Evolution and success of antlions (Neuropterida: Neuroptera, Myrmeleontidae)

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Abstract:

Myrmeleontidae comprise the largest and most widespread family of Neuroptera owing to their ability to exploit a wide range of habitats including sand. A psammophilous existence was facilitated by several larval autapomorphies in the groundplan of Neuroptera that pre-adapted antlions to a life in sand and ensured their evolutionary success. The progression from arboreal habitats to psammophily may reflect the phylogeny of the family and hold the key to the unresolved higher classification of Myrmeleontidae. Additional information is also forthcoming from historical biogeography. Classifications, morphological adaptations, life histories, predation strategies and distribution patterns are reviewed and discussed as a contribution to elucidating relationships within the Myrmeleontidae.

Key words: Myrmeleontidae, higher classification, subfamilies, evolution, biogeography, biology, psammophily.

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Introduction

Myrmeleontidae are a highly evolved family of Neuroptera whose larvae have adopted a variety of predation strategies that enable them to exploit a wide range of habitats relative to other families. This versatility has ensured their evolutionary success as the largest and most widespread group, rivalled only by Chrysopidae, in the neuropteroid lineage. There are currently about 2000 described species of antlions distributed throughout the world, but especially in the arid regions of the globe (ASPÖCK H. et al. 1980). Many of these species names are synonyms, but they are being offset by new discoveries that will eventually yield a far higher number of extant taxa. The family also includes some of the largest and most striking of all insects, with wingspans ranging from 30-170 mm. Many have ornately patterned wings (Fig. 1) that enhance the camouflage and cryptic behaviour of these great insects.

The range of habitats and predation strategies reflect evolutionary trends within the Myrmeleontidae, from plesiomorphic arboreal habitats to the apomorphic occupation of sand. This was facilitated by a unique morphological adaptation that set Neuroptera on an evolutionary course and engendered a remarkable order of predatory insects. Enigmatically, this specialisation was not restrictive, but resulted in the radiation of Neuroptera into an impressive array of morphologically and biologically diverse taxa that comprise 17 families. It also provided a larval autapomorphy to underpin the monophyly of Neuroptera, and established them as a highly effective functional group of predators.

Myrmeleontidae, in particular, have exploited the specialised larval mouthparts that pre-adapted them to a variety of habitats, culminating in psammophily (Fig. 2). This was the key to the evolutionary success of antlions. Occupation of different habitats enabled these „sit and wait" ambush predators to develop many tactics to improve their efficiency as predators. These range from lurking camouflaged on rocks and vegetation, in tree-holes, concealed in dust and sand, under rock overhangs, in animal burrows and ultimately the ability to modify the immediate sandy environment into traps.

The abundance of antlions and their voracious feeding habits are an important influence in the regulation of populations of ground-dwelling and arboreal arthropods. In arid areas such as the Kalahari savannah of southern Africa, the biomass of large predatory larvae of Palparini (Figs 3-5) and other tribes could well exceed that of vertebrate predators. Larval and adult antlions, in turn, are a sustainable food resource for invertebrates and vertebrates in natural ecosystems. Many species are restricted to specific habitats and biomes, and are sensitive to ecological disturbance,

Fig. 1: *Palpares speciosus* (LINNAEUS), Western Cape Province, South Africa. Length = 70 mm

Fig. 2: Larva of *Crambomorphus* MCLACHLAN, Kalahari Savannah, South Africa, displaying the psammophilous habit. Length = 30 mm.

Fig. 3: Larva of *Golafrus oneili* (Péringuey), Kalahari Savannah, South Africa. Length = 35 mm. (Photo: A.S. Schoeman).

Fig. 4: Larva of *Crambomorphus* McLachlan, Kalahari Savanna, South Africa. Length = 30 mm.

Fig. 5: Larva of *Palpares annulatus* Stitz, Kalahari Savannah, South Africa. Length = 25 mm. (Photo: R.G. Oberprieler).

rendering them excellent bio-indicators of environmental degradation. This is of particular concern in South Africa where large-scale habitat fragmentation and application of pesticides threaten several endemic populations such as the vulnerable genus *Pamexis* Hagen (Fig. 6). Apart from their obvious biological significance, Myrmeleontidae are ideal subjects for the study of insect behaviour, physiology, biogeography and evolution, and is consequently a group that urgently warrants study and conservation.

