jacquemin, G., Leconte, R., Luquet, G. C., Mora, F., Noël, F., … Ruffoni, A. (2011). Synthèse des observations récentes et anciennes de *Libelloides coccajus* (Denis & Schiffermüller) et *L. longicornis* (Linné) dans la moitié nord de la France (Neuroptera, Ascalaphidae). *Bulletin De La Société Entomologique De France*, *116*, 365–387.

Ardila Camacho, A., & Jones, J. R. (2012). A new species of *Haploglenius* Burmeister, 1839 (Neuroptera: Ascalaphidae) from the Colombian Orinoquía. *Zootaxa*, *3268*, 40–46. https://doi.org/10.11646/zootaxa.3268.1.4

Aspöck, U., Aspöck, H., & Haring, E. (2015). *Stilbopteryx* meets *Pseudimares* – a challenging hypothesis (Neuropterida: Neuroptera: Myrmeleontidae. Paper presented at 7th Dresden Meeting on Insect Phylogeny, September 25–27, 2015, Dresden, Germany.

Aspöck, U., & Aspöck, H. (2008). Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology*, *33*, 97–127. https://doi.org/10.1111/j.1365-3113.2007.00396.x

Aspöck, U., Plant, J. D., & Nemeschkal, H. L. (2001). Cladistic analysis of Neuroptera and their systematic position within Neuropterida (Insecta:

Holometabola: Neuropterida: Neuroptera). *Systematic Entomology*, *26*, 73–86. https://doi.org/10.1046/j.1365-3113.2001.00136.x

Badano, D., Aspöck, H., Aspöck, U., & Haring, E. (2017). Eyes in the dark … shedding light on the antlion phylogeny and the enigmatic genus *Pseudimares* Kimmins (Neuropterida: Neuroptera: Myrmeleontidae). *Arthropod Systematics & Phylogeny*, *75*, 535–554.

Badano, D., Aspöck, U., Aspöck, H., & Cerretti, P. (2017). Phylogeny of Myrmeleontiformia based on larval morphology (Neuropterida: Neuroptera). *Systematic Entomology*, *42*, 94–117. https://doi.org/10.1111/syen.12200

Badano, D., & Pantaleoni, R. A. (2014). The Larvae of European Ascalaphidae (Neuroptera). *Zootaxa*, *3796*, 287–319.

Banks, N. (1899). A classification of the north American Myrmelionidae. *The Canadian Entomologist*, *31*, 67–71.

Banks, N. (1909). New genera and species of tropical Myrmeleonidae. *Journal of the New York Entomological Society*, *17*, 1–4.

Banks, N. (1911). Notes on African Myrmeleonidae. *Annals of the Entomological Society of America*, *4*, 1–31.

Banks, N. (1927). Revision of the Nearctic Myrmeleonidae. *Bulletin of the Museum of Comparative Zoology*, *68*, 1–84.

Belušič, G., Pirih, P., & Stavenga, D. G. (2013). Acute and highly contrast sensitive superposition eye – the diurnal owlfly *Libelloides macaronius*. *Journal of Experimental Biology*, *216*, 2081–2088. https://doi.org/10.1242/jeb.084194

Beutel, R. G., Friedrich, F., & Aspöck, U. (2010). The larval head of Nevrorthidae and the phylogeny of Neuroptera (Insecta). *Zoological Journal of the Linnean Society*, *158*, 533–562. https://doi.org/10.1111/j.1096-3642.2009.00560.x

Borkent, A. (2018). The state of phylogenetic analysis: Narrow visions and simple answers—examples from the diptera (flies). *Zootaxa*, *4374*, 107–143. https://doi.org/10.11646/zootaxa.4374.1.7

Brauer, F. (1866). Zusätze und Berichtigungen zu Hagen's Hemerobidarum Synopsis Synonymica und Beschreibung einer neuen Nymphiden-gattung: *Myiodactylus osmyloides* aus Australien. *Verhandlungen Der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, *16*, 983–992.

