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Eyes in the dark … Shedding light on the antlion phylogeny and the enigmatic genus *Pseudimares* Kimmins (Neuropterida: Neuroptera: Myrmeleontidae)

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Abstract

The systematic position of the antlion *Pseudimares* Kimmins has been disputed since description of the genus. *Pseudimares* is one of the most enigmatic and unusual members of Myrmeleontidae and probably of all Neuroptera. The taxon has been usually tied to the antlion subfamily Palparinae, although its phylogenetic affinities have never been thoroughly investigated and the monophyly of the subfamily as a whole has never been corroborated. We reconstruct for the first time the phylogenetic affinities of *Pseudimares* based on both morphological and molecular genetic data. The widely accepted subfamily level subdivision of antlions (Stilbopteryginae, Palparinae, Myrmeleontinae) is refuted in all our analyses, since Stilbopteryginae in the traditional sense are recovered as deeply nested within Myrmeleontidae forming a monophylum with Palparinae, while Myrmeleontinae are poorly supported by the parsimony analysis. In our morphology-based parsimony analysis, *Pseudimares* is the sister taxon of *Stilbopteryx* and *Aeropteryx*, which makes the traditional Palparinae paraphyletic. This result is further supported by our phylogenetic reconstruction based on molecular data, which found a clade including *Pseudimares* and *Stilbopteryx*, which is nested within the traditional Palparinae. The high genetic distances measured among the analysed taxa suggest that these groups quickly diverged in ancient times, although they remained morphologically homogeneous. In conformity with the results of the phylogenetic analyses, we propose a new classification scheme for antlions, one that merges *Stilbopteryx* and *Aeropteryx* into an expanded concept of the subfamily Palparinae.

Key words

Systematics, Myrmeleontiformia, Palparinae, Stilbopteryginae, Pseudimarini, antlion, West Palaearctic.

1. Introduction

In the torrid August nights of the Moroccan and Iranian deserts, one may catch a passing glimpse of spectral bluish eyes reflecting light in the darkness. It is not an illusion, but an encounter with the most spectacular antlion, *Pseudimares* Kimmins, 1933. A small, poorly known genus, it comprises two species: *Pseudimares iris* Kimmins, 1933, from Iran, and the recently described *Pseudimares aphrodite* H. Aspöck & U. Aspöck, 2009, from the Western Foothills of the Haut-Atlas in Morocco (H. Aspöck & U. Aspöck 2009). Few species of lacewings have attained an almost mythical status among specialists, such as these antlions, due to their impressive habitus, their rarity and

Fig. 1. *Pseudimares aphrodite* H. Aspöck & U. Aspöck, 2009, female: habitus. (Scale bar: 10 mm)

their mysterious affinities. Unique among extant Neuropterida, *Pseudimares* is indeed characterized by huge, bewitching eye-spots at the apex of fore- and hindwings (Fig. 1; Kimmins 1933; Stange 2004; H. Aspöck & U. Aspöck 2009). Among Neuroptera, true wing eye-spots are only documented in the Mesozoic fossil family Kalligrammatidae (Handlirsch 1906–1908; Handlirsch & Beier 1936; Grimaldi & Engel 2005; Yang et al. 2014; Labandeira et al. 2016). The similarity in wing pattern between *Pseudimares* and kalligrammatids hints that these Mesozoic lacewings might have evolved wing eye-spots under similar predatory pressures, suggesting that these ancient neuropterans were also nocturnal, thus they were not exact ecologically convergent to butterflies. This unusual wing pattern is so remarkable and spectacular that it has even inspired artists (Monserrat 2010; Nicoli Aldini & Pantaleoni 2012). As noted by Stange (2004), aside from the wing pattern, this genus is no less impressive due to its unusual combination of characters, in particular its huge size, unusually bulging eyes and extremely long legs. *Pseudimares* is exceedingly rare and poorly known and other than the type specimens of both species, few additional specimens of *P. aphrodite* have been later collected in August 2009 and 2013 by H. and U. Aspöck, R. Bläsius, A. Steiner, and A. Werno at the type locality or photographed by a herpetologist (Pantaleoni et al. 2012). The extraordinary rarity of this antlion so far has hampered the study of its relationship among myrmeleontids.

In the original description of the genus, Kimmins (1933) noted a strong similarity in wing shape and venation between *Pseudimares* and two geographically distant genera of Myrmeleontidae: the South American *Dimares* Hagen and the South African endemic *Palparidius* Peringuey. As the name itself implies, Kimmins suggested a close affinity of *Pseudimares* with *Dimares* that was based not only on shared venational characters, but also supposedly the shape of male genitalia. Afterwards, few authors have investigated the relationships of this taxon. Markl (1954), in a fundamental work on the tribal classification of Myrmeleontidae, included *Pseudimares* in a dedicated, monotypic tribe, Pseudimarini, and proposed a tribal classification: Palparidiini, which only includes *Palparidius*, and Palparini, which in turn comprises a vast array of genera widely distributed in the Afrotropical, Palaearctic and Oriental regions. Hölzel (1972) instead directly placed *Pseudimares* within the latter group, which he considered as the subfamily Palparinae. Finally, Stange & Miller (1990) and Stange (2004) re-organized all the previous classification attempts, retaining a subfamily Palparinae which included Palparini and three much smaller tribes: Palparidiini, Dimarini, comprising the South American genera *Dimares* and *Millerleon* Stange and the Old World genus *Echthromyrmex* McLachlan, and finally Pseudimarini, which included only *Pseudimares*. In a preliminary molecular analysis aimed to unveil the relationships of *Pseudimares aphrodite*, U. Aspöck et al. (2015) found a unexpected relationship between *Pseudimares* and *Stilbopteryx*, raising interesting questions not only on the affinities of this unusual genus but also on the relationships among antlion tribes.

In the present study, we explore the affinities of *Pseudimares* through phylogenetic analyses based on both morphological characters and DNA sequences, intending to clarify the phylogentic position of this spectacular insect within antlions.

2. Systematization of Myrmeleontidae

The phylogeny and the reciprocal affinities within Myrmeleontidae remain a poorly investigated topic, especially by means of modern quantitative analyses with only two most recent exceptions (Badano et al. 2017a; Michel et al. 2017). Indeed, the most important works

on the internal relationships of this diverse family of Neuroptera are qualitative studies subdividing the family into several subfamilies or tribes mostly based on comparison of adult characters, especially wing venation (Mansell 1999). Since the first subdivision of Myrmeleontidae by Banks (1899), almost every author working on the group proposed a different classification scheme, disagreeing in the number, delimitation and rank of suprageneric taxa, therefore a broadly accepted consensus among specialists could hardly be reached (see Mansell 1999; New 2003; Michel et al. 2017 for thorough reviews). Markl (1954) compared the morphology (mainly based on wing-venation) of most genera of Myrmeleontidae known at the time and subdivided the family in several tribes, not considering subfamily-level categories. Although useful to delimit groups for identification purposes, the classification of Markl (1954) is too artificial and was only partly followed by later authors (Mansell 1999). Afterwards, the inclusion of larval characters by Stange & Miller (1990) and Stange (1994) represented a great step forward in our understanding of the relationships within Myrmeleontidae, as their larvae often present unique morphological characters useful to delimit groupings. The catalogue of Stange (2004), which serves as the basis of the present treatment, proposed a convincing classification scheme based on both adult and larval characters and it was quickly accepted by most specialists, with few exceptions (Krivokhatsky 2011; Kuznetsova et al. 2015). Stange (1992, 2004) subdivided the family in 3 subfamilies and 16 tribes: Stilbopteryginae (1 tribe), Palparinae (4 tribes) and Myrmeleontinae (11 tribes). While Palparinae were recognized since the first classification attempts of the family due to their unmistakable habitus (New 2003), the affinities of the Australian endemic subfamily Stilbopteryginae have been one of the most debated topics of Neuroptera systematics (New 1982a). This small but remarkable subfamily only includes the genera *Stilbopteryx* Newman and *Aeropteryx* Riek, which show a strong morphological and behavioural parallelism with Ascalaphidae (New 1982a). Indeed, *Stilbopteryx* was originally considered a member of Ascalaphidae due to a superficial resemblance with the unusual South American ascalaphid *Albardia* Weele (Lefebvre 1842; van der Weele 1909; Navás 1912; Tillyard 1916). However, already in the second half of the 19th century, Hagen (1866) recognized the myrmeleontid affinities of *Stilbopteryx*, a solution followed by McLachlan (1873). Kimmins (1940) again considered Stilbopteryginae as belonging to Myrmeleontidae and suggested ties with subfamily Palparinae. Nevertheless, most authors preferred to consider Stilbopterygidae a dedicated family to accommodate these Australian oddities (Tillyard 1926; Riek 1968, 1976; H. Aspöck et al. 1980). Finally, New (1982a) comparing the morphology of male and female genitalia, convincingly debated the status of Stilbopterygidae stating that *Stilbopteryx* and *Aeropteryx* were indeed myrmeleontids, but *Albardia* was actually just a peculiar ascalaphid. The myrmeleontid affinities of *Stilbopteryx* were also supported by larval morphology, being characterized by the presence of the non-homoplasious apomorphies of this family (New 1982b; Stange 1994; Badano et al. 2017a). Few studies have investigated the phylogeny of Myrmeleontidae by means of quantitative methods and none of them included *Pseudimares* in the analyses. In the first cladistic study of the family, Stange (1994) did not support the monophyly of Palparinae, which were reconstructed as paraphyletic, with Palparini and Palparidiini as sister to all other remaining antlions, including Stilbopteryginae and Dimarini. Badano et al. (2017a) investigated the phylogeny of Myrmeleontiformia exclusively by means of larval morphological characters through parsimony and Bayesian analyses. In both analyses, *Stilbopteryx* was found to be the sister group to *Palpares* + Myrmeleontinae. In the first large molecular phylogeny of the whole family, Michel et al. (2017) similarly retrieved *Stilbopteryx* as sister group to all remaining antlions, suggesting that this position is consistent with a family-level status. Their results favoured the delimitation of a further monophyletic subfamily, Acanthaclisinae – supporting a previous concept of New (1985b) – and in turn the subfamily was retrieved as sister to Palparinae + Myrmeleontinae (Michel et al. 2017).

3. Materials and methods

3.1. Morphological examination and pictorial documentation

All specimens examined (two males, five females) have been taken on the type locality (Morocco, Haut Atlas, coastal foothills, ca 20 km N Agadir, 230 m) in August 2009 and 2013. Specimens were examined with a Leica® MZ 9.5 stereomicroscopes. Genitalia were macerated in 10% KOH (potassium hydroxide) at room temperature and later rinsed in acetic acid and water. To enhance the contrast of minute morphological features, genitalia were stained with chlorazol black prior to examination. Finally, they were preserved in glycerol. Specimens and morphological structures were then photographed with a Canon® EOS 600D digital camera equipped with Canon® lens MP-E 65 mm. The resulting images were processed and stacked with the software Zerene® Stacker. Terminology mainly follows Stange (1970) for body and wing morphology and U. Aspöck & H. Aspöck (2008) for genitalia, while Stange (2004) served as the basis for the taxonomic treatment of Myrmeleontidae.

3.2. Cladistic analysis

To reconstruct the phylogenetic affinities of *Pseudimares* we selected a sample of 29 representatives of Myrmeleontiformia. *Nymphes myrmeleonoides* (Leach) (Nym-

Table 1. Specimens analysed genetically in the present study and sequences downloaded from GenBank. GenBank = accession numbers for *cox1*, *cox3* and *28S*; gb = sequences derived from GenBank.