Antlions and their habits have captured the attention of scientists since early times, and are entrenched in folklore (Wheeler 1930, Kevan 1992). Despite this, the global systematics and phylogenetic relationships of Myrmeleontidae remain obscure owing to the dynamic evolutionary state of the group and the consequent plethora of synonyms in the literature. These issues are currently being addressed by several researchers, and some phylogenetic analyses have already been carried out (e.g. Mansell 1992, Stange 1994).

Various authors have attempted to arrange the Myrmeleontidae into subfamilies, tribes and subtribes, but no consensus has been reached, as most classifications lack a sound phylogenetic basis. The variety of lifestyles and biogeography of antlions may, however, reflect evolutionary trends within the family that could contribute to resolving their higher classification. The current paper consequently reviews information on supra-generic classification, morphology, biology and historical biogeography, particularly vicariance events, as a contribution to elucidating the phylogeny and classification of the family.

Fig. 6: *Pamexis karoo* MANSELL, Karoo National Park, South Africa. Wing length = 34 mm

Higher classification of Myrmeleontidae

Supra-generic classification of Myrmeleontidae was initiated by BANKS (1899) who distinguished two groups, Myrmeleoni and Dendroleoni. In his study of African antlions BANKS (1911) elevated these two groups to the subfamilies Myrmeleoninae and Dendroleoninae, each comprising two tribes, Palparini and Myrmeleonini and Dendroleoni and Nemoleonini respectively.

NAVÁS (1912a, 1912b, 1913, 1914a, 1914b, 1926) added eight more tribes, while TILLYARD (1916) recognized Banks' two subfamilies and added two more tribes in studies on the Australian fauna. ESBEN-PETERSEN (1918) divided the Myrmeleontidae into two sections, Archaemyrmeleonida and Neomyrmeleonida, the former including only the Palparini, and the latter comprising the Myrmeleontinae with four tribes and Dendroleontinae with six. BANKS (1927) raised the Palparini and Macronemurini to subfamily status and added two more tribes, and subsequently elevated the Acanthaclisini to subfamily level (BANKS 1943).

More recent contributions have been those of MARKL (1956) who classified the genera of the world into 23 tribes, adding 10 new tribes in the process. He did not mention subfamilies in his treatise, but it had had the important effect of focussing attention to the higher classification of Myrmeleontidae, and providing a basis for future discussions. STANGE (1961) mentioned three subfamilies, Acanthaclisinae, Macronemurinae and Dendroleontinae, but did not deal with Myrmeleontinae or Palparinae. In 1967 and 1970a, STANGE referred to four subfamilies, omitting Macronemurinae, and then (STANGE 1970b) synonymized Dendroleontinae and Macronemurinae with Myrmeleontinae. HÖLZEL (1969) established the tribe Isoleontini, and in 1970 he also included the tribes of Dendroleontinae in Myrmeleontinae. RIEK (1970) placed the Australian Myrmeleontidae in four subfamilies, Dendroleontinae, Macronemurinae, Acanthaclisinae and Myrmeleontinae, but did not mention tribes. HÖLZEL (1972) recognised three subfamilies, Palparinae, Myrmeleontinae and Echtromyrmecinae, and STANGE (1976) listed Acanthaclisinae, Palparinae and Myrmeleontinae. WILLMANN (1977) and ASPÖCK H. et al. (1980) reduced the number of subfamilies to two, Palparinae and Myrmeleontinae, but the latter did not provide a tribal classification. NEW (1982) relegated the family Stilbopterygidae to subfamily status, assigning *Albardia* VAN DER WEELE to the Ascalaphidae, and *Stilbopteryx* NEWMAN and *Aeropteryx* RIEK to the subfamily Stilbopteryginae within Myrmeleontidae. At this stage some consensus appeared to be emerging regarding subfamilial classification, but none of these subfamilies was based on sound phylogenetic characters, and still require appraisal. The tribes were also subjectively defined and in considerable disarray, but recently STANGE & MILLER (1990) and STANGE (1994) have attempted to rationalise them by examining larval characters. They listed three subfamilies, Palparinae, Myrmeleontinae and Stilbopteryginae, but were not able to substantiate the monophyly of any of these. STANGE & MILLER (1990) enumerated nine tribes, and STANGE (1994) added a further two. The tribes documented by these authors are generally well defined and are recognised for the following discussions.