Bremer, K. (1994). Branch support and tree stability. *Cladistics*, *10*, 295–304.

Burmeister, H. C. C. (1839). *Handbuch der Entomologie. Zweiter Band. Besondere Entomologie. Zweite Abtheilung. Kaukerfe. Gymnognatha. (Zweite Hälfte; vulgo Neuroptera)*. Berlin, Germany: Theodor Christian Friedrich Enslin.

Canard, M., Aspöck, H., & Mansell, M. W. (1992). Nomenclatural note: Myrmeleontidae vs Myrmeleonidae. In M. Canard, H. Aspöck, & M. W. Mansell (Eds). *Current Research in Neuropterology. Proceedings of the Fourth International Symposium on Neuropterology (24–27 June 1991, Bagnères-de-Luchon, Haute-Garonne, France)* (pp. 253–254). Toulouse, France: Privately Printed.

Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, *17*, 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Castresana, J. (2002). Gblocks Server. Version 0.91b. http://molevol.cmima.csic.es/castresana/Gblocks_server.html

Costa, A. (1855). Fauna del Regno di Napoli ossia enumerazione di tutti gli animali che abitano le diverse regioni di questo regno e le acque che le bagnano e descrizione de' nuovi o poco esattamente conosciuti con figure ricavate da originali viventi e dipinte al naturale. Nevrotteri. (3) Famiglia degli Ascalafidei. Napoli.

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*(8), 772. https://doi.org/10.1038/nmeth.2109

Engel, M. S., Winterton, S. L., & Breitkreuz, L. C. V. (2018). Phylogeny and evolution of Neuropterida: Where have wings of lace taken us? *Annual Review of Entomology*, *63*, 531–551. https://doi.org/10.1146/annurev-ento-020117-043127

Esben-Petersen, P. (1918). Results of Dr. E.Mjöberg's Swedish scientific expeditions to Australia 1910–1913. *Neuroptera and Mecoptera. Arkiv För Zoologi*, *11*, 1–37.

Esben-Petersen, P. (1919). Help-notes towards the determination and the classification of the European Myrmeleonidae. *Entomologiske Meddelelser*, *12*, 97–127.

Fabricius, J. C. (1775). Systema entomologiae, sistens insectorvm classes, ordines, genera, species, adiectis synonymis, locis, descriptionibvs, observationibvs. Flensbvrgi et Lipsiae.

Fetz, R. (1999). Untersuchungen zur Biologie and Habitatoptimierung von *Libelloides coccajus* (Neuroptera: Ascalaphidae) auf Muschelkalkhängen des Taubertales bei Rothenburg o.d.T. *Schriftenreihe Bayerisches Landesamt Für Umweltschutz*, *150*, 183–192.

Gao, X.-Y., Cai, Y.-Y., Yu, D.-N., Storey, K. B., & Zhang, J.-Y. (2018). Characteristics of the complete mitochondrial genome of *Suhpalacsa longialata* (Neuroptera, Ascalaphidae) and its phylogenetic implications. *PeerJ*, *6*, e5914. https://doi.org/10.7717/peerj.5914; https://doi.org/10.7287/peerj.preprints.27183v1

Gerstaecker, A. (1885). [not 1884]). Vier Decaden von Neuropteren aus der Familie Megaloptera Burm. *Mitteilungen Aus Dem Naturwissenschaftlichen Verein Für Neu-Vorpommern Und Rugen*, *16*, 1–49.

Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, *24*, 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x

Guindon, S., & Gascuel, O. (2003). A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood". *Systematic Biology*, *52*, 696–704.

Hacker, H. (1913). Some field notes on Queensland insects. *Memoirs of the Queensland Museum*, *2*, 96–100.

Hagen, H. A. (1866). Hemerobidarum Synopsis Synonymica. *Stettiner Entomologische Zeitung*, *27*, 369–462.

Hagen, H. A. (1888). Stray notes on Myrmeleonidae, Part 4. *Canadian Entomologist*, *20*, 34–38, 57–60, 72–74, 93–97.