Family	Species	Sampling locality	Labcode	GenBank		
Subfamily				*cox1*	*cox3*	*28S*
Myrmeleontidae						
Palparinae	*Pseudimares aphrodite*	Morocco, Haut Atlas, Costal Hills, Paradise Valley	Pseaph-1	MG334605	MG334601	MG334619
Palparinae	*Palpares angustus*	Morocco, Tamaloukt	Palang-1	MG334606	MG334602	MG334620
Palparinae	*Palpares libelluloides*	Italy, Liguria	Pallib-1	MG334607	MG334603	MG334621
Palparinae	*Millerleon bellulus*	Peru, Puerto Morin	Milbel-1	MG334608	MG334604	MG334622
Myrmeleontinae	*Euroleon nostras*	Austria, Dürnstein	Eurnos-1	MG334609	MG334600	MG334618
Myrmeleontinae	*Distoleon tetragrammicus*	Austria, Eichkogel	Distet-1	MG334611	MG334598	MG334616
Myrmeleontinae	*Dendroleon pantherinus*	Austria, Brand-Laaben	Denpan-1	MG334610	MG334597	MG334615
Myrmeleontinae	*Macronemurus appendiculatus*	Italy, Liguria	Macapp-1	MG334612	MG334599	MG334617
Stilbopteryginae	*Stilbopteryx costalis*	—	gb	EU839773.1		
Ascalaphidae	*Libelloides macaronius*	Austria, Eichkogel	Libmac-1	MG334613	MG334596	MG334614
	Ascalohybris subjacens	—	gb	KC758703.1	KC758703.1	
Nymphidae	*Nymphes myrmeleonoides*	—	gb	NC_021428.1	NC_021428.1	
Nemopteridae	*Chasmoptera hutti*	—	gb	KT425069.1	KT425069.1	
Ithonidae	*Rapisma zayuanum*	—	gb	NC_023363.1	NC_023363.1	

phidae) was chosen as outgroup, while other closely related families of Myrmeleontiformia, i.e. Nemopteridae and Ascalaphidae, were included to provide adequate comparisons and to test the evolution of some morphological traits. We sampled 25 species of Myrmeleontidae representing all antlion subfamilies and the main tribes. The data matrix including 48 characters and 121 states was assembled in MESQUITE version 3.03 (MADDISON & MADDISON 2015) (see Supplement Table S4). Inapplicable and unknown states were coded as '–' and '?', respectively. Cladistic parsimony analyses were conducted with TNT version 1.5 (GOLOBOFF & CATALANO 2016). The analyses were run under equal weighs, selecting the 'traditional search' option, enforcing the following parameters: general RAM of 1000 Mbytes, memory set to hold 1,000,000 trees, setting 1000 replicates with tree bisection-reconnection (TBR) branch swapping and saving 1000 trees per replicate. Multistate characters were treated as unordered and zero-length branches were collapsed. Unambiguous character state changes were mapped on the most parsimonious tree using WINCLADA version 1.00.08 (NIXON 2002). Bremer support values were calculated in TNT from 10,000 trees up to 10 steps longer than the shortest trees obtained from a 'traditional search', using the 'trees from RAM' setting. Consistency and retention indices were computed in MESQUITE version 3.03 (MADDISON & MADDISON 2015).

3.3. DNA analysis

Our set of genetically analysed samples (nine specimens) represents eight genera of the family Myrmeleontidae (Table 1). Tissue samples were taken from the thorax (wing muscles) from alcohol-preserved specimens with sterile forceps. Vouchers are stored at the Entomological Department of the Natural History Museum Vienna (NHMW). Remaining DNA is stored in the DNA and Tissue Collection of the Central Research Laboratories at the NHMW. The specimens analysed are listed in Table 1 together with sequences derived from GenBank representing five additional genera of the families Ascalaphidae, Nymphidae, Nemopteridae, as well as Ithonidae (Table 1) which were used to root the trees.

3.3.1. Marker sequences and laboratory procedures

Two mitochondrial marker sequences were amplified using primers listed in Table 2: (1) A partial sequence of the *cytochrome c oxidase subunit 3* gene (*cox3*) which has been also used in previous studies on Neuropterida as well as Raphidioptera (HARING & ASPÖCK 2004; HARING et al. 2011) and (2) the complete sequence of the *cytochrome c oxidase subunit 1* gene (*cox1*) plus partial sequences of the adjacent tRNA genes. Additionally, a partial sequence of the nuclear *28S rRNA* gene (*28S*) was analysed. The amplicon lengths of *cox1* sequences ranged from 1604–1610 bp (length variation due to indels in the flanking tRNA genes). The final alignment comprised the complete *cox1* gene and had a length of 1534 positions. The amplicon length of the *cox3* sequence was 712 bp (final alignment 667 positions). The amplicon length of the 28S sequence ranged from 1230–1316 bp (final alignment 1356 positions).

DNA extraction was performed using the DNeasy-Blood and tissue Kit (QUIAGEN) according to the manufacturer's instructions. The final volume of elution buffer was 40 µl. DNA solutions were stored in aliquots to avoid too frequent thawing. Control extractions with pure extraction buffer (without tissue) were prepared PCR was carried out with an Eppendorf Thermocycler. PCR reactions had a volume of 25 µl, containing 1 unit Taq Polymerase (5 units/reaction; QIAGEN, Hilden,

Table 2. Primers used. a: Haring & Aspöck (2004); b: Haring et al. (2011).

Gene	Primer	Sequence (5′–3′)	Reference
cox3 external primers			
	Arth-cox3-fwd	5′-TAGTTGATTATAGACCATGACC-3′	a
	Raph-cox3-fwd	5′-TAGTCCATGACCHTTAACAGG-3′	a
	Arth- cox3-rev	5′-ACATCAACAAAATGTCAATATCA-3′	a
	Cox3-Myr-fwd	5′-TAGTTGATTATAGCCCTTGACC-3′	present study
cox1 external primers			
	Tyr-myr-1+	5′-CCCATAAATAAATTTACAGTTTA-3′	present study
	Leu-Myr-1–	5′-GCACTATTCTGCCATATTAG-3′	present study
28S external primers			
	Raph-28S1+	5′-CAGGGGTAAACCTGAGAAA-3′	b
	Raph-28S-4–	5′-AGCGCCAGTTCTGCTTACC-3′	b
28S internal primers			
	Raph28S-3+	5′-AGCTTTGGGTACTTTCAGGA-3′	b
	Raph28SF3_Lib	5′-TTATACTATATTACTGTCAGT-3′	present study
	Raph28S5F_Lib	5′-TCTTGTAGGACGTCGCGACCCGT-3′	present study
	Raph28S-2–	5′-ACATGCTAGACTCCTTGGT-3′	b
	Raph28S6R_Lib	5′-TATTTATACCGTCAAACAATTG-3′	present study
	Raph28SR4_Lib	5′-TCATTTTGCCTTTGGGTTTCAT-3′	present study

Germany), 1 µM of each primer, and 0.2 mM of each dNTP, 1.5 mM $MgCl_2$, 5 µl Q-Solution, 2.5 µl 10 × PCR buffer and 1 µl of template DNA. The following PCR protocols were used: *cox3*: initial denaturation 94°C (3 min); 35 cycles: 94°C (60 sec) / 50°C (30 sec) / 72°C (60 sec); final extension at 72°C (10 min). *cox1*: initial denaturation 94°C (3 min); 35 cycles: 94°C (60 sec) / 50°C (30 sec) / 72°C (60 sec); final extension at 72°C (10 min). *28S*: initial denaturation 94°C (3 min); 35 cycles: 94°C (60 sec) / 55°C (30 sec) / 72°C (60 sec); final extension at 72°C (10 min); Negative PCR controls were carried out to screen for contaminated reagents: (1) control extractions without tissue were carried out which were used in a subsequent PCR (i.e. instead of template DNA) to test extraction ingredients; (2) PCR reactions with distilled water instead of template were performed to text PCR ingredients. PCR products were purified with the QIAquick PCR Purification Kit (QIAGEN, Hilden, Germany) prior to sequencing. Sequencing (both directions) was performed at Microsynth (Vienna, Austria) using the PCR primes as well as various internal primers (Table 2). Sequences obtained in the present study are deposited in GenBank under the accession numbers listed in Table 1.

3.3.2. Phylogenetic analyses

Raw sequences were manually aligned in BioEdit v.7.1.3 (Hall 1999) and checked for errors. The alignment was straightforward for the two mitochondrial marker sequences (*cox1*, *cox3*) since there were no insertions or deletions. The alignment of *28S* sequences was done in ClustalX (Larkin & Blackshields 2007) using default parameters and corrected manually. Bayesian Inference (BI) was used for calculating phylogenetic trees. The best fitting substitution model was determined for each of the three genes, as well as for the three codon positions in the protein coding genes separately using JModelTest v.2.1.10 (Darriba et al. 2012) and chosen based on the corrected Akaike information criterion (AICc). Bayesian inference (BI) analyses were calculated using MrBayes v.3.2.1 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Phylogenetic trees were calculated first for each marker sequence separately and subsequently with the concatenated alignment of all three sequences. For the mitochondrial genes, several outgroup species were included, from which sequences are available in GenBank. Since no *28S* sequences were available for those taxa, we used solely *Libelloides macaronius*, a representative of Ascalaphidae, as outgroup for the *28S* trees as well as for the concatenated tree. BI analyses were run for 6×10^6 generations (two runs each with four chains, one of which was heated), sampling every 100th tree. The first 25% of trees were discarded as burnin and a 50% majority rule consensus tree was calculated from the remaining trees.

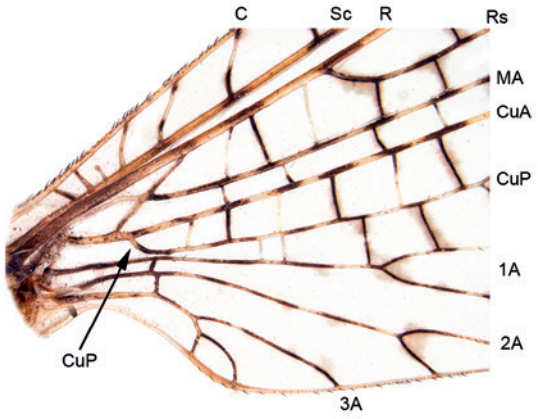
3.4. Character description

1. Compound eye, size relative to frons width: **(0)** eye radius smaller or subequal to frons width; **(1)** eye radius larger than frons width. — In Ascalaphidae and in a few Myrmeleontidae, such as Stilbopteryginae (*sensu* Stange 2004) (*Stilbopteryx* and *Aeropteryx*) and in the genus *Pseudimares*, the eyes are huge, covering most of the lateral sides of the head (Riek 1968: pl. 1; Tjeder 1992: figs. 3–8) (Fig. 2).

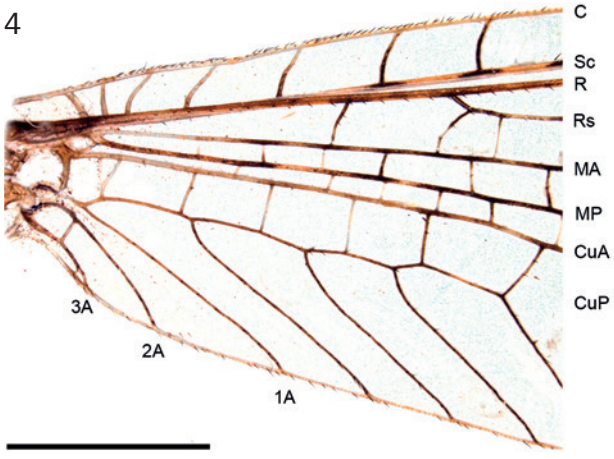
2. Antenna, shape: **(0)** filiform; **(1)** clavate; **(2)** apically clubbed. — The antenna is primitively filiform in Neuroptera, as observed in *Nymphes* and *Chasmoptera*. In most Myrmeleontidae (including all the investigated species) the antenna is clavate, gradually and progressively widening toward the apex (Stange

2

3



4



Figs. 2–4. *Pseudimares aphrodite* H. Aspöck & U. Aspöck, 2009, female: details of head and wings. **2**: Detail of the head, ventral view. **3**: Base of fore wing. **4**: Base of hindwing. — ***Abbreviations***: **C** – Costa, **Sc** – Subcosta, **R** – Radius, **Rs** – Radius sector, **MA** – Media anterior, **MP** – Media posterior, **CuA** – Cubitus anterior, **CuP** – Cubitus posterior, **A** – Anal vein. (Scale bar: 0.5 mm)

1994: fig. 36) (Fig. 1). In most Ascalaphidae the antenna is narrow and abruptly swollen near the apex, forming a distinct apical knob (resembling the antenna of butterflies) (TJEDER 1992: figs. 19–24). A few taxa of both families diverge from the common condition having the apex of antenna not prominently swollen (e.g. TJEDER 1992: fig. 19).