Morphology and Feeding

Autapomorphic mouthparts, comprising the elongated mandibles and maxillary lacinia that fit together along their entire lengths to form a piercing and sucking apparatus (Fig. 7), has been the key factor in the rise of Neuroptera as a group of specialist predators. Adaptations derived from this attribute include: smooth curved mandibles in larvae of Chrysopidae, Hemerobiidae, Nemopteridae and Psychopsidae; short or long straight stylets in Coniopterygidae, Sisyridae, Osmylidae, Dilaridae, Berothidae and Mantispidae; and the curved toothed jaws of Myrmeleontoidea (Myrmeleontidae, Ascalaphidae and Nymphidae). The straight mandibles and maxillae are apomorphic (ASPÖCK U. 1992), and curved jaws with teeth are another derivation from the simple curved-jaw condition. Such attributes equipped neuropteran larvae for widely divergent predation strategies in a variety of habitats. These range from aquatic, semiaquatic, arboreal, corticolous, detritis-dwelling, under stones, tree-holes and sheltered rock ledges and caves, to inquilines in colonies of termites, ants and wood-boring beetles, parasites in the nests of spiders, culminating in psammophily in Myrmeleontidae and Nemopteridae. A psammophilous habit does not, however, infer a close relationship between these two families (MANSELL 1996).

The mouthparts engendered further autapomorphic characteristics in larval Neuroptera, including loss of labial palps, mouth opening reduced to a shallow slit, a sealed midgut, modification of the malpighian tubules for silk production and cryptonephry (HENNIG 1981). Each of these attributes further enhanced the ability of antlions to thrive in hot, dry sandy habitats.

The mouthparts and feeding mechanism are unique to Neuroptera. When prey is captured, the sharp tips of the mandibles pierce the cuticle and enzymes are infused into the body through the mandibular/maxillary canals. This kills the prey and dissolves the soft internal tissues, the resulting fluid being drawn up through the sucking tubes into the alimentary canal of the larva. The food consequently never comes into contact with the substrate and is not contaminated with chitin, sand or other indigestible debris that would accumulate from biting and chewing mouthparts. Sand grains would also impede a chewing motion and this is obviated, as is the need for a mouth opening that would become filled with sand. The ingestion and digestion of food is consequently so efficient that the midgut is sealed and no solid waste, only excess fluid, is voided during larval life. This exempts some of the malpighian tubules from an excretory role, enabling them to produce silk for cocoon construction.

Fig. 7: Jaw structure of *Palpares inclemens* (WALKER), ventral aspect, showing grooved mandible and lacinia of maxilla. Jaw length = 8 mm.

The major constraint to life in hot, dry, sandy conditions is desiccation, but the excretory system of antlions prevents unnecessary moisture loss through faeces, and the cryptonephridial malpighian tubes regulate the volume of fluid excreted. A silken cocoon, incorporating sand grains, is spun on the substrate where the larva lived, or in sand. The cocoon provides a tough impenetrable shelter that protects the pupa from parasites, predators, excess soil moisture (rain) and desiccation, and the sand grains provide effective camouflage. Behavioural traits such as diurnal rhythms that regulate movement through the sand, and larval coloration (Fig. 3) also protect psammophilous antlions from excessive heat and desiccation. These attributes have enabled the great majority of antlions to exploit the limitless sandy environments of the world, leading to their radiation under the protective mantle of sand.

