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ANTLION ASSEMBLAGES (NEUROPTERA: MYRMELEONTIDAE) OF TWO ARID HABITATS IN TUNISIA

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The antlion fauna was investigated by black-lighting in late spring and late summer at two sites in southern Tunisia, representing pre-Saharan acacia savanna and dwarf shrub semi-desert of the Sahara, respectively. The species compositions recorded differed very markedly between sites and seasons, with few species encountered in both habitats or in both collecting periods. Diversity was distinctly lower at the semi-desert site, where only 21 species, but a high number of individuals, were caught, with a strong dominance of one species each in the two seasons. At the acacia savanna location, 26 species were found, a few of which may, however, be associated with adjoining biotopes of oasis vegetation, ravines and hillside grassland. The species assemblage of the savanna is compared to a previous, similarly rich sample from the same region. Some taxonomic and faunistic remarks are given regarding the species collected.

Key words: Myrmeleontidae, North Africa, habitat preferences, phenology, systematics

INTRODUCTION

Knowledge of the North African antlion fauna is still very incomplete, compared to other regions of the Palaearctic eremial. For the Middle East and Arabia, HÖLZEL (1972, 1981, 1982, 1983, 1988) has provided thorough revisions of the family Myrmeleontidae. KRIVOKHATSKY (*e.g.* 1990, 1992, 1994, 1996, also KRIVOKHATSKY & ZAKHARENKO 1994) has extensively investigated the myrmeleontid fauna of Central Asian deserts, and those of Mongolia are well known through the works of HÖLZEL (1970*a, b*) and KRIVOKHATSKY *et al.* (1996). When attempting to identify North African myrmeleontids, though, we as yet still depend on the insufficient and highly scattered information from numerous works by NAVÁS (1921*a, b*, 1928, 1930, 1931, 1933, 1934, 1936 and many others). The species hitherto reported from North Africa have recently been catalogued (ASPÖCK & HÖLZEL 1996, ASPÖCK *et al.* 2001).

While research on European Myrmeleontidae now comprises several works on reproductive biology (*e.g.* YASSERI 1994, YASSERI & PARZEFALL 1996, YASSERI *et al.* 1998), adult and larval feeding (*e.g.* STELZL & GEPP 1990, LACKINGER 1973) and habitat choice (*e.g.* STEFFAN 1971, YASSERI *et al.* 1997), work on Palaearctic eremial antlions has hitherto been virtually exclusively taxonomic. Information on ecology and phenology is present within the collection data in taxonomic and faunistic publications but these have mostly not been analysed. KRIVOKHATSKY *et al.* (1996) give an overview of habitat preferences for Mongolian Myrmeleontidae, and KRIVOKHATSKY (1998) summarizes data on seasonality at the generic level for the Palearctic. The study of collection data is impeded by the fact that most material (with the exception of much of that dealt with by the latter author) was usually not collected by the specialists themselves.

During two recent visits to southern Tunisia, I was able to collect numerous Myrmeleontidae, mainly by light-trapping. The two sites investigated during these trips represent distinctly different habitats within the Maghrebinian arid zone, namely remnants of acacia savanna on one hand and an ecotone of dwarf shrub semi-desert and erg (sandy desert) on the other. The excursions took place in August/September 1998 and in May/June 1999, so that information on the seasonal occurrence of species could be obtained. Coincidentally, the only comparatively large sample of antlions hitherto collected in Northern Africa originates from the immediate vicinity of the savanna site newly investigated. This material, procured by C. DUMONT in 1927, thus enables an interesting comparison with the recent sample, especially as information on the month of collecting accompanies the specimens.

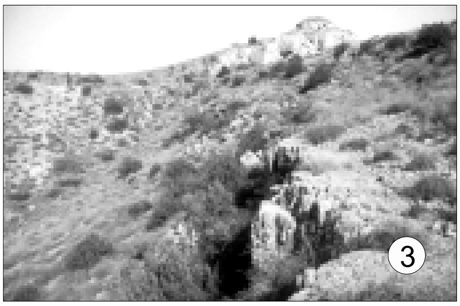
The material gathered also gives new insights on numerous taxonomic questions regarding the Myrmeleontidae of North Africa. However, a full revision that can assign valid names to all species reported here will depend on the reinvestigation of all historic material, particularly all extant NAVÁS types.