Handlirsch, A. (1906–1908). *Die fossilen Insekten und die Phylogenie der rezenten Formen*. Leipzig, Germany: W. Engelmann.

Haring, E., & Aspöck, U. (2004). Phylogeny of the Neuropterida: A first molecular approach. *Systematic Entomology*, *29*, 415–430. https://doi.org/10.1111/j.0307-6970.2004.00263.x

Henry, C. S. (1976). Some aspects of the external morphology of larval owlflies (Neuroptera: Ascalaphidae), with particular reference to *Ululodes* and *Ascaloptynx*. *Psyche*, *83*, 1–31.

Henry, C. S. (1977). The behavior and life histories of two North American ascalaphids. *Annals of the Entomological Society of America*, *70*, 179–195.

Henry, C. S. (1978a). An evolutionary and geographical overview of repagula (abortive eggs) in the Ascalaphidae (Neuroptera). *Proceedings of the Entomological Society of Washington*, *80*, 75–86.

Henry, C. S. (1978b). The egg, repagulum, and larva of *Byas albistigma* (Neuroptera: Ascalaphidae): Morphology, behavior and phylogenetic significance. *Systematic Entomology*, *3*, 9–18.

Henry, C. S. (1978c). An unusual ascalaphid larvae (Neuroptera: Ascalaphidae) from southern Africa, with comments on larval evolution within the Myrmeleontoidea. *Psyche*, *85*, 265–274.

Jones, J. R. (2014). *Taxonomic revisions of six genera of entire-eyed owlflies (Ascalaphidae: Haplogleniinae), and first large-scale phylogeny of the owlflies*. Ph.D. Dissertation. College Station, TX: A&M University.

Jones, J. R., & Oswald, J. D. (2013). On the nomenclature of the genus name *Ululodes*. *Bulletin of Zoological Nomenclature*, *70*, 285–290.

Katoh, K., Kuma, K., Toh, H., & Miyata, T. (2005). MAFFT version 5: Improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research*, *33*, 511–518. https://doi.org/10.1093/nar/gki198

Kimmins, D. E. (1933). A new genus and species of the family Myrmeleonidae. *Annals and Magazine of Natural History*, *10*(11), 244–246.

Kimmins, D. E. (1940). The genus *Stilbopteryx* Newman (Neuroptera). *Annals and Magazine of Natural History*, *11*(5), 449–462.

Lan, X.-E., Chen, S., Li, F.-H., & You, P. (2016). The complete mitochondrial genome of *Bullanga florida* (Neuroptera: Myrmeleontidae). *Mitochondrial DNA Part B*, *1*(1), 632–634. https://doi.org/10.1080/23802359.2016.1214548

Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*(6), 1695–1701. https://doi.org/10.1093/molbev/mss020

Latreille, P. A. (1802). *Histoire naturelle, générale et particulière de Crustacés et des Insectes*. Vol. 3. Familles naturelles des genres. Paris, France: F. Dufart.

Lefèbvre, A. (1842). G. Ascalaphe. Ascalaphus. Fabricius. vel Azesia. A Lefèbvre. *Magasin De Zoologie, D'anatomie Comparée Et De Palaeontologie (Guérin-Méneville)*, *4* (text to Plate 92), 1–10.

Linnaeus, C. (1758). *Systema natura per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Tomus I. Holmiae: Salvii.

Linnaeus, C. (1767). *Systema natura per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio duodecima reformata. Tom. I. Pars II (pp. 533–1327). Holmiae: Laurentii Salvii.

Machado, R. J. P., Gillung, J. P., Winterton, S. L., Garzón-Orduña, I. J., Lemmon, A. R., Lemmon, E. M., & Oswald, J. D. (2018). Owlflies are derived antlions: Anchored phylogenomics supports a new phylogeny and classification of Myrmeleontidae (Neuroptera). *Systematic Entomology*, *44*, 418–450. https://doi.org/10.1111/syen.12334

MacLeod, E. G. (1964). *A comparative morphological study of the head capsule and cervix of larval Neuroptera (Insecta)*. Ph.D. dissertation. Cambridge, UK: Harvard University.