Habitats of Myrmeleontidae

The progression of Myrmeleontidae can be traced through examples from a diversity of lifestyles. These include: arboreal, living exposed on vegetation or in tree holes; exposed on rock surfaces; in fine dust and detritus under rock overhangs and small caves; detritus in animal burrows; freeliving in sand and psammophilous pit-builders. Larvae of *Neulatus* NAVÁS live in *Puya* (Bromeliaceae) plants in Chile, while *Jaffuelia* NAVÁS live camouflaged on boulders (STANGE 1994). The larvae of these two genera resemble Ascalaphidae and may represent the archetypal mode of existence of antlions. The close relationship of Ascalaphidae with Myrmeleontidae has frequently been emphasized (STANGE & MILLER 1990, STANGE 1994). Gnopholeontini larvae live fully exposed on rocks or tree bark and rely on camouflage for protection (MILLER 1990), similar to the *modus operandi* of Ascalaphidae. From there it would have been a simple advance to living in tree holes and then to dust and detritus on rock ledges under protective overhangs and detritus in animal burrows. Several genera inhabit tree holes, *Elicura* NAVÁS (STANGE 1994), *Dendroleon* BRAUER and *Cymothales* GERSTÄCKER (MANSELL 1987). Many occupy sheltered dusty ledges, including *Bankisus* NAVÁS (MANSELL unpubl.), *Tricholeon* ESBEN-PETERSEN (MANSELL 1988a) and some *Neuroleon* NAVÁS in southern Africa, and *Eremoleon* BANKS (STANGE & MILLER 1990) in the New World. Larvae of a few genera, *Cymothales* (*C. spectabilis* ESBEN-PETERSEN, *C. eccentros* (WALKER)) (MANSELL unpubl.) and *Elicura* and *Eremoleon* (STANGE & MILLER 1990, STANGE 1994) live both in tree holes and on rock ledges. *Bankisus* larvae are found on rock ledges and on tree roots under sandy overhangs (MANSELL unpubl.). One of the most enigmatic larvae is that of *Navasoleon boliviana* BANKS, from Bolivia, that lives upside down on bare rock on the ceilings of caves and has adapted its pupal emergence procedure accordingly (MILLER & STANGE 1985). This habit resembles that of *Proctolyra* TJEDER (Ascalaphidae) whose larvae also live upside down but under stones in the Karoo biome of South Africa (MANSELL unpubl.), and may emphasise the close relationship between Ascalaphidae and Myrmeleontidae. *Eremoleon nigribasis* Banks has progressed further to living in animal burrows (MILLER 1990), a habit that could have been exploited by those adapted to living in cave mouths. This diversity of habitats reflects, even within a single genus, the versatility of certain groups of antlions, but could also indicate that they are less specialized than the psammophilous species, by not being confined to one restricted habitat. They also retain several plesiomorphic traits such as abdominal scoli and slender jaws.

Arboreal and freeliving larvae conform to the general groundplan of Neuroptera manifest in other large families including Ascalaphidae, Chrysopidae, Hemerobiidae, Coniopterygidae, Psychopsidae and, many other insects. In most insect orders true psammophily (freeliving, completely immersed in sand) is a rare phenomenon that could be considered a derived condition. Beyond the Neuroptera, it occurs mainly in Diptera and Coleoptera, both highly evolved holometabolous orders. The majority of antlion tribes, Acanthaclisini, Dimarini, Palparidini, Palparini, Stilbopterygini, Myrmeleontini and most Myrmecaelurini and Nemoleontini are psammophiles. This could be considered an autapomorphy for this section of Myrmeleontidae that supports the status of a subfamily Myrmeleontinae, with another other major clade comprised of non-psammophilous forms in the subfamily Dendroleontinae (MANSELL 1996). Morphological characters, including loss of scoli, development of fossorial appendages and setae on abdominal segment 8, increased tooth number in most Palparini, and the ability to move rapidly backwards through sand (Fig. 2), are commensurate with a sand-dwelling existence and could be considered autapomorphies as additional support for the Myrmeleontinae. This subfamily has advanced further in being able to modify the immediate sandy environment into pitfall traps to improve their predatory skills. A pit-building habit, although a derived feature, is extremely ancient, but it further enhanced the success of antlions, in their psammophilous habit (MANSELL 1996). It is limited to the Myrmeleontini and a few genera in other tribes such as Myrmecaelurini. There are several variations to the pit-building adaptation that has been carried to extremes by the Australian antlion *Callistoleon manselli* NEW, 1993 (MANSELL 1988b). Further characters, unsegmented tarsi, sensory setae for detection of vibrations, a highly flexible cervical region and eyes borne on protuberances (secondarily reduced in *Myrmeleon* and other pit-builders), are general myrmeleontoid features that also pre-adapted myrmeleontid larvae for psammophily.

The Dendroleontinae are not as clearly supported, although the long slender legs and opposable pretarsal claws in adults could be considered, along with slender form of the larval jaws. A closer study of the rich Australian fauna would certainly reveal additional characters to clarify the status of this subfamily.