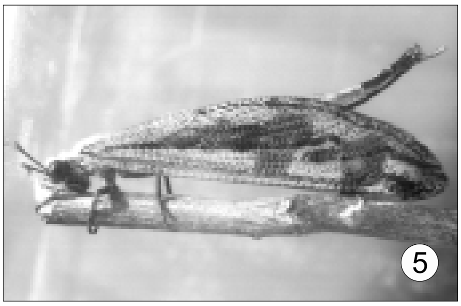
MATERIAL AND METHODS

Localities

Collecting took place at two sites, both declared Tunisian national parks. Bou Hedma National Park (about 34°29'N 9°39'E, currently 116 km^2) is the oldest protected area existing in Tunisia, a forest reserve since 1936, incorporating the only considerable remnant of acacia savanna still extant in the country (Fig. 1). Elsewhere, acacia (*Acacia raddiana* (SAVI) BRENAN) had been removed virtually completely by the end of the 19th century, and natural vegetation communities have undergone further heavy degradation, mainly by grazing. With an annual precipitation of about 250 mm, Bou Hedma is situated near the dry limit for the growth of acacia trees. Since about 1985, Bou Hedma National Park has focused on the establishment of semi-wild stocks of bovid species (*e.g. Addax nasomaculatus* (DE BLAINVILLE, 1816) and *Oryx dammah* (CRETZSCHMAR, 1827)) and of ostrich (*Struthio camelus* LINNAEUS, 1758), all native to this part of North Africa but extinct there since the 19th century. Besides savanna plain with acacia trees, the Bou Hedma mountain chain adjoining to the north, with peaks up to about 800 m elevation is also incorporated in the park (Figs 1, 3).

Along the northern border of the Grand Erg Oriental in southern Tunisia, about 50 km south of the oasis of Douz, a section which is not subject to any specific landuse has been recently set aside as the Jbil National Park (around 33°N 9°E; a more commonly encountered transcription is "Djebil"). It incorporates the northern rim of the Sahara sandy desert (erg) as well as adjoining semi-desert of chamaephytes and perennial grasses (Fig. 4). Here, annual precipitation is distinctly below 100 mm which is often given as the defining border of the Sahara. The national park is projected to eventually cover about 1500 km^2, but details on its precise extension are not currently available from Tunisian authorities.





Figs 1–5. 1 = *Acacia* savanna at Bou Hedma National Park with the Bou Hedma range in the background. 2 = Oasis vegetation adjoining a brook (nearly dry in summer) at the foot of the Bou Hedma mountains. 3 = Open stand of juniper at about 500 m elevation in the Bou Hedma chain. 4 = Dwarf shrub semi-desert with grass tussocks at the border of the Grand Erg Oriental in the Jbil region. 5 = "*Palpares*" *germaini* male at Jbil

Black-lighting

For the collection of adult antlions, a light-trap of commonly used design was employed, consisting of a metal frame carrying a cylindrical piece of transparent drapery cloth surrounding the light source at its center. A mixed light fluorescent lamp with strong UV emission (20 W) was used, accompanied by a pure ultraviolet light (18 W) during the 1999 trip. Usually all Myrmeleontidae settling on the trap or flying in the vicinity were collected. In a few instances, numbers of very abundant species attracted on a particular evening were estimated and not all specimens taken. Wind conditions permitting, the light-trap was usually operated from around sunset (about 19h20 local time in late spring, shortly after 20h00 in late summer) until numbers of antlions newly attracted dropped noticeably. This happened consistently between 0h30 and 1h30, if winds remained low throughout.

In the acacia savanna and the dwarf shrub semi-desert, 4 stations each were selected to carry out black-lighting. No significant differences between these were apparent within the very uniform habitat at Jbil – this was confirmed by the catch results – even though the maximum distance between two of them was about 15 km. Only one of these 4 locations was visited during the second investigation period in spring 1999. At Bou Hedma, in contrast, the 4 stations within a radius of only 2 km represented two distinctly different kinds of biotopes. While two stations were in open savanna, the two northerly ones were situated at the foot of the mountain range, adjacent to two clumps of oasis vegetation. These were supported by a watercourse descending from the mountains to the savanna plain (Fig. 2) and by an artificial catchment from a source on the lower slopes, respectively.