MacLeod, E. G. (1970). The Neuroptera of the Baltic Amber. I. Ascalaphidae, Nymphidae, and Psychopsidae. *Psyche*, *77*, 147–180. https://doi.org/10.1155/1970/45459

Maddison, W. P., & Maddison, D. R. (2011). Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org

Mansell, M. W. (1992). The systematic position of the Nemopteridae (Insecta: Neuroptera: Myrmeleontidae). In M. Canard, H. Aspöck, & M. W. Mansell (Eds). *Current Research in Neuropterology. Proceedings of the Fourth International Symposium on Neuropterology (24–27 June 1991, Bagnères-de-Luchon, Haute-Garonne, France)* (pp. 233–241). Toulouse, France: Privately Printed.

Markl, W. (1954). Vergleichend-morphologische Studien zur Systematik und Klassifikation der Myrmeleoniden (Insecta, Neuroptera). *Verhandlungen Der Naturforschende Gesellschaft in Basel*, *65*, 178–263 [Errata, 66, 140].

McLachlan, R. (1871). An attempt towards a systematic classification of the family Ascalaphidae. *Journal of the Linnean Society of London, Zoology*, *11*, 219–276. https://doi.org/10.1111/j.1096-3642.1871.tb02588.x

Meglič, A., Škorjanc, A., & Zupančič, G. (2007). The dynamics of light adaptation in *Ascalaphus* (*Libelloides macaronius*; Neuroptera). *Acta Biologica Slovenica*, *50*, 71–84.

Michel, B., Clamens, A.-L., Béthoux, O., Kergoat, G. J., & Condamine, F. L. (2017). A first higher-level time-calibrated phylogeny of antlions (Neuroptera: Myrmeleontidae). *Molecular Phylogenetics and Evolution*, *107*, 103–116. https://doi.org/10.1016/j.ympev.2016.10.014

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov 2010 (pp. 1–8). New Orleans, LO: Institute of Electrical and Electronics Engineers (IEEE).

Müller, M., Schlegel, J., & Krüsi, B. O. (2012). Der Libellen-Schmetterlingshaft *Libelloides coccajus* (Denis & Schiffermüller, 1775) (Neuropterida: Neuroptera: Ascalaphidae) im Kanton Aargau: Aktuelles Vorkommen und Empfehlungen zum Artenschutz. *Mitteilungen Der Schweizerischen Entomologischen Gesellschaft*, *85*, 177–199.

Navás, L. (1909). Notas neuropterológicas. X. Sobre Ascaláfidos. *Butlletí De La Institució Catalana D'història Natural*, *9*(1), 52–57.

Navás, L. (1912a). Ascaláfidos (Ins. Neur.) sudamericanos. *Brotéria (Zoológica)*, *10*, 203–233.

Navás, L. (1912b). Sinopsis de los Ascaláfidos (Ins. Neur.). *Arxius De L'institut De Ciències, Institut D'estudis Catalans, Secció De Ciències*, *1*, 45–143.

Navás, L. (1919). Algunos insectos Neurópteros de la República Argentina. Serie tercera [III]. *Revista De La Real Academia De Ciencias Exactas Fisicas Y Naturales De Madrid*, *17*, 287–305.

New, T. R. (1982). A reappraisal of the status of the Stilbopterygidae (Neuroptera: Myrmeleontoidea). *Journal of the Australian Entomological Society*, *21*, 71–75. https://doi.org/10.1111/j.1440-6055.1982.tb01768.x

New, T. R. (1984). Revision of the Australian Ascalaphidae. *Australian Journal of Zoology, Supplementary Series*, *100*, 1–86.

New, T. R. (1991). Neuroptera (lacewings). In I. D. Naumann, (Ed). *The Insects of Australia*. 2nd Edition. *1*, 525–542. Melbourne: Melbourne University Press.