Biogeography

The 12 tribes of Myrmeleontidae, as delimited by STANGE & MILLER (1990) and STANGE (1994) manifest distinctive lifestyles that were reviewed by MANSELL (1996), and distributions that could provide further phylogenetic information. The tribe Myrmeleontini includes *Myrmeleon* LINNAEUS, the only genus that occurs throughout the world – on all continents and islands that support Myrmeleontidae. There are a number of closely related pit-building genera that possess features indicating a close relationship with this genus. The distributions of *Myrmeleon* and its allies suggest that psammophily and pit-construction evolved very early in the myrmeleontid lineage, before the separation of the continents (MANSELL 1996). The tribe Acanthaclisini is not as widespread as *Myrmeleon*, but is nonetheless represented on all continents by different genera. The tribe is comprised entirely of psammophiles and is also an ancient lineage, as indicated by the distributions of its constituent genera. Psammophily is not manifest in Dendroleontini, a tribe that occurs throughout the world, although individuals are rare. This tribe is also an ancient lineage (STANGE & MILLER 1990, MANSELL 1996) whose members may manifest an early stage in the transition from arboreal habits to psammophily. Dendroleontini have undergone a great radiation in Australia, a continent that has long been separated, and a detailed study of this phylogenetically significant fauna is urgently needed. The possibility that Stilbopterygini, a relictual tribe confined to Australia, were precursors to psammophilous antlions cannot be ignored. The larva of *Stilbopteryx linearis* NAVÁS from South Australia resembles those of Ascalaphidae, including well developed scoli, yet it has a psammophilous habit (MCFARLAND 1968), and other myrmeleontid traits are also manifest. Unfortunately, only one larva of Stilbopterygini is currently known, and it has not been comprehensively described. Myrmecaelurini appear to be confined to the Old World and are psammophilies, with several pit-builders (MANSELL 1996). Dimarini and Brachynemurini are psammophiles confined to the Americas, while Gnopholeontini and Lemolemini live mainly on rocks or are arboreal and are confined to the New World. Nemoleontini occur throughout the world and manifest a wide range of larval habits. At present little information can be gained from consideration of this tribe, as it is certainly polyphyletic. STANGE & MILLER (1990) include Palparidini in Palparini, but on adults characters the three species of *Palparidius* PÉRINGUEY, all endemic to southern Africa, are closer to the Dimarini. Maulini comprises three Afrotropical genera whose larvae remain unknown. The tribe Palparini is clearly monophyletic and has radiated since the breakup of Gondwanaland (MANSELL 1992, 1996). The protective covering of sand has enabled palparines to evolve into some of the largest and most efficient psammophilous predators in the Insecta. The resultant large adults, in turn, had to adapt by developing cryptic coloration, resulting in the magnificient wing patterns of all Palparini that enhance the camouflage of these great insects which are certainly a recent myrmeleontoid innovation.

The idea of two clades of Myrmeleontidae, represented by the subfamilies Myrmeleontinae and Dendroleontinae is reiterated. Psammophily has been the key to success in the majority of antlions, and can be used to distinguish the two groups. Myrmeleontinae are well supported by apomorphic features, but this is not as clear in Dendroleontinae where the larvae of many taxa are still unknown. The two clades were already well established before the breakup of the continents, as reflected by the distributions of Myrmeleontini, Acanthaclisini and Dendroleontini. These are the only tribes that occur in all the areas occupied by antlions. Other tribes may have appeared after the commencement of continental separation, as manifest by the radiation of Palparini on the African continent. The current distribution of Palparini, and their vicariance biogeogaphy were discussed by MANSELL (1996).

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Zusammenfassung

Die Myrmeleontiden stellen die größte und am weitesten verbreitete Familie der Neuroptera dar; dies steht im Zusammenhang damit, daß sie ein großes Spektrum von Habitaten – einschließlich Sand – besiedelt haben. Die Adaption an den Sand wurde durch eine Reihe larvaler Autopormophien im Grundplan der Neuroptera ermöglicht und war letztlich das Erfolgsrezept in der Evolution der Myrmeleontiden. Der Übergang von arboralen Habitaten zum Psammophilie spiegelt sich in der Phylogenie der Familie wider und ist möglicherweise der Schlüssel für das Verständnis bisher ungelöster Fragen der Klassifikation der Familie. Wichtige Information ist zudem von biogeographischen Analysen von Verbreitungsmustern von Myrmeleontiden zu erwarten. Konzepte der Klassifikation, morphologische Anpassungen, Entwicklungszyklen, Beutefangstrategien und Verbreitungsbilder von Myrmeleontiden werden besprochen und im Lichte der Aufklärung von Verwandtschaftsbeziehungen diskutiert.

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