In Table 1, the successful trapping days (defined as producing at least 10 specimens) are listed with some temperature data. The climate was generally slightly cooler in May/June than in August/September, except for one day (02.06.) at the semi-desert site. Early September 1998 at Bou Hedma was characterized by exceptionally high humidity. In complement to the samples from late spring and late summer, other workers have procured some specimens, using the same kind of light trap in autumn 1999 both at Bou Hedma (05–07.10.) and at Jbil (11–15.10.), and at hand-held oil-lamps in early spring 2001 at Jbil (03.04.).

Table 1. Dates of light-trapping in Tunisia with indication of temperature ranges for the day and during black-lighting sessions

sites	1998 trapping dates	20h00 (top) and 1h00 (bottom) temp.	daily max. (top) and min. (bottom) temp.	1999 trapping dates	19h30 (top) and 1h00 (bottom) temp.	daily max. (top) and min. (bottom) temp.
Bou Hedma	21–24.08.	29–31°C	40–42°C	25–26.05.	21–24°C	39°C
(savanna stations)		22–27°C	20–22°C		18–20°C	17–18°C
Jbil	26–27.08.	31–38°C	45–49°C	30.05.–02.06.	31–38°C	42–44°C
(semi-desert /erg)	31.08.–02.09.	24–31°C	19–21°C		25–31°C	19–23°C
Bou Hedma	04–06.09.	34°C	39–40°C	06.06.	29°C	40°C
(oasis stations)		27–29°C	24°C		24°C	21°C

Other collecting methods

Antlions were also occasionally found during the day, flying actively, or when beating vegetation. These, however amounted to less than 4% of the specimens from Bou Hedma, while at Jbil only 1 individual was thus detected. Numerous larvae of pit-building species were collected at Bou Hedma and some later raised. These are not included in the numeric totals given in the results section. The quest for non-pit-building larvae unfortunately proved largely futile at the investigated localities.

Historic samples

In the late 1920s, C. DUMONT collected a variety of insects in south-central Tunisia, among these a large number of Myrmeleontidae. The latter were treated mainly by NAVÁS (1930), with additions and repetitions in NAVÁS (1931, 1933, 1934, 1936). As NAVÁS' concepts regarding species delimitation and denomination are very insufficient, it has been necessary to reinvestigate DUMONT's material, preserved chiefly at the Museum National d'Histoire Naturelle, Paris (MNHN), in order to gain a data set suitable for comparison to the present sample from Bou Hedma. At MNHN, a total of 458 specimens of Myrmeleontidae labeled "Maknassy 1927" were investigated, with additional indication of the month of collecting (between May and August) for 446 of them. The town of Maknassy is situated north of the Bou Hedma range, a direct distance of less than 15 km from Bou Hedma NP. Some further specimens belonging to this series have been seen in the Naturhistorisches Museum Basel (NHMB) and further ones may be present in other museums. There are, in MNHN, additional Myrmeleontidae collected by DUMONT labeled "Maknassy 1929" (June to November, 105 specimens) and "Bou Hedma 1929" (May and June, 43 specimens). Only a few specimens of the latter series have been published by NAVÁS (1931, 1933, 1934). These samples are not evaluated specifically in the present paper though some reference is made in the following as concerns species of interest not present among the "Maknassy 1927" series.

RESULTS

The collecting yielded a total of 42 species from the two investigated areas as listed below. The purpose of this contribution is not predominantly in the field of taxonomy, thus I relegate systematic and faunistic notes regarding the taxa concerned to an appendix to this paper.

"*Palpares*" *angustus* MCLACHLAN, 1898
"*Palpares*" *germaini* NAVÁS, 1921
Fadrina sp.
Centroclisis punctulata NAVÁS, 1912
Centroclisis cervina (GERSTAECKER, 1863)
Phanoclisis longicollis (RAMBUR, 1842)
Myrmecaelurus cf. *lachlani* NAVÁS, 1912
Myrmecaelurus medius NAVÁS, 1913
Nohoveus lepidus (KLUG, 1834)
Nohoveus palpalis (KLAPÁLEK, 1914)
Nophis teillardi NAVÁS, 1912
Lopezus arabicus HÖLZEL, 1972
Maracanda lineata NAVÁS, 1913
Gepus invisus NAVÁS, 1912
Gepus tersus NAVÁS, 1919
Solter liber NAVÁS, 1912
Cueta lineosa (RAMBUR, 1842)
Cueta pallens (KLUG, 1834)
Cueta sp. 3
Myrmeleon hyalinus OLIVIER, 1811