3. Antenna, length relative to forewing length: **(0)** short, less than half of forewing length; **(1)** long, more than half of forewing length. — With a single exception (*Albardia*), all Ascalaphidae have very long antennae (TJEDER 1992: p. 59).
4. Labial palpus, length relative to head length (from occiput to frons): **(0)** shorter than head; **(1)** much longer than head. — In some Myrmeleontidae, such as *Echthromyrmex*, *Dimares*, *Millerleon*, *Palpares* (examined species), *Annulares* and *Goniocercus*, the labial palp is extremely elongate, much longer than the head. For discussion about this character in Palparini, see MANSELL (1992: figs. 10–11) and BADANO et al. (2017b: 44).
5. Apical labial palpomere, shape: **(0)** subcylindrical; **(1)** spindle-shaped; **(2)** clavate. In Nemopteridae (*Chasmoptera*) the apical palpomere is subcylindrical, not medially swollen (TJEDER 1967: figs. 1901, 1902). — In the analysed genera of Nymphidae, Ascalaphidae and most Myrmeleontidae, the apical labial palpomere is spindle-shaped, being medially swollen and restricting at the apex. In some taxa of Myrmeleontidae, the apical palpomere is clavate, gradually swollen apically and without an apical narrowing. Among the included taxa, the latter condition is present in *Acanthaclisis*, *Echthromyrmex*, *Dimares*, *Millerleon*, *Palpares*, *Annulares* and *Goniocercus* (INSOM & CARFÌ 1988: figs. 86–95; MANSELL 1992: figs. 10–13). Some species of *Palpares* that were not included have spindle-shaped apical palpomeres (INSOM & CARFÌ 1988: figs. 83–85; MANSELL 1992: figs. 6, 7, 9).
6. Apical labial palpomere, sensory area: **(0)** absent; **(1)** present. — Nemopteridae lack a sensory pit on the apical palpomere (TJEDER 1967: figs. 1901, 1902; STANGE 1994: 68).
7. Apical labial palpomere, sensory area (if present), shape: **(0)** rounded; **(1)** slit-like. — The sensory pit on apical palpomere is rounded in shape in Nymphidae, Ascalaphidae and most genera of Myrmeleontidae. In Acanthaclisini, such as *Acanthaclisis*, and in several Palparinae, such as *Dimares*, *Millerleon*, *Palparidius*, *Echthromyrmex*, *Goniocercus*, *Annulares* and some species of *Palpares* (including examined taxa) the sensory area is elongate and slit like. See also INSOM & CARFÌ (1988: figs. 83–85), MANSELL (1992: figs. 10–13), STANGE (1994: 68) and BADANO et al. (2017b: 44).
8. Pronotum length/width ratio, taken at midline: **(0)** longer than wide; **(1)** as long as wide; **(2)** wider than long. — In Nymphidae, Nemopteridae and some genera of Myrmeleontidae (*Dendroleon*, *Pseudimares*), the pronotum is noticeably longer than wide at midline (Fig. 1). In most myrmeleontids, the pronotum is squarish, as long as wide. In Ascalaphidae and the myrmeleontid subfamilies Stilbopteryginae and Palparinae (with the exception of *Pseudimares*), the

pronotum is noticeably short, much wider than long (see also Riek 1968: pl. 1; Tjeder 1992: figs. 25, 26; Mansell 1992: 245; Stange 1994: 68).

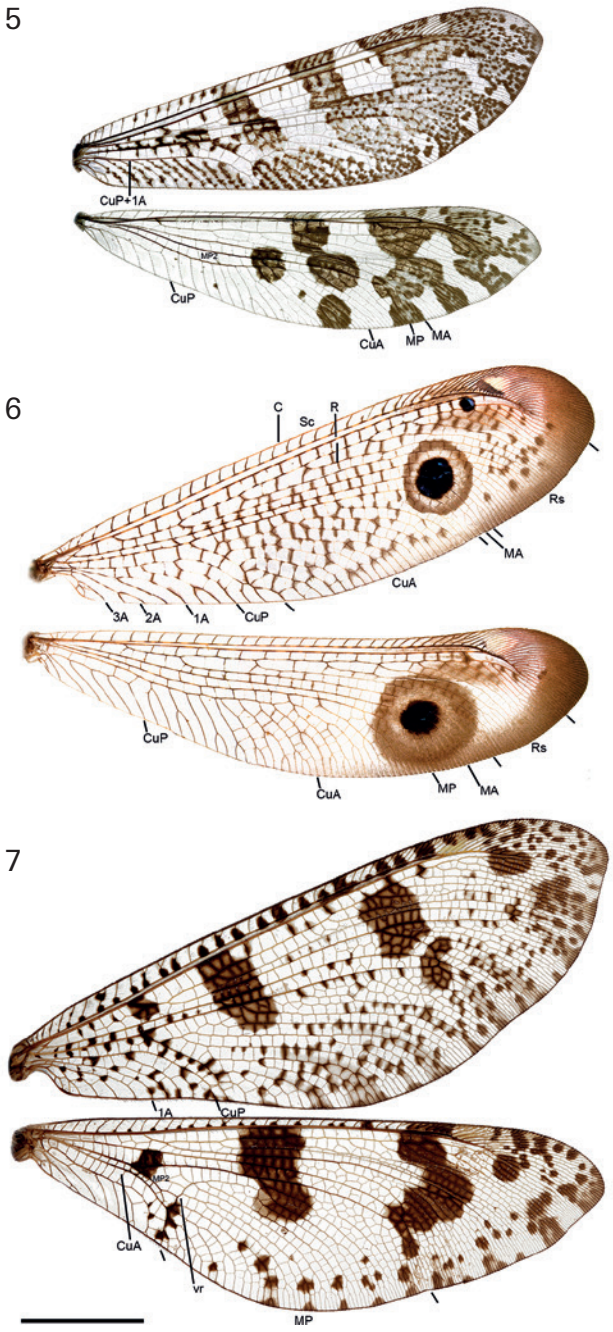
9. Prothoracic femur, hair-like sensillum (hair-like seta, *sensu* Stange 1994): **(0)** absent; **(1)** present. — The presence of a hair-like sensillum on prothoracic femur is characteristic of Myrmeleontinae. See also Stange (1994: 68) and Badano et al. (2017b: 45).

10. Wing colour pattern: **(0)** mostly hyaline; **(1)** costal area darkened; **(2)** markings in delimited wing areas; **(3)** eye-spots; **(4)** large markings covering most of the membrane; **(5)** wing membrane almost completely pigmented. — The wing pattern is variable across Myrmeleontiformia. Most Nymphidae and Nemopteridae, as well as several Myrmeleontidae (e.g. included species of *Aeropteryx*, *Myrmeleon*, *Myrmecaelurus*, *Macronemurus*) are characterized by a mostly hyaline wing membrane (H. Aspöck et al. 1980: figs. 215, 225, 229). Several Ascalaphidae (*Ascalohybris*) and the ascalaphid-like antlion *Stilbopteryx* have a strongly pigmented costal area (Tillyard 1926: pl. 24). In many Myrmeleontidae, wing membrane is marked in delimited areas (e.g. gradates, radial and cubital areas), such as in the examined species of *Dendroleon*, *Distoleon*, *Scotoleon*, *Euroleon*, *Acanthaclisis*, *Cueta* and *Solter* (H. Aspöck et al. 1980: figs. 212, 213, 217, 218, 228, 241). Eye spots are unique to *Pseudimares* (Figs. 1, 6). Most Palparinae are instead characterized by a membrane mostly shaded by large markings (H. Aspöck et al. 1980: fig. 211) (Figs. 5, 7). In a few taxa, such as the butterfly-like *Libelloides*, the wing membrane is almost completely pigmented (H. Aspöck et al. 1980: aqu. 17, 18). The myrmeleontid *Dimares elegans* is unusual due to its striking sexual dimorphism: the male has hyaline wings while in the female, the wings are heavily marked with large stripes marks and shades (Stange 1994).

11. Forewing, origin of Rs from R: **(0)** at 1/10 of wing length; **(1)** at 1/4 of wing length; **(2)** at 1/3 of wing length. — Forewing vein Rs originates near the wing base in Nymphidae (Shi et al. 2015). In Nemopteridae, Ascalaphidae and Myrmeleontidae, the origin of Rs is distal to wing base at 1/4 or 1/3 of wing length. See also Badano et al. (2017b: 45).

12. Forewing, origin of CuP relative to basal crossvein (= vein H in Markl 1954: fig. 36): **(0)** at or proximal of basal crossvein; **(1)** distal of basal crossvein. — Forewing vein CuP originates at or proximal of basal crossvein in Nymphidae, Nemopteridae, Ascalaphidae and most Myrmeleontidae. In a few groups of antlions, such as Brachynemurini and *Pseudimares aphrodite* (but not in *P. iris*), CuP originates distal of basal crossvein. See also Stange (1994: 69) (Fig. 3).

13. Forewing, vein CuP: **(0)** long vein running independently from 1A for all its length; **(1)** short vein, parallel to 1A for a short distance and then merging with it. In Nymphidae and Nemopteridae, forewing vein CuP is a distinct, independent long vein (Tjeder 1967: figs. 1924, 1925). — This condition is also present in several genera of Myrmeleontidae, such as *Stilbopteryx*, *Aeropteryx*, *Pseudimares* and in all Palparini (*Palpares*, *Goniocercus*, *Palparellus*, *Annulares*) (Riek 1976: figs. 2, 3) (Figs. 3, 6, 7). In several ascalaphids and in all the other antlions, including *Echthromyrmex*, *Dimares* and *Millerleon*, this vein is short, amalgamating with 1A, usually just after



Figs. 5–7. Wings of Palparinae. **5**: *Millerleon bellulus* (Banks, 1908). **6**: *Pseudimares aphrodite* H. Aspöck & U. Aspöck, 2009. **7**: *Palpares libelluloides* (Linnaeus, 1764). — ***Abbreviations***: **C** – Costa, **Sc** – Subcosta, **R** – Radius, **Rs** – Radius sector, **MA** – Media anterior, **MP** – Media posterior, **MP2** – Media posterior branch, **CuA** – Cubitus anterior, **CuP** – Cubitus posterior, **A** – Anal vein. (Scale bar: 10 mm)

origin (Fig. 5). The genus *Palparidius* is exceptional under this respect, as it includes both: species with a long CuP (*P. capicola*) and species with a short CuP, merging with 1A (*P. concinnus*). See also TJEDER (1992: figs. 36, 38), STANGE (1994: 69) and BADANO et al. (2017b: fig. 5A).

14. Forewing, vein 2A, curvature: **(0)** gently curved; **(1)** strongly bent. — Forewing vein 2A is evenly curved downward in Nymphidae, Nemopteridae and several genera of Myrmeleontidae. In the antlion tribes Nesoleontini (*Cueta*), Myrmeleontini (*Myrmeleon*, *Euroleon*) and Nemoleontini (*Distoleon*, *Macronemurus*) 2A is characteristically angled. See also STANGE (1994: 69) and BADANO et al. (2017b: fig. 5A).

15. Hindwing, overall shape: **(0)** similar to forewing; **(1)** different from forewing (i.e. exceptionally elongate and narrow). — Nemopteridae are characterized by elongated, ribbon-like or even filiform hindwings, although some genera, including *Chasmoptera*, are characterized by large dilatations (e.g. KOCH 1967).