Newman, E. (1838). Entomological Notes. *Entomological Magazine, London*, *5*, 168–181, 372–402, 483–500.

Newman, E. (1853). Proposed division of Neuroptera into two classes. *Zoologist*, *11* (Appendix), clxxxi–cciv.

Orfila, R. N. (1949). Notas criticas sobre Ascalaphidae (Neurop.). *Anales De La Sociedad Científica Argentina*, *148*, 187–194.

Oswald, J. D. (1993). Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). *Journal of the New York Entomological Society*, *101*, 143–299.

Penny, N. D. (1982). Review of the generic level classification of the New World Ascalaphidae (Neuroptera). *Acta Amazonica*, *11*, 391–406. https://doi.org/10.1590/1809-43921981112391

Rambaut, A. (2014). *FigTree v1.4.1*. [Computer software and manual]. Edinburgh, Scotland, UK: Ashworth Laboratories, Institute of Evolutionary Biology. Retreived from http://tree.bio.ed.ac.uk/software/figtree/

Rambaut, A., Drummond, A. J., & Suchard, M. (2013). *Tracer v1.6. MCMC trace analysis package*. [Computer software and manual]. Edinburgh, Scotland, UK: Ashworth Laboratories, Institute of Evolutionary Biology. Retrieved from http://tree.bio.ed.ac.uk/software/tracer/

Rambur, J. P. (1842). *Histoire Naturelle des Insectes, Névroptères. Librairie encyclopédique de Roret*. Paris, France: Fain Et Thunot.

Randolf, S., Zimmermann, D., & Aspöck, U. (2014). Head anatomy of adult *Nevrorthus apatelios* and basal splitting events in Neuroptera (Neuroptera: Nevrorthidae). *Arthropod Systematics & Phylogeny*, *72*, 111–136.

Rehn, A. C. (2003). Phylogenetic analysis of higher-level relationships of Odonata. *Systematic Entomology*, *28*, 181–239. https://doi.org/10.1046/j.1365-3113.2003.00210.x

Riek, E. F. (1968). A new genus and key to the species of Australian Stilbopterygidae (Neuroptera). *Journal of the Australian Entomological Society*, *7*, 105–108. https://doi.org/10.1111/j.1440-6055.1968.tb00713.x

Riek, E. F. (1976). The family Stilbopterygidae (Neuroptera) in Australia. *Journal of the Australian Entomological Society*, *15*, 297–302. https://doi.org/10.1111/j.1440-6055.1976.tb01710.x

Ronquist, F., & Huelsenbeck, J. P. (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Senčič, L. (2006). Intensity of wing pigmentation and identification of pigments in wings of owl-fly *Libelloides macaronius* (Scopoli, 1763) (Neuroptera: Ascalaphidae). *Acta Entomologica Slovenica*, *14*, 5–10.

Smith, J. B. (1900 [not 1899]). Insects of New Jersey: A list of species occurring in New Jersey, with notes on those of economic importance. *Annual Report of the New Jersey State Board of Agriculture*, *27*(Supplement), 1–755.

Song, N., Li, X.-X., Zhai, Q., Bozdoğan, H., & Yin, X.-M. (2019). The mitochondrial genomes of neuropteridan insects and implications for the phylogeny of neuroptera. *Genes*, *10*, 108 (1–18). https://doi.org/10.3390/genes10020108

Song, N., Lin, A., & Zhao, X. (2018). Insight into higher-level phylogeny of Neuropterida: Evidence from secondary structures of mitochondrial rRNA genes and mitogenomic data. *PLoS ONE*, *13*(1), e0191826. https://doi.org/10.1371/journal.pone.0191826

Stamatakis, A. (2014). RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*(9), 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stange, L. A. (1989). Review of the New World Dimarini with the description of a new genus from Peru (Neuroptera: Myrmeleontidae). *Florida Entomologist*, *72*, 450–461. https://doi.org/10.2307/3495183

Stange, L. A. (1994). Reclassification of the New World antlion genera formerly included in the tribe Brachynemurini (Neuroptera: Myrmeleontidae). *Insecta Mundi*, *8*, 67–119.