Myrmeleon fasciatus (NAVÁS, 1912)
Myrmeleon pseudofasciatus HÖLZEL, 1981
Macronemurus elegantulus MCLACHLAN, 1898
Mesonemurus harterti NAVÁS, 1920
Geyria lepidula (NAVÁS, 1912)
Geyria saharica ESBEN-PETERSEN, 1920
Neuroleon tenellus (KLUG, 1834)
Neuroleon leptaleus (NAVÁS, 1912)
Neuroleon dumontinus (NAVÁS, 1930)
Neuroleon sp. 3
Neuroleon numidus NAVÁS, 1928
Quinemurus cf. *cinereus* KIMMINS, 1943
Distoleon sp. 1
Distoleon cf. *annulatus* (KLUG, 1834)
Delfimeus scriptus NAVÁS, 1912
Creoleon cf. *arenosus* NAVÁS, 1934
Creoleon alternus NAVÁS, 1933
Creoleon sp. 3
Creoleon sp. 4
Creoleon sp. 5
Pseudoformicaleo gracilis (KLUG, 1834)
Ganguilus pallescens NAVÁS, 1912

At Bou Hedma, 26 of these species were collected represented by 222 specimens. Of these, 57 are from May/June, 154 from August/September and 11 from October. The numbers for Jbil were 505 specimens of 21 species. However, two of these, *Maracanda lineata* (in May/June) and *Geyria lepidula* (in August/September) were so abundant that not all specimens attracted to the light source were taken. *G. lepidula* was in fact the most numerous insect in one of the collecting nights (26.08.98) with up to about 250 present at the light trap. The estimated total for Jbil, considering specimens actually attracted, was thus about 450 Myrmeleontidae for May/June and over 700 for August/September; 23 each were collected in April and October.

Markedly different species arrays could be demonstrated at the two arid sites. Only 5 species were found at both (marked with X in Fig. 6), 3 of which were common to abundant at Jbil while represented by single or very few specimens in the Bou Hedma material. *Neuroleon dumontinus* (1 specimen at Bou Hedma) may have to be added to this group as it is possibly identical to *Neuroleon* sp. 3 from Jbil (see appendix). *Gepus invisus* was encountered more commonly at Bou Hedma than at Jbil, while *Distoleon* cf. *annulatus* is the only species almost equally represented at both localities. It is, however, seasonally peculiar, as it was virtually restricted to the October material. This very small but remarkably distinctive sample added 1 species to the Bou Hedma and 3 to the Jbil list, these latter representing over half of the individuals caught in October. The single but numerous species flying at Jbil in April, *Lopezus arabicus*, is also restricted to that time of the year.

A conspicuous segregation is also obvious between the two main collecting seasons, noticeable at both localities (Fig. 6). Only 6 species at Bou Hedma, and 3 at Jbil, were found both in late spring and late summer, most of which showed a clear preference for one of those periods.

The lower number of species and higher number of individuals at Jbil, mainly attributable to the above-mentioned very high numbers of two of the species, also account for a marked difference in dominance patterns between the two locations,