16. Hindwing, presectoral area: **(0)** absent; **(1)** present. — In Nymphidae, hindwing vein Rs originates proximally of wing length (SHI et al. 2015) and there is no presectoral area, while in the other families it branches off distally (Fig. 4) and there is a large presectoral area. Not applicable to Nemopteridae due to their highly modified hindwings.

17. Hindwing, presectoral area, number of crossveins: **(0)** 1–2; **(1)** > 3. — The presectoral area of the hindwings is basal to the origin of Rs. In several genera of Myrmeleontidae (*Pseudimares*, *Dimares*, *Millerleon*, *Echthromyrmex*, *Palparidius*, *Dendroleon*, *Brachynemurus*, *Scotoleon*, *Distoleon*, *Macronemurus*) this area is crossed by one or two crossveins (Figs. 4, 5, 6), while in all the other antlions and examined Ascalaphidae it is divided by more than 4 crossveins (H. ASPÖCK et al. 1980: figs. 213, 215, 218). Not applicable to Nymphidae and Nemopteridae, as they lack crossvein.

18. Hindwing, vein MP2: **(0)** as a long posterior branch; **(1)** as a short vein (i.e. crossvein-like). — In Nymphidae, Ascalaphidae and several genera of Myrmeleontidae, the hindwing vein MP obviously forks in one anterior branch and in one long posterior oblique branch. In some genera of Myrmeleontidae, such as *Stilbopteryx*, *Aeropteryx*, *Pseudimares*, *Echthromyrmex*, *Dimares*, *Millerleon* and *Palparidius*, the posterior fork of MP strikingly resembles a crossvein (MARKL 1954: figs. 62, 64, 65, labelled as M; RIEK 1976: figs. 2, 3, labelled as M) (Figs. 5, 6). It should be noted that in some small-sized antlions or in species with a narrow posterior section of the hindwing, MP2 is also relatively short but it is not crossvein-like, as it is evident by the shape of surrounding wing cells. Not applicable to Nemopteridae.

19. Hindwing, vein CuA: **(0)** ending at or before MP2; **(1)** continuing beyond MP2. — In Nymphidae, Ascalaphidae and most Myrmeleontidae, hindwing vein CuA reaches the posterior wing margin before or in proximity of MP2. In Acanthaclisini (*Acanthaclisis*) CuA directly connects with MP2, but in most antlions the two veins are usually separated by crossveins (STANGE 2004: 371). The angle of CuA varies according to genus, from oblique to parallel but it always ends at MP2 (see BADANO et al. 2017b: fig. 4). However, in some antlion genera, CuA continues as a long vein well beyond MP2, in some cases almost reaching the wing apex (Figs. 5–7). The latter condition is only present in the members of the traditional subfamilies Stilbopteryginae and Palparinae (KIMMINS 1940: figs. 3–5; MARKL 1954: figs. 62–65; RIEK 1976: figs. 2–3) (Figs. 5–7). Not applicable to Nemopteridae.

20. Hindwing, vein CuA, shape, if continuing beyond MP2: **(0)** parallel to MP1; **(1)** divergent from MP1 (*vena recurrens*). — In the members of the tribe Palparini (*Palpares*, *Annulares*, *Palparellus*, *Goniocercus*), hindwing vein CuA runs toward MP2 as an oblique vein and then abruptly curves upward after the posterior branch (KIMMINS 1940: figs. 2, 5; MARKL 1954: fig. 63; MANSELL 1985a: fig. 6) (Fig. 7). In other antlions with long CuA, the vein continues parallel to MP1 (KIMMINS 1940: figs. 1, 3, 4).

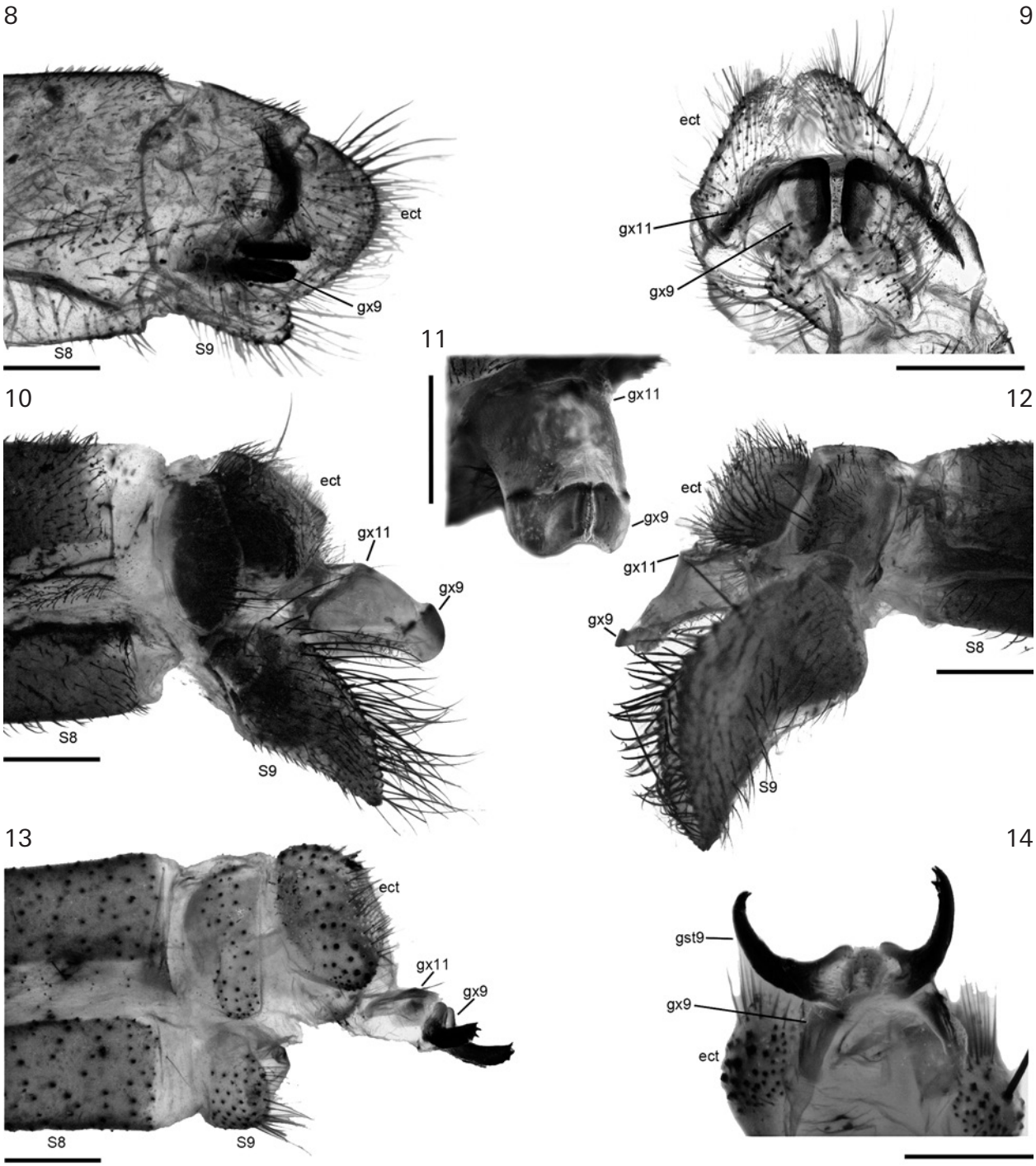
21. Hindwing, vein 1A: **(0)** not thicker than surrounding veins and not bent upward; **(1)** thicker than surrounding veins and bent upward. — In the genus *Echthromyrmex*, vein 1A is noticeably thicker and bent upward (MARKL 1954: fig. 64). An autapomorphic character here included to better delimit this taxon.

22. Pilula axillaris: **(0)** absent; **(1)** present. — The pilula axillaris is a small, usually hairy, knob in proximity of the wing base characteristic of most male Myrmeleontidae but absent in several lineages, including the tribe Nemoleontini and, among the included genera, *Dimares* and *Scotoleon*. See also STANGE (1994: 69) and BADANO et al. (2017b: 58).

23. Male, abdominal swelling in proximity of the 4th segment: **(0)** absent; **(1)** present. — In the males of Stilbopteryginae *sensu* STANGE (2004) (*Stilbopteryx* and *Aeropteryx*), the abdomen has a very large and prominent swelling in proximity of abdominal segment 4 (RIEK 1968: pl. 1).

24. Male, gonocoxites 9 and 11: **(0)** gonocoxites 11 as a transverse arch, gonocoxites 9 at the ventral end of this arch; **(1)** gonocoxites 11 arranged longitudinally and dorsally to gonocoxites 9, forming a complex. — In Ascalaphidae and Myrmeleontidae, gonocoxites 9 and 11 are strictly associated into a complex. In Nymphidae and Nemopteridae, these gonocoxites are independent and distinct sclerites. See U. ASPÖCK & H. ASPÖCK (2008) for a thorough treatment of this character.

25. Male, sternite 9: **(0)** small, without a spoon-like projection; **(1)** very large, with a spoon-like projection. — In the males of Stilbopteryginae *sensu* STANGE (2004) (*Stilbopteryx* and *Aeropteryx*), sternite 9 is extremely large and prominent (RIEK 1968: pl. 1) (Figs. 10, 12).



Figs. 8–14. Male genitalia of Palparinae. **8**, **9**: *Pseudimares aphrodite* H. Aspöck & U. Aspöck, 2009, **8**: apex of the abdomen, lateral view, **9**: complex of gonocoxites 9 + gonocoxites 11, ventral view. **10, 11**: *Stilbopteryx costalis* Newman, 1838, **10**: apex of the abdomen, lateral view, **11**: complex of gonocoxites 9 + gonocoxites 11, dorso-posterior view. **12**: *Aeropteryx monstrosa* Riek, 1968, apex of the abdomen, lateral view. **13**, **14**: *Dimares elegans* (Perty, 1833), **13**: apex of the abdomen, lateral view, **14**: complex of gonocoxites 9 + gonocoxites 11, ventral view. — ***Abbreviations***: **ect** – ectoproct, **S8** – sternite 8, **gx8** – gonocoxite 8, **S9** – sternite 9, **gx9** – gonocoxite 9, **gst9** – gonostylus 9, **gx11** – gonocoxite 11. (Scale bar: 0.5 mm)

26. Male, median hook-like structure on sternite 9: **(0)** absent; **(1)** present. — In the males of *Palparidius*, sternite 9 is equipped with a sclerotized upward hooked process.

27. Male, complex of gonocoxites 9 and 11, shape: **(0)** not fused; **(1)** shaped in a straight cone-like structure; **(2)** shaped in a tube strongly curved upward. — In most Myrmeleontidae, gonocoxites 9 and 11 are not fused and easily recognizable as independent genital sclerites. In Stilbopteryginae (*Stilbopteryx*, *Aeropteryx*) and Palparini (*Palpares*, *Palparellus*, *Goniocercus*, *Annulares*), the gonocoxites are amalgamated in a cone-like structure (Insom & Carfì 1988: figs. 34–62; Mansell 1992: figs. 14, 15) (Figs. 10–11).

In other antlions, such as *Myrmecaelurus* and *Cueta* gonocoxites 9 and 11 are also fused but markedly differ from the above mentioned condition in shape, being a tube-like structure usually curved upward (H. Aspöck et al. 1980: figs. 799, 800).

28. Male, gonarcal bulla (*sensu* Mansell 1992): **(0)** absent; **(1)** present. — The males of some Palparini (*Annulares*, *Palparellus*, some *Palpares*) are characterized by a prominent dorsal swelling on gonocoxite 11 (Insom & Carfì 1988: figs. 34, 37, 40; Mansell 1992: figs. 15, 16).

29. Male, gonocoxites 9, shape (caudal view): **(0)** with branched apex; **(1)** without branched apex. — In Nymphidae and Nemopteridae gonocoxites 9 appear rod-shaped with a branched apex, often of complex shape, in caudal view (cf. U. Aspöck & H. Aspöck 2008). In Myrmeleontidae and Ascalaphidae, the gonocoxites 9 are compact and unbranched (Badano et al. 2017b: fig. 8A,C,E,G) (Figs. 9, 11).