Stange, L. A. (2004). A systematic catalog, bibliography and classification of the world antlions (Insecta: Neuroptera: Myrmeleontidae). *Memoirs of the American Entomological Institute*, *74*, i–565.

Swofford, D. L. (2002). *PAUP* Phylogenetic Analysis Using Parsimony (*and other methods). Version 4.0b10*. Sunderland, MA: Sinauer Associates.

Tillyard, R. J. (1916). Studies in Australia Neuroptera. No. II. Descriptions of new genera and species of the families Osmylidae, Myrmeleontidae, and Ascalaphidae. *Proceedings of the Linnean Society of New South Wales*, *41*, 41–70.

Tillyard, R. J. (1926). *The insects of Australia and New Zealand*. Sydney, NSW: Angus and Robertson.

Tjeder, B. (1972). Two necessary alterations in long-established genus nomenclature in Ascalaphidae (Neuroptera). *Entomologica Scandinavica*, *3*, 153–155.

Tjeder, B. (1992). The Ascalaphidae of the Afrotropical Region (Neuroptera). 1. External morphology and bionomics of the family Ascalaphidae, and taxonomy of the subfamily Haplogleniinae including the tribes Proctolyrini n. tribe, Melambrotini n. tribe, Campylophlebini n. tribe, Tmesibasini n. tribe, Allocormodini n. tribe, and Ululomyiini n. tribe of Ascalaphidae. *Entomologica Scandinavica*, *41*(Supplement), 3–169.

van der Weele, H. W. (1903). Description of a new genus and species of holophthalmous Ascalaphidae. *Notes from the Leyden Museum*, *23*, 234–236.

van der Weele, H. W. (1909 [not 1908]). Ascalaphiden. *Collections Zoologiques Du Baron Edm. De Selys Longchamps, Catalogue Systématique Et Descriptif*, *8*, 1–326.

von der Dunk, K. (2012). Contribution on the biology of Libelloides coccajus (D&S) (Neuroptera, Ascalaphidae). *Galathea, Berichte Des Kreises Nürnberger Entomologen, E. V. 28*.

Wang, Y., Liu, X., Garzón-Orduña, I. J., Winterton, S. L., Yan, Y., Aspöck, U., … Yang, D. (2017). Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida. *Cladistics*, *33*, 617–636. https://doi.org/10.1111/cla.12186

Weissmair, W. (2004). Der Schmetterlingshaft Libelloides macaronius (Scopoli 1763) (Insecta: Neuroptera: Ascalaphidae) in den Ennstaler Voralpen (Oberösterreich): Verbreitung – Schutz – Management. In U. Aspöck (sci. ed.). *Entomologie und Parasitologie. Festschrift zum 65. Geburtstag von Horst Aspöck* (13, pp. 269–275) Denisia.

Winterton, S. L., Hardy, N. B., & Wiegmann, B. M. (2010). On wings of lace: Phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. *Systematic Entomology*, *35*, 349–378. https://doi.org/10.1111/j.1365-3113.2010.00521.x

Winterton, S. L., Lemmon, A. R., Gillung, J. P., Garzon, I. J., Badano, D., Bakkes, D. K., … Oswald, J. D. (2018). Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). *Systematic Entomology*, *43*, 330–354. https://doi.org/10.1111/syen.12278

Withycombe, C. L. (1925). Some aspects of the biology and morphology of the Neuroptera. With special reference to the immature stages and their possible phylogenetic significance. *Transactions of the Royal Entomological Society of London*, *72*, 303–411.

Zhang, L., & Yang, J. (2017). The mitochondrial genome of *Gatzara jezoensis* (Neuroptera: Myrmeleontidae) and phylogenetic analysis

of Neuroptera. *Biochemical Systematics and Ecology*, *71*, 230–235. https://doi.org/10.1016/j.bse.2017.02.009

SUPPORTING INFORMATION

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