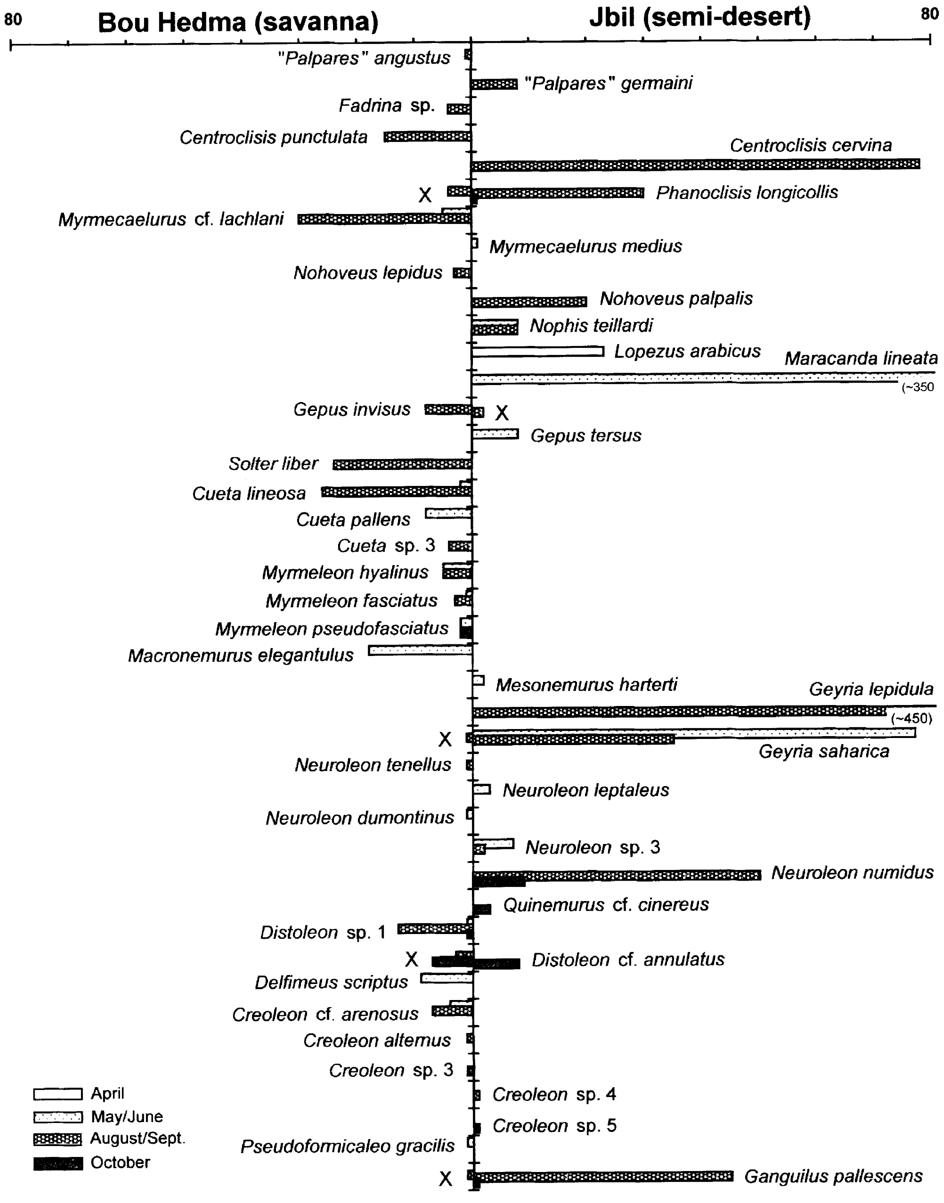


Fig. 6. Species and numbers of individuals of Myrmeleontidae caught at Bou Hedma and Jbil in 1998, 1999 and 2001, subdivided by season. X: species recorded at both sites

the acacia savanna showing a higher diversity. In May/June, *Maracanda lineata* accounted for over 3/4 of the catch at the semi-desert, and *Geyria lepidula* for over 60% in August/September. Just 2 species in late spring (5 in late summer) contributed well over 90% of specimens. In contrast, the single most numerous species at Bou Hedma were represented with only 1/3 and 1/5 of individuals in May/June and August/September, respectively. The three most common species contributed only just over 60% in the earlier and 50% in the later period, in which these 3 were caught in almost equal numbers.

The higher diversity of antlions at Bou Hedma in comparison to the semi-desert/erg ecotone at Jbil is certainly in part a reflection of the ecological circumstances. However, it needs to be noted that the effect is enhanced by the chosen black-lighting locations at Bou Hedma representing two distinct kinds of habitat. This can be demonstrated by comparing results from the 2 acacia savanna loca-