30. Male, gonocoxites 9, medial fusion: **(0)** not fused; **(1)** fused, in a Y-shaped structure; **(2)** fused in an upward hook-shaped structure. — Gonocoxites 9 are fused into a Y-shaped structure in the antlion tribe Nemoleontini (*Distoleon* and *Macronemurus*) (H. Aspöck et al. 1980: fig. 853; Badano et al. 2017b: fig. 8H). In the genus *Cueta* they are fused into an upward hook (H. Aspöck et al. 1980: fig. 806).

31. Male, gonocoxites 9, internal margin: **(0)** without teeth; **(1)** with small teeth. — In Dimarini (*Dimares* and *Millerleon*), the internal margin of gonocoxites 9 is equipped with small teeth, which in *Dimares* are arranged on the conspicuous projection of gonocoxites 9.

32. Male, gonocoxites 9, lobes: **(0)** absent; **(1)** present. — The male gonocoxites 9 extend in a lobe in the genus *Palparidius*.

33. Male, ectoproct, paired ventrocaudal projection: **(0)** absent; **(1)** present. — In several antlion lineages, including the genera *Palpares*, *Palparellus*, *Goniocercus*, *Annulares*, *Palparidius*, *Brachynemurus*, *Scotoleon*, *Macronemurus*, *Acanthaclisis*, *Myrmecaelurus* and *Cueta*, the ectoproct has a posterior process (H. Aspöck et al. 1980: figs. 779, 780, 791, 792; Mansell 1992: figs. 4, 5; Stange 1994: fig. 45; Badano et al. 2017b: fig. 8G, H). These structures are absent in the other examined antlions (Figs. 8–13).

34. Male, ectoproct, ventrocaudal projection (if present), shape: **(0)** very short, as long as the ectoproct; **(1)** long, more than 3 × the length of the ectoproct; **(2)** extremely long, at least 1/3 of abdomen length. — In the males of some antlion genera, such as *Acanthaclisis*, *Myrmecaelurus* and *Cueta*, the ventrocaudal projection is as long as the ectoproct (H. Aspöck et al. 1980: figs. 791, 792, 796, 797, 802). — In *Brachynemurus*, *Scotoleon*, *Macronemurus*, *Palpares*, *Palparellus*, *Goniocercus* and *Annulares*, this projection is very long and clasper-like (H. Aspöck et al. 1980: figs. 779, 780; Insom & Carfì 1988: figs. 2–14; Mansell 1992: figs. 4, 5; Stange 1994: fig. 45). Unique to *Palparidius*, the projections of the ectoproct are spectacularly developed reaching 1/3 of abdomen length.

35. Female, paired process on segment 8: **(0)** absent; **(1)** present. — Several antlion genera, including *Dendroleon*, *Brachynemurus*, *Scotoleon*, *Myrmeleon* and *Euroleon* are equipped with setiferous processes at base of gonocoxites 8 (U. Aspöck & H. Aspöck 2008; Badano et al. 2017b: p. 46).

36. Female, gonocoxites 8: **(0)** unpaired plate-like; **(1)** paired processes. — Gonocoxites 8 are flattened and plate-like in Nymphidae, Nemopteridae and Ascalaphidae (see U. Aspöck & H. Aspöck 2008 for a thorough description of this character). In Myrmeleontidae, gonocoxites 8 are shaped as paired prominences (Badano et al. 2017b: figs. 7B, 9) (Figs. 15–20).

37. Female, gonocoxites 8 (if paired processes): **(0)** not prominent; **(1)** prominent (longer than wide). — Gonocoxites 8 are not prominent, being wider than long in *Palparidius* and Palparini (*sensu* Stange 2004) (Figs. 19, 20). In all other antlions they are longer than wide, often digitiform in shape (Badano et al. 2017b: figs. 7B, 9) (Figs. 15–18).

38. Female, gonocoxites 8, chaetotaxy: **(0)** thin setae; **(1)** stout setae; **(2)** long robust setae curved downward. — With a few exceptions (e.g. *Dendroleon*), antlion females are equipped with stout digging setae on gonocoxites 8. In some genera, such as *Solter*, *Acanthaclisis*, *Myrmecaelurus* and *Cueta*, these setae are very long and curved downward (H. Aspöck et al. 1980: figs. 808, 809) (see also Stange 1994: p. 70).

39. Female, paired processes on segment 9: **(0)** absent; **(1)** present. — Some antlion genera, such as *Pseudimares*, *Dendroleon*, *Cueta* and *Myrmecaelurus* are equipped with setiferous processes at base of gonocoxites 9 (Badano et al. 2017b: p. 46) (Figs. 15, 16).

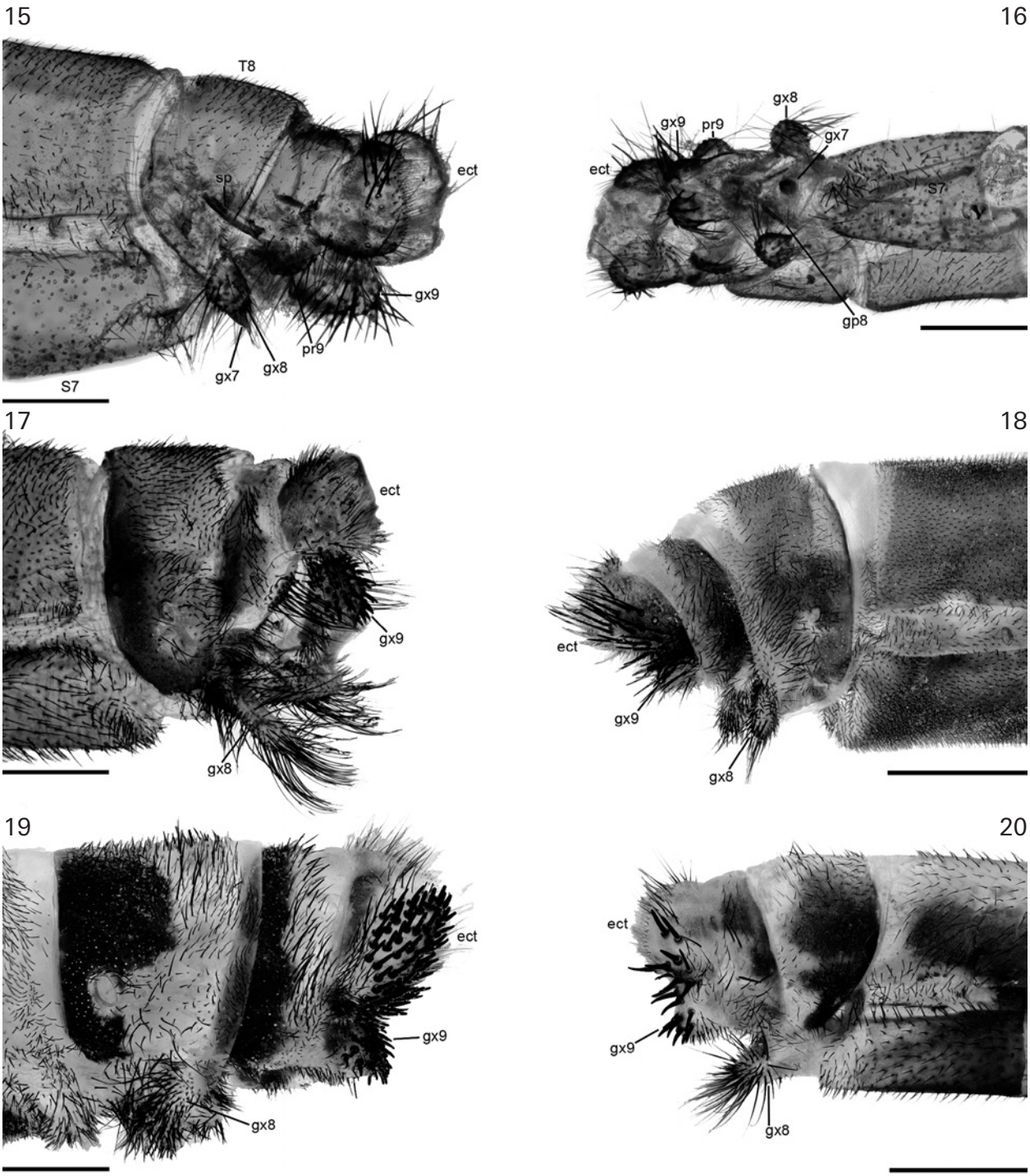
40. Larva, ocular tubercle: **(0)** absent; **(1)** present. — The larvae of Ascalaphidae and Myrmeleontidae have stemmata that are raised on a prominent tubercle (Badano et al. 2017a: figs. 6E,F, 10E).

41. Larva, fringe of extremely long setae on the lateral side of the mandible: **(0)** absent; **(1)** present. — Pit-building antlion larvae (*Myrmeleon*, *Euroleon*, *Cueta*, *Myrmecaelurus*) are characterised by the presence of a fringe of long setae on the external margin of the mandible (Badano et al. 2017a: fig. 6F).

42. Larva, fringe of extremely long setae on meso- and metathoracic leg: **(0)** absent; **(1)** present. — In some antlion genera, including *Solter*, *Acanthaclisis*, *Myrmecaelurus*, *Cueta*, *Myrmeleon* and *Euroleon*, meso- and metathoracic legs are provided with a fringe of long setae (Badano et al. 2017a: fig. 7G).

43. Larva, metathoracic leg: **(0)** similar to mesothoracic leg; **(1)** more robust than mesothoracic leg. — In Myrmeleontidae the metathoracic pair is noticeably larger than the mesothoracic leg (Badano et al. 2017a: fig. 8F).

44. Larva, metathoracic leg, articulation of tibia and tarsus: **(0)** articulated; **(1)** fused. — In Myrmeleontidae



Figs. 15–20. Female genitalia of Palparinae. **15**, **16**: *Pseudimares aphrodite* H. Aspöck & U. Aspöck, 2009, apex of the abdomen, **15**: lateral view, **16**: ventral view. **17**: *Stilbopteryx costalis* Newman, 1838, apex of the abdomen, lateral view. **18**: *Millerleon bellulus* (Banks, 1908), apex of the abdomen, lateral view; **19**: *Palpares libelluloides* (Linnaeus, 1764). **20**: *Palparidius concinnus* (Peringuey, 1910) apex of the abdomen, lateral view. — ***Abbreviations***: **ect** – ectoproct, **S7** – sternite 7, **gx7** – gonocoxites 7, **T8** – tergite 8, **gx8** – gonocoxite 8, **sp** – spermatheca, **pr9** – process of segment 9; **gx9** – gonocoxite 9. (Scale bar: 0.5 mm).

and Ascalaphidae, metathoracic tibia and tarsus are fused (Badano et al. 2017a: fig. 7G).

45. Larva, metathoracic leg, tarsal claws: **(0)** not enlarged; **(1)** enlarged. — The larvae of Myrmeleontidae are characterised by enlarged tarsal claws (Badano et al. 2017a: fig. 7G).

46. Larva, abdominal setiferous processes: **(0)** absent; **(1)** present. — The larvae of Nymphidae, Myrmeleontidae and Ascalaphidae have prominent setae-bearing protuberances on the lateral side of the abdomen (Badano et al. 2017a: fig. 8E,F).

47. Larva, abdominal segments 1–7, type of dorsal setiferous processes: **(0)** scolus-like; **(1)** tubercle-like. — The setiferous processes of the dorsal series are scolus-like in the larvae of Nymphidae and Ascalaphidae, while in most Myrmeleontidae they are

short and tubercle-like (BADANO et al. 2017a: fig. 8C,D).

48. Larva, abdominal segment 8, odontoid processes: **(0)** absent; **(1)** present. — The odontoid processes, or "submedial teeth" (STANGE 1994), are paired, tooth-like sclerotizations present on sternite 8 in Nemopteridae Nemopterinae, Ascalaphidae and most Myrmeleontidae (BADANO et al. 2017a: fig. 9B).

49. Larva, abdominal segment 9, shape: **(0)** longer than wide; **(1)** wider than long. — The abdominal segment 9 is longer than wide in Nymphidae, Nemopteridae, Ascalaphidae and in a few Myrmeleontidae (*Dendroleon*) (BADANO et al. 2017a: fig. 9D), while in most members of the latter family, segment 9 is wider than long (BADANO et al. 2017a: fig. 9B).

50. Larva, rastra: **(0)** absent; **(1)** present. — The rastra is a pair of sclerotizations at the apex of sternite 9 and is present in most Myrmeleontidae and all Ascalaphidae (BADANO et al. 2017a: fig. 9B).

51. Larva, rastra (if present), digging setae: **(0)** unfused; **(1)** partly fused; **(2)** fused. — In most Myrmeleontidae – including the first instar larva of *Palpares*, see BADANO et al. (2017a: fig. 9E), and *Millerleon*, see STANGE (1989: fig. 12) – and all Ascalaphidae, rastra are equipped with an apical set of unfused, triangular digging setae (STANGE 1994; BADANO et al. 2017a: fig. 9E). In *Dimares*, the apical digging setae of rastra are partly fused (STANGE 1989: fig. 15). Later instars of *Palpares* are characterized by very large, heavily sclerotized rastra whose apical setae are fused into a shovel-like structure termed fossoria (BADANO et al. 2017a: 9F).

4. Results

4.1. Taxonomy

***Pseudimares aphrodite* H. Aspöck & U. Aspöck, 2009**

Figs. 1–4, 6, 8, 9, 15, 16

Diagnostic description of male. H. ASPÖCK & U. ASPÖCK (2009) (original description).

Diagnostic description of female. ***Head***: Vertex narrowing anteriorly, blackish (Fig. 1). Frons reddish brown, paler toward the clypeus. Clypeus, labrum and genae light brown (Fig. 2). Maxillary and labial palpi light brown. Apical segment of the labial palp spindle-shaped, with a rounded sensorial pit (Fig. 2). Eyes very large and globose, eye radius larger than frons width (Fig. 2). Distance between antennae smaller than scape width. Antennae with reddish brown scape and pale brown flagellum.

Thorax: Uniformly reddish brown (Fig. 1). Pronotum longer than wide. Thorax covered with pale hair-like setae. Legs very long and slender, reddish brown with darker tarsi (Fig. 1). In all legs, the first tarsomere is of comparable length to the second and third tarsomeres together. Tibial spurs as long as the first tarsomere. Legs thickly covered with short black setae sparsely interspersed with longer sensilla.

Wings: Relatively long and broad with rounded apex. Length of forewing 48–55 mm. Membrane hyaline with conspicuous markings and shades, including very large eye-spots (Fig. 6). Venation brown with alternating pale dashes. Forewing with radius sector originating at 1/5 of wing length, much before cubital fork (Fig. 3). Cubitus posterior originating after basal crossvein and running independently from first anal vein (Fig. 3). First anal vein gently curving toward the posterior part of the wing. Most wing veins shaded with brown. Apex of the forewing shaded with brown. Pterostigma bicoloured, dark basally and whitish proximally. Hypostigmatic area with a black dot characterized by bluish iridescence (Fig. 6). Gradates and posterior margin of the wing apex with brown spots. Radial area with a very large eye-spot with a brown perimeter encircling a slightly shaded "iris" and a large blackish "pupilla" with a blue iridescence (Fig. 6). Hindwing with short presectoral area, crossed by one crossvein (Fig. 4). Longitudinal veins relatively straight and sub-parallel. Medial fork not evident, as the media posterior (MP) is crossvein-like (Fig. 6). Cubitus anterior parallel to the media and running toward the wing apex. First anal vein parallel to cubitus anterior (Fig. 6). Shading of hindwing veins less marked than in the forewing. Pterostigma whitish. Black dot of hypostigmatic area smaller than in forewing (sometimes faded). Apex of the hindwing shaded with brown. Eye-spot slightly wider than in forewing and not as contrasted, with the "iris" fading in the circular perimeter (Fig. 1).

Abdomen: Entirely reddish brown (Fig. 1). Abdomen chaetotaxy constituted by black and short setae. Ectoproct pale reddish brown.

Female genitalia: Female gonocoxites 7 unpaired, relatively small, triangle-shaped and strongly sclerotized (Figs. 15, 16). Gonocoxites 8 paired, prominent and longer than wide, yet relatively stout, covered with long, hair-like setae (Figs. 15, 16). Gonapophyses 8 appearing in ventral view as narrow, oblique rods converging caudally (Fig. 16). Segment 9 with a pair of prominent processes arranged anteriorly to gonocoxites 9, relatively rounded in shape being as long as wide (Figs. 15, 16). These processes are covered with hair-like setae. Gonocoxites 9 separated (not fused medially), ventrally covered with long and robust digging setae. Ectoproct comparatively small, oval-shaped, covered with long and robust digging setae (Fig. 15).

4.2. Phylogenetic reconstruction based on morphology

The cladistic analysis resulted in one most parsimonious tree, on which we mapped the inferred character changes (Fig. 21), with a tree length of 108 steps, a consistency index (CI) of 0.59 and a retention index (RI) of 0.8.

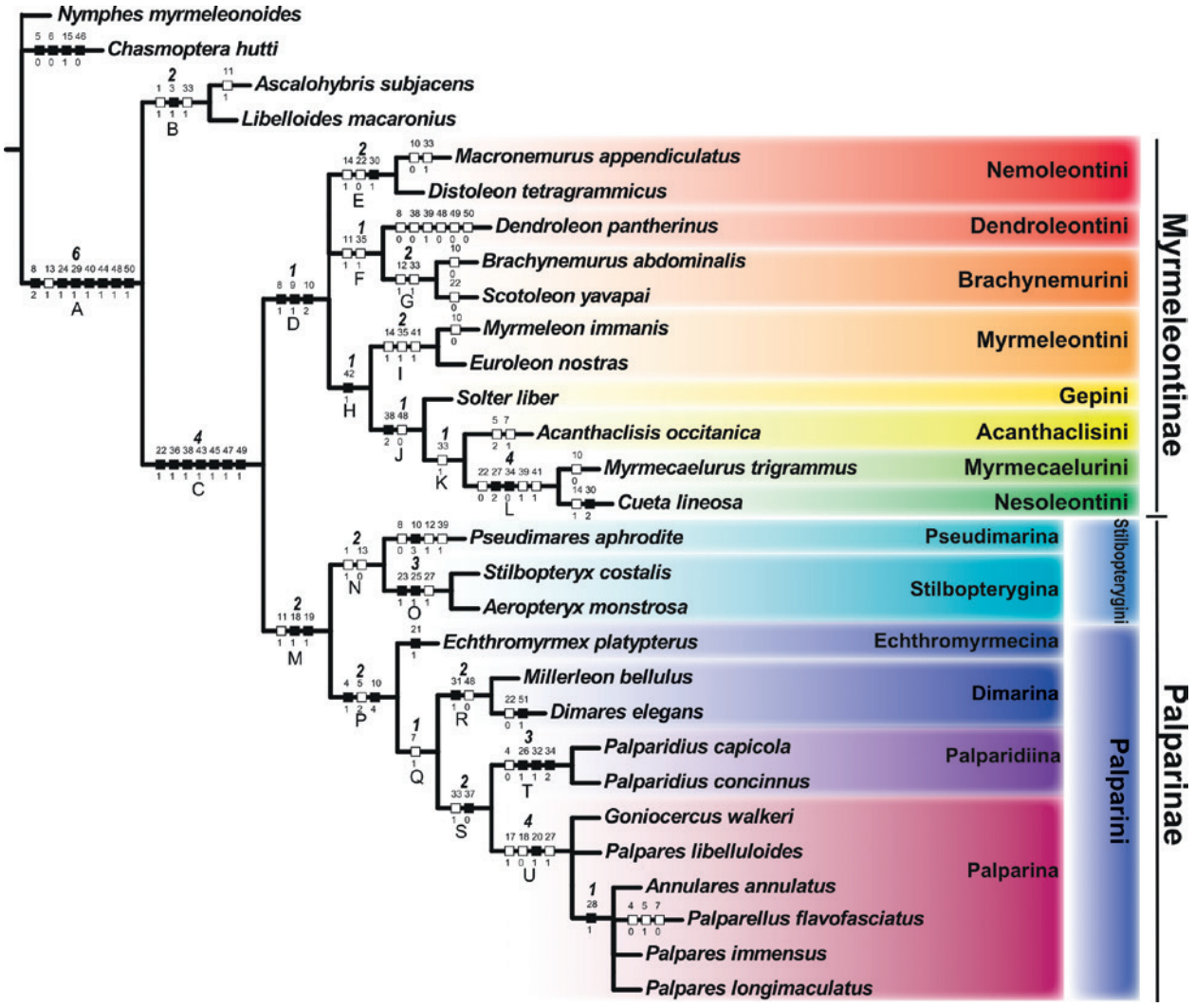


Fig. 21. Morphology based phylogeny of Myrmeleontidae. The single tree resulting from the parsimony analysis with unambiguous characters mapped on branches. Numbers above branches indicate Bremer supports. Letters below branches are main clades discussed in the text. The new proposed classification scheme for Myrmeleontidae is reported on the right side.

The analyses confirmed a sister group relationship between Myrmeleontidae and Ascalaphidae (clade A). The clade including Ascalaphidae + Myrmeleontidae is based on 7 non-homoplasious apomorphies (8 : 2, prothorax wider than long; 24 : 1, male gonocoxites 9 and 11 forming a complex; 29 : 1, male gonocoxites 9 short without branched apex; 40 : 1, larva, ocular tubercle present; 44 : 1, larva with fused metathoracic tibia and tarsus; 48 : 1, larva with abdominal segment 8 equipped with odontoid processes; 50 : 1, larva equipped with rastra) and 1 homoplasious apomorphy (13 : 1), and the clade received a Bremer support value of 6.

Monophyly of Ascalaphidae (clade B) relied on one non-homoplasious apomorphy (3 : 1, antenna long, more than half forewing length) and two homoplasious apomorphies (1 : 1 and 33 : 1) and received a Bremer support value of 3.

The family Myrmeleontidae (clade C) is confirmed as monophyletic based on 7 non-homoplasious apomorphies (22 : 1, pilula axillaris present; 36 : 1, female gonocoxites 8 as paired processes; 38 : 1, female gonocoxites 8 with stout setae; 43 : 1, larva with metathoracic leg more robust than mesothoracic leg; 45 : 1, larva with enlarged claws of the metathoracic leg; 47 : 1, larva with abdominal setiferous processes tubercle-like; 49 : 1, larva with abdominal segment 9 wider than long) and obtained a Bremer support value of 4. The analysis found evidence of two subclades (D and M). Myrmeleontinae (clade D) are very weakly recovered as monophyletic based on 3 non-homoplasious apomorphies (8 : 1, prothorax as long as wide; 9 : 1, prothoracic femur with hair like sensillum; 10 : 2, wing with markings in delimited areas) and received a Bremer support value of 1. The relationships within Myrmeleontinae (clade D) remained unresolved. Nemoleontini (clade E), including *Distoleon* + *Macronemurus*, emerged as monophyletic based on 1 non-homoplasious apomorphy (30 : 1, male gonocoxites 9 fused in a Y-shaped structure) and 2 homoplasious apomorphies (14 : 1; 22 : 0). The parsimony analysis retrieved a weakly supported clade (F) including Dendroleontini (*Dendroleon*) and Brachynemurini (Clade G, including *Brachynemurus* and *Scotoleon*) based on 2 homoplasious apomorphies (11 : 1; 35 : 1), which received