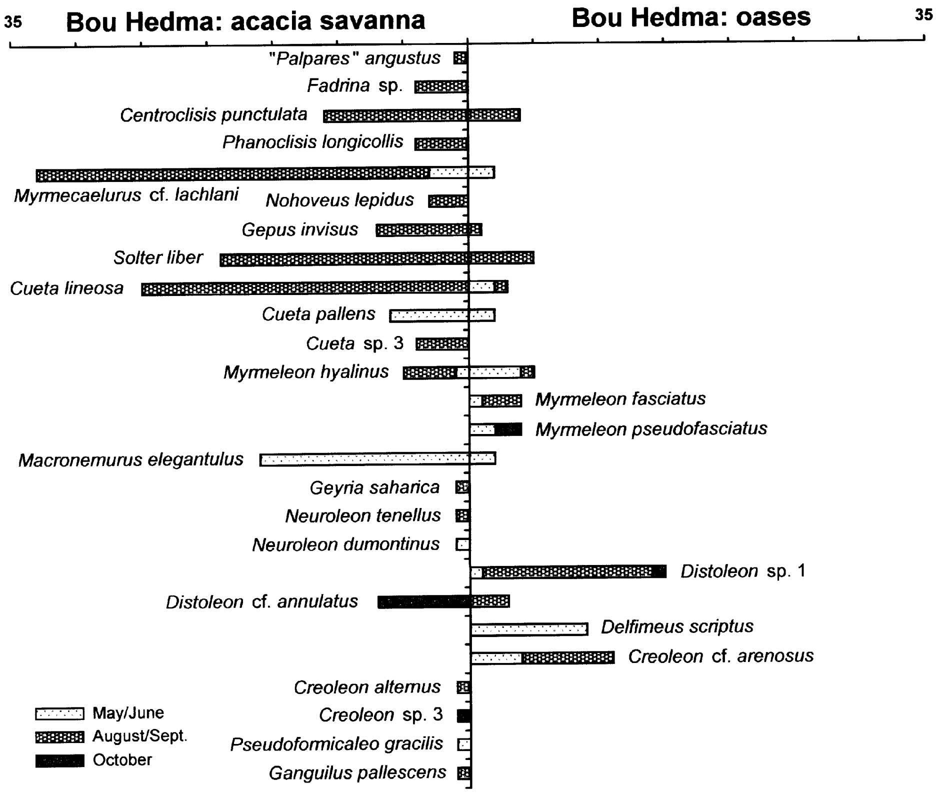


Fig. 7. Species and numbers of individuals of Myrmeleontidae caught at acacia savanna and oases light-trapping stations at Bou Hedma, subdivided by season

tions with those from the 2 locations at the mountain-base oases (Fig. 7). While those species represented by at least 5 specimens at the acacia savanna also occurred at the oasis sites, 5 species were found only at the latter, 3 of which constituted the most numerous ones there.