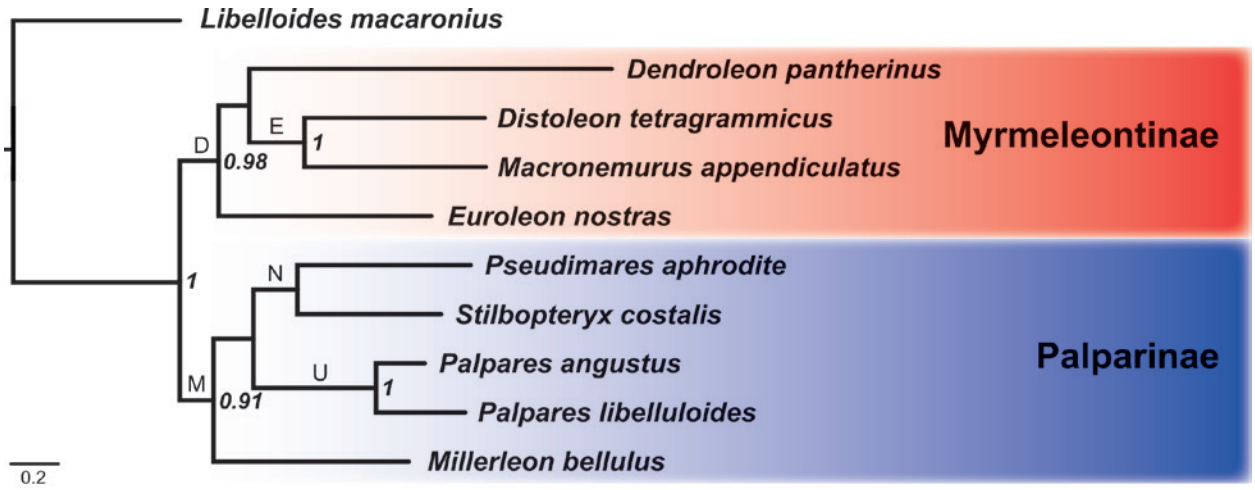


Fig. 22. DNA based phylogeny of Myrmeleontidae. 50% Majority rule tree resulting from the Bayesian analysis of the combined dataset (*cox1*, *cox3*, *28S*). Support values near nodes are Bayesian Posterior Probabilities (> 0.90). Letters below branches indicate main clades agreeing with the morphological analysis.

a Bremer support value of 1. Taxa belonging to several antlion tribes clustered together in the weakly supported clade H, based on 1 homoplasious apomorphy (42 : 1, larva with a fringe of extremely long setae on meso- and metathoracic leg), and received a Bremer support value of 1. This group includes the families with the larvae showing the most specialized digging adaptations. Monophyly of Myrmeleontini (clade I, including *Myrmeleon* and *Euroleon*) relied on 3 homoplasious apomorphies (14 : 1; 35 : 1; 41 : 1) and received Bremer support value of 2. In turn, Myrmeleontini (clade I) are recovered as the sister group to clade J, including members of the tribes Gepini (*Solter*), Acanthaclisini (*Acanthaclisis*), Myrmecaelurini (*Myrmecaelurus*) and Nesoleontini (*Cueta*). This group was reconstructed as monophyletic based on 1 non-homoplasious apomorphy (38 : 2, female gonocoxites 9 provided with large robust setae curved downward) and 1 homoplasious apomorphy (48 : 0) and garnered a Bremer support value of 1. *Acanthaclisis* was reconstructed as the sister taxon to clade L, including *Myrmecaelurus* + *Cueta*. Monophyly of *Myrmecaelurus* + *Cueta* (clade L) is based on 2 non-homoplasious apomorphies (27 : 2, male gonocoxites 9+11 shaped in a tube strongly curved upward; 34 : 0, male ectoprocts with very short ventrocaudal process) and 3 homoplasious apomorphies (22 : 0; 39 : 1; 41 : 1), obtaining a Bremer support value of 4.

The analysis found evidence of a clade (clade M), including members of Stilbopteryginae and Palparinae (*sensu* STANGE 2004). Monophyly of this group relied on 2 non-homoplasious apomorphies (18 : 1, hindwing vein MP2 short, crossvein-like; 19 : 1, longitudinal vein after MP2 present) and 1 homoplasious apomorphy (11 : 1) and obtained a Bremer support value of 2. Within this group, two subclades were retrieved by both analysis: clade N, including *Pseudimares* + clade O (Stilbopteryginae *sensu* STANGE 2004), and clade P including the remainder of Palparinae. *Pseudimares* clustered together with *Stilbopteryx* + *Aeropteryx* (clade O) based on 2 homoplasious apomorphies (1 : 1; 13 : 0). This clade was supported by a Bremer support value of 2. Stilbopteryginae (in the sense of STANGE 2004) were recovered as monophyletic based on 2 non-homoplasious apomorphies (23 : 1, male abdomen swollen in proximity of segment 4; 25 : 1, male sternite 9 spoon-like) and 1 homoplasious apomorphy (27 : 1), obtaining a Bremer support value of 3.

All other Palparinae (*sensu* STANGE 2004, exclusive of *Pseudimares*) formed a clade (clade P) based on 2 non-homoplasious apomorphies (4 : 1, labial palpus much longer than the head; 10 : 4, wings with large markings covering most of the membrane) and 1 homoplasious apomorphy (5 : 2). In the parsimony analysis, *Echthromyrmex* was reconstructed as the sister taxon to all other members of the clade Q, based on 1 homoplasious apomorphy (7 : 1). In turn, clade R (*Dimares* + *Millerleon*) took up a position as the sister group to clade S, including *Palparidius* + Palparini (*sensu* STANGE 2004). The monophyly of clade R (*Dimares* + *Millerleon*) relied on one non-homoplasious apomorphy (31 : 1, internal margin of male gonocoxites 9 with small teeth) and 1 homoplasious apomorphy (48 : 0), receiving a Bremer support value of 2.

Clade S, including *Palparidius* (clade T) and Palparini (*sensu* STANGE 2004) (clade U) was supported by one non-homoplasious apomorphy (37 : 0, female gonocoxites 8 not prominent) and 1 homoplasious apomorphy (30 : 1) garnering a Bremer support value of 2. The monophyly of *Palparidius* is supported by 3 non-homoplasious apomorphies (26 : 1, male with a hook-like structure on sternite 9; 32 : 1, male gonocoxites 9 lobe-like; 34 : 2, male with ventrocaudal projections of the ectoproct as long as 1/3 of the abdomen length) and 1 homoplasious apomorphy (4 : 0) and received a Bremer support value of 3. Palparini (*sensu* STANGE 2004) (clade U) were strongly supported as monophyletic in all analyses, being based on 1 non-homoplasious apomorphy (20 : 1, longitudinal vein after MP2 curved) and 3 homoplasious apomorphies (17 : 1; 18 : 0; 27 : 1) and garnering a Bremer support value of 4. The analysis found evidence that the genus *Palpares* is paraphyletic.

4.3. Phylogenetic reconstruction based on DNA sequences

The trees based on single genes did not show a good resolution and contained only few highly supported nodes (Fig. S1). Palparinae + Stilbopteryginae *sensu* Stange (1994, 2004) were found highly supported in the *cox1* tree. This clade corresponds to clade M in the morphological analysis. In the *28S* tree this group was present, too, but poorly supported and in the *cox3* tree it was distorted by *Chasmoptera hutti*. Yet, the clustering of *C. hutti* is not significant since the nodes in the *cox3* trees in general lack support, which might be explained by high saturation of this marker sequence. The Palparinae clade again received high support in the combined tree based on the two mitochondrial sequences. In that tree Ascalaphidae, which clustered with high support, were confirmed to be the sister group of Myrmeleontidae (Fig. S2).

The tree based on three genes (*cox1*, *cox3*, *28S*) generally had the highest support (Fig. 22). Palparinae were monophyletic, yet with low support (0.91 posterior probability). This might be due to the fact that only a partial *cox1* sequence was available for *S. costalis*, which clustered in the tree with *P. aphrodite*. After omitting *S. costalis* from the alignment, the Palparinae node had a PP value of 0.99 (Fig. S3). Palparina (*Palpares libelluloides* + *P. angustus*) were strongly supported group, with a posterior probability of 1. Within the Palparinae clade, *Millerleon bellulus* (Dimarina) emerged as the sister group of the other members of clade. Myrmeleontinae *sensu* Stange (1994, 2004), corresponding to Clade D in the morphological analysis, and the Palparinae clade obtained a posterior probability value of 0.98. Yet, this result is not conclusive since only few representatives of the subfamily were included. Within the Myrmeleontinae clade, only the sister group relationship between *D. tetragrammicus* + *M. appendiculatus*, i.e., Nemoleontini, was highly supported (posterior probability 1.0).

Genetic distances between taxa in the various genes are given in Tables 3–5 illustrating that the representatives of both subfamilies (Myrmeleontinae, Palparinae) are distantly related (e.g., with distances mainly around 20% among taxa of both subfamilies).

5. Discussion

5.1. A new phylogenetic classification scheme for Myrmeleontidae

All our phylogenetic analyses based on a comprehensive morphological data set convincingly reconstructed Ascalaphidae and Myrmeleontidae as monophyletic sister groups, in agreement with previous studies based on morphological data (Henry 1978; Mansell 1992; Stange 1994; U. Aspöck et al. 2001; Beutel et al. 2010; Randolf et al. 2014; Badano et al. 2017a). The molecular phylogenetic trees, albeit they included a much smaller taxon sample, are in accord with this finding. A similar result was retrieved by most DNA-based phylogenies (Haring & U. Aspöck 2004; Winterton et al. 2010; Michel et al. 2017), although the first reconstruction based on whole mitochondrial genomes yielded these families as paraphyletic, with Ascalaphidae nested within Myrmeleontidae (Wang et al. 2016). In another study using mitochondrial genomes of Neuroptera, Zhang & Yang (2017) recovered a monophyletic Myrmeleontidae in the phylogenetic analyses based on mitochondrial protein coding genes and rRNA genes, but the family was again reconstructed as paraphyletic with respect to Ascalaphidae when analysing mitochondrial protein coding genes only. An immanent problem concerning phylogenetic relationships of these two families is their taxon richness and the fact that many genera appear in the DNA based trees as old lineages which probably radiated within a short period of time. This is exemplified by the high genetic distances among most taxa.

In a first preliminary study on the affinities of *Pseudimares* based on DNA sequences, U. Aspöck et al. (2015) unexpectedly found evidence of a possible relationship between *P. aphrodite* and *Stilbopteryx costalis*, shaking the widely accepted internal subdivisions of the family Myrmeleontidae (Stange 2004). This result was a surprise comparable to the amazement of D.E. Kimmins when he saw for the first time *Pseudimares* (H. Aspöck & U. Aspöck 2009). We can confirm now this noteworthy result both in our morphological and molecular based phylogenetic analyses, a result which affects the internal subdivisions of the Myrmeleontidae (Figs. 21, 22). Indeed, our cladistic analysis (Fig. 21) reconstructed *Stilbopteryx* + *Aeropteryx* as constituting a monophyletic subtribe Stilbopterygina (clade O), and in turn are the sistergroup to *Pseudimares*, which represents the subtribe Pseudimarina, together these two subtribes form the tribe Stilbopterygini (clade N). Stilbopterygini are the sistergroup to clade P, which corresponds to the tribe Palparini. A similar relationship is confirmed by our DNA-based phylogeny (Fig. 22), which retrieved a monophyletic tribe Stilbopterygini, including *Stilbopteryx* + *Pseudimares*. We suggest attributing the name Palparinae to the new monophylum (clade M) composed of Stilbopterygini + Palparini. Palparini (clade P), in turn comprise 4 subtribes: Echthromyrmicina (*Echthromyrmex*), Dimarina (*Dimares* + *Millerleon*, clade R), Palparidiina (*Palparidius*, clade T), Palparina (clade U) (Fig. 21). Therefore, our results contradict previous phylogenetic analyses of Myrmeleontidae, such as Badano et al. (2017a) and Michel et al. (2017), which retrieved Stilbopteryginae (*sensu* Stange 2004) as the sister group to all other Myrmeleontidae, although both studies did not include in their respective datasets other members of Palparinae aside from Palparini (*sensu* Stange 2004) and likewise did not include *Pseudimares*. In contrast, Stange (1994) in a morphology-based cladistic analysis, interestingly recovered Palparinae as paraphyletic, and Stilbopteryginae were reconstructed as deeply nested

Table 3. Distance matrix (p distances) of *cox1* sequences included in the present study.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1 *Pseudimares aphrodite*													
2 *Palpares angustus*	18.08												
3 *Palpares libelluloides*	18.79	17.80											
4 *Millerleon bellulus*	14.69	17.09	17.94										
5 *Stilbopteryx costalis*	15.68	16.81	17.23	18.08									
6 *Euroleon nostras*	16.81	15.25	15.82	15.82	17.94								
7 *Dendroleon pantherinus*	18.08	18.22	19.35	17.51	19.21	16.53							
8 *Distoleon tetragrammicus*	16.95	18.64	17.37	14.83	19.49	12.99	14.69						
9 *Macronemurus appendiculatus*	17.80	17.37	17.94	16.10	18.22	13.56	13.28	13.56					
10 *Libelloides macaronius*	17.23	18.64	16.67	16.24	19.07	14.97	17.09	16.10	15.25				
11 *Ascalohybris subjacens*	17.66	17.80	17.94	15.68	18.79	14.83	14.41	14.83	12.85	13.70			
12 *Chasmoptera hutti*	20.48	21.89	19.92	18.64	21.33	18.36	18.79	19.21	18.50	15.82	18.93		
13 *Nymphes myrmeleonoides*	20.76	21.19	20.48	17.66	21.05	15.68	15.82	13.84	13.98	17.09	15.11	17.66	
14 *Rapisma zayuanum*	22.03	21.19	20.76	20.62	23.16	17.09	18.79	15.25	17.09	18.79	17.66	19.77	13.98

Table 4. Distance matrix (p distances) of *cox3* sequences included in the present study.

	1	2	3	4	5	6	7	8	9	10	11	12
1 *Pseudimares aphrodite*												
2 *Palpares angustus*	18.51											
3 *Palpares libelluloides*	17.91	16.24										
4 *Millerleon bellulus*	18.82	19.73	18.51									
5 *Dendroleon pantherinus*	22.15	21.55	22.15	21.09								
6 *Distoleon tetragrammicus*	20.79	19.12	18.21	18.51	17.75							
7 *Macronemurus appendiculatus*	19.73	19.12	18.36	17.75	21.85	17.00						
8 *Euroleon nostras*	20.03	17.75	18.06	16.54	17.91	15.63	15.33					
9 *Libelloides macaronius*	18.82	20.18	19.12	19.27	21.09	17.45	17.60	18.36				
10 *Ascalohybris subjacens*	20.33	22.00	19.58	19.88	21.70	16.24	16.54	18.51	17.60			
11 *Nymphes myrmeleonoides*	22.76	23.98	23.98	21.09	22.15	18.82	20.18	17.15	22.15	21.40		
12 *Chasmoptera hutti*	22.91	20.79	21.09	19.73	22.00	20.33	22.00	18.36	20.94	20.94	22.31	
13 *Rapisma zayuanum*	28.07	27.92	27.62	25.80	25.64	23.07	26.56	23.37	26.40	25.49	18.66	25.34

Table 5. Distance matrix (p distances) of *28S* sequences included in the present study.

	1	2	3	4	5	6	7	8
1 *Pseudimares aphrodite*								
2 *Palpares angustus*	4.95							
3 *Palpares libelluloides*	4.08	2.17						
4 *Millerleon bellulus*	4.69	5.22	4.29					
5 *Euroleon nostras*	6.92	6.88	5.82	6.12				
6 *Dendroleon pantherinus*	6.33	5.60	5.69	6.82	7.14			
7 *Distoleon tetragrammicus*	5.19	5.05	4.94	5.00	6.46	5.97		
8 *Macronemurus appendiculatus*	5.82	6.86	6.34	6.06	5.90	6.88	4.33	
9 *Libelloides macaronius*	7.09	6.87	6.63	7.18	7.98	7.34	6.76	6.95

within Myrmeleontidae. MANSELL (2004) noted that the widely accepted monophyly of Palparinae (*sensu* STANGE 2004) actually relies on synapomorphies of Palparini (see below), making it difficult to characterize the entirety of the subfamily. An affinity between Palparinae and Stilbopteryginae (*sensu* STANGE 2004) was previously suggested by KIMMINS (1940) – who thoroughly delimited these groups – as well as by MANSELL (1992). Nonetheless, this suggestion has remained untested and unverified. Myrmeleontinae (clade D), the third extant subfamily of Myrmeleontidae according to STANGE (2004), is also seriously challenged by our morphology-based analyses, since it is retrieved as monophyletic but with very low support (Fig. 21). The fact that Myrmeleontinae were strongly supported as monophyletic in the DNA-based phylogenetic reconstruction has to be taken with caution since it included few members of this group (Fig. 22). Although our analyses were strictly aimed to reconstruct the relationship of *Pseudimares*, they cast serious doubts on the widely accepted classification scheme of Myrmeleontidae and challenge the subdivision into three subfamilies (STANGE 2004). A more comprehensive taxon sampling, considering both morphological characters and DNA sequences is necessary to further clarify the status

of the groups presently included within Myrmeleontinae and their reciprocal relationship, however it is beyond the aim of the present study.

5.2. *Pseudimares* within expanded Palparinae

On morphological grounds, the monophyly of Palparinae (clade M) is based on synapomorphic characters of the hindwing, in particular the vein MP2 as an inconspicuous, usually oblique, crossvein-like vein, while a longitudinal vein continues CuA beyond MP2 and runs toward the apex of the wing (Figs. 5–7). In Myrmeleontinae (clade D), the hindwing vein MP is long, as a distinct fork, and CuA ends in proximity of the fork (in Acanthaclisini even coalescing with the latter, see Stange 2004). In contrast with previous classification schemes, we retrieved *Pseudimares* as the sister taxon to *Stilbopteryx* and *Aeropteryx*, making Palparinae as conceived in the traditional sense (*sensu* Stange 2004) paraphyletic and supporting the new proposed division of this group into two sister tribes: Stilbopterygini (clade N, including Stilbopterygina and Pseudimarina) and Palparini (clade P) (Fig. 21). Indeed, *Pseudimares* shares with *Stilbopteryx* and *Aeropteryx* a series of homoplasious apomorphies, such as large globose eyes (also present in Ascalaphidae) (Fig. 2) and a long forewing vein CuP running independently from vein 1A (Fig. 6). The latter character is also present in Palparina, while in Dimarina and *Echthromyrmex* this vein merges with 1A (Fig. 5). Noteworthy is that *Palparidius* is highly unusual in this respect, since it comprises species with long CuP (*P. capicola*, *P. fascipennis*) and with short CuP fusing with 1A (*P. concinnus*) (Stange 2004). Kimmins (1933) originally suggested a relationship of *Pseudimares iris* and *Millerleon subdolus* (sub *Dimares*) based on wing venation and genitalia, although he also noted the above-mentioned differences in the shape of forewing vein CuP between these genera. Nevertheless, the genitalia of both genera of Dimarina are highly apomorphic since their gonocoxites 9 are prominent and provided with small teeth (Figs. 13, 14). *Millerleon* is characterized by a series of small teeth on the internal margin of gonocoxites 9, while in *Dimares* gonocoxites 9 are unusually prominent, being hook-like and with few small teeth arranged on the internal margin of the apex (Stange 1989) (Figs. 13, 14). However, the gonocoxites 9 of *Pseudimares* are less derived, resembling the plate-like condition widespread across several antlion lineages (Fig. 9). Female genitalia are considered of notable importance in the systematics of myrmeleontids, especially in some tribes (e.g. Dendroleontini, Brachynemurini) (Miller 1991; Stange 1994, 2004). In the case of *Pseudimares*, they are not particularly informative concerning phylogenetic affinities, although they noteworthy differ from all the other members of clade M because segment 9 is equipped with a short setiferous process arranged ventrally to gonocoxites 9 (Figs. 15, 16). This setiferous process is also present in several genera of other tribes of myrmeleontids (e.g. Mansell 1988), supporting the notion that it evolved in different occasions within the family. In our morphology-based cladistic analysis, Stilbopterygina are recovered well nested within Myrmeleontidae, suggesting that their highly specialized life-style and morphology as aerial predators, which so confused earlier authors (van der Weele 1909; Navás 1912; Tillyard 1916), evolved in parallelism to Ascalaphidae.

Palparini (*sensu novo*), exclusive of *Pseudimares* (clade P) are best characterized by a long labial palpus with slit-shaped palpimacula (although several genera of Palparina show a reversal, see Mansell 1992) and the wing pattern. In our analysis, the Old World genus *Echthromyrmex* is retrieved as a relatively isolated genus, placed outside Dimarina, supporting the classification of Markl (1954), Hölzel (1972) and H. Aspöck et al. (2001). *Echthromyrmex* differs from the other members of the clade P by the thickened and bent hindwing vein 2A (Markl 1954). Dimarina in the restricted sense, i.e. only including the genera *Dimares* and *Millerleon* (clade R), are reconstructed as monophyletic based on the strongly apomorphic male genitalia (Figs. 13, 14). This subtribe represents an exclusively American lineage. The genus *Palparidius* (clade T) is recovered as the sistergroup to Palparina (clade U), based on the not prominent female gonocoxites 8 (Fig. 20). Noteworthy is that the males of *Palparidius* and Palparina share very long ventrocaudal projections of the ectoproct, which reach a spectacular size in *Palparidius*. In compliance with previous studies (Mansell 1992, 2004; Michel et al. 2017), Palparina are confirmed as monophyletic, based on the strongly curved longitudinal vein after MP2 (vena recurrens) on hindwing (Fig. 7) and larva with the setae of rastra fused to fossoria. Although differing in shape and proportion, the 3rd instar larva of *Dimares* also shows a partial fusion of the digging setae of rastra (see Stange 1989), therefore further studies of the larvae of this group appear necessary to better understand the evolution of this trait, which might be associated with large sized larvae. In compliance with previous studies (Insom & Carfì 1988; Mansell 1992, Michel et al. 2017), we found evidence of paraphyly of the genus *Palpares*, despite our limited taxon sampling, suggesting that this genus needs a profound revision.

6. Conclusions

The classification of extant Myrmeleontidae has always been notoriously controversial due to the paucity of phylogenetic studies (Mansell 1999; New 2003). Moreover, the phylogenetic value of several characters commonly used by taxonomists to delimit and distinguish genera or suprageneric groups has been rarely tested, making it difficult to assess their suitability in unveiling the affinities between antlions, a particularly evident problem for genera with highly distinctive morphology (Badano et al. 2017b).

The genus *Pseudimares*, which was apostrophized by STANGE (2004) as "one of the mystery groups of antlions", is particularly representative for these difficulties. On the one hand, inclusion of morphological and molecular genetic data of this genus in our study has deeply impacted our understanding of the phylogeny of Myrmeleontidae. On the other hand, it also severely questions the currently accepted classification of the group and challenges old conventions, raising unexpected scenarios. Thus, the study of *Pseudimares* has induced substantial challenges concerning the phylogeny of Myrmeleontidae.

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Electronic Supplement Files

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File 1: badano&al-myrmeleontidaephylogeny-asp2017-electronic supplement-1.pdf — **Fig. S1.** BI trees based on single gene sequences: *cox1* (top), *cox3* (middle), *28S* (bottom). Support values near nodes are Bayesian Posterior Probabilities (> 0.90). — **Fig. S2.** BI tree based on the two combined mitochondrial sequences *cox1* and *cox3*. Support values near nodes are Bayesian Posterior Probabilities (> 0.90). — **Fig. S3.** BI tree based on three combined mitochondrial sequences *cox1*, *cox3* and *28S* without *Stilbopteryx costalis*. Support values near nodes are Bayesian Posterior Probabilities (> 0.90).

File 2: badano&al-myrmeleontidaephylogeny-asp2017-electronic supplement-2.nex — **Table S4.** Data matrix for the morphological phylogenetic analysis.