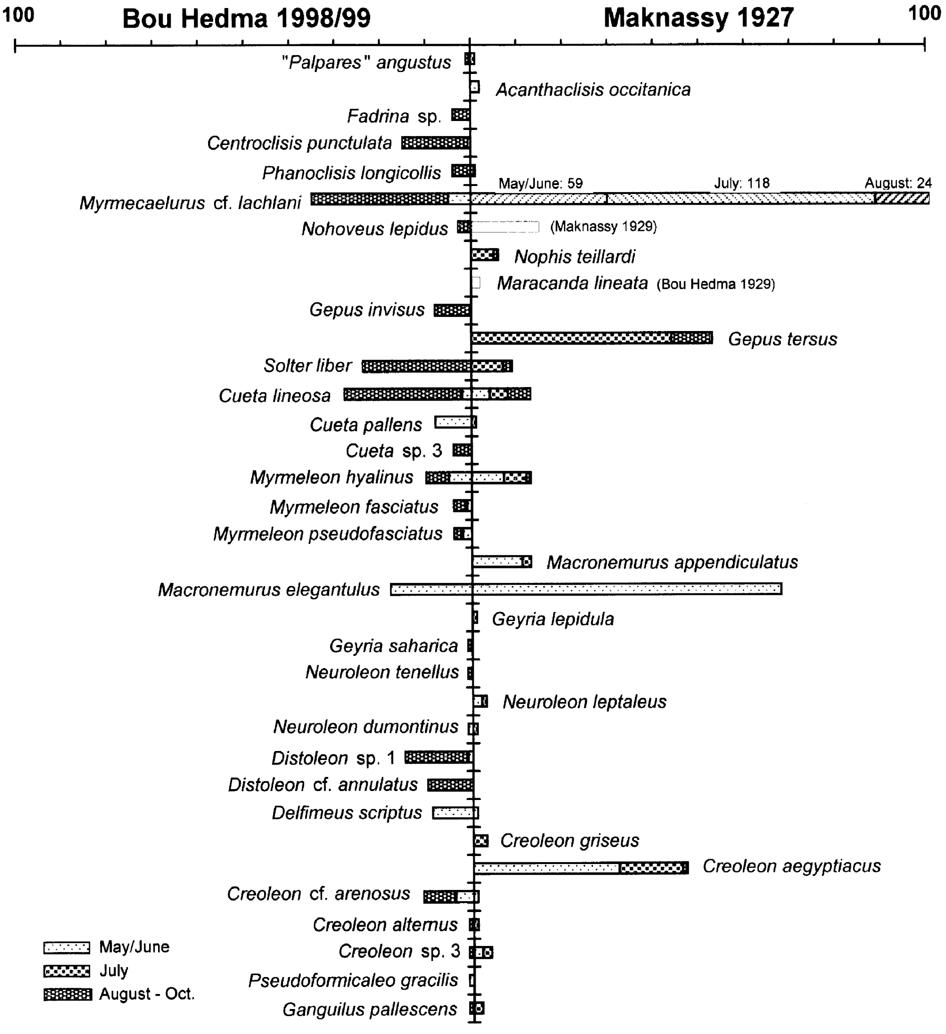


Fig. 8. Species and numbers of individuals of Myrmeleontidae caught at Bou Hedma (present study) and at Maknassy (C. DUMONT leg. 1927), subdivided by season. *Nohoveus lepidus* and *Maracanda lineata* added from other samples by DUMONT. Column size for *Myrmecaelurus* cf. *lachlani* on right hand side reduced by one half

Predictably, C. DUMONT's large sample of antlions from the year 1927 from Maknassy shows many similarities in species composition and abundance to the present collections from nearby Bou Hedma (Fig. 8). The *Myrmecaelurus* species is the most numerous in both, though a lot more dominant in the older material (nearly 50% compared to 16% over all seasons). This is partly because DUMONT collected 60% of the individuals of this species in July, obviously its main period of occurrence, during which I have not collected at Bou Hedma. In that month, the species accounted for more than 70% of specimens. *Macronemurus elegantulus* dominates in May/June, holding about 30% in both samples. Several moderately numerous species are about equally represented, showing the same seasonal preferences. The absence or near-absence of a few species in DUMONT's material is noteworthy. They are, on one hand, those which occur at Bou Hedma mainly or exclusively at the oases trapping locations (e.g. *Distoleon* sp. 1, *Myrmeleon fasciatus*, *M. pseudofasciatus*), on the other hand the two acanthaclisine species *Centroclisis punctulata* and *Fadrina* sp. Those species which are present only in the Maknassy sample also represent different groups. There are some further species which are shown here to be typical for the dwarf shrub semi-desert in addition to those also found sparsely in recent Bou Hedma material (e.g. *Nophis teillardi*, *Geyria lepidula*, with *Maracanda lineata* being added from DUMONT's small Bou Hedma sample). Again, these are represented by very few specimens, with the exception of *Gepus tersus*. More intriguing are *Acanthaclisis occitanica* (VILLERS, 1789), *Macronemurus appendiculatus* (LATREILLE, 1807) and *Creoleon aegyptiacus* (RAMBUR, 1842), the latter being the fourth-most numerous species in the Maknassy sample. These species are to be considered associated to Mediterranean-type habitats and are, in Tunisia, otherwise restricted to the northern third of the country. A further species restricted to DUMONT's collection is *Creoleon griseus* (KLUG, 1834).

DISCUSSION

The total of 42 antlion species found in the two areas explored, is remarkable in comparison to only 37 species recorded by ASPÖCK *et al.* (2001) for the whole of Tunisia, about 6 of which are to be regarded as Mediterranean faunal elements ordinarily not expected in the savanna and desert zone in question (but see below). However, the species number reported reflects to a large part the very limited collecting activities in Tunisia up to now, and also the country's small size compared to its neighbours. In fact, the Myrmeleontidae recorded from Algeria, Tunisia and Libya combined amount to 93 species (ASPÖCK *et al.* 2001). This includes numerous names published by NAVÁS many of which will prove to be synonyms as far as they still can be elucidated, certainly more than offsetting the number of species still to be discovered. Thus, I reckon that there occur about 80 species of Myrmeleontidae in the mentioned 3 countries. Up to 70 of these may pertain to the eremial realm, so more than half of this prospected number occur at Bou Hedma and Jbil combined. The Maghrebinian fauna is obviously less rich than that of the sub-Saharan savanna belt where nearly 80 species were discovered in a restricted area of southern Mali alone (MICHEL 1999) – admittedly more humid than the region treated here. To cite another comparison, there are 113 species known from the Arabian Peninsula (HÖLZEL 1998), but no figures have been published for single localities there.

Habitat association

Few previous studies of myrmeleontid faunas in parts of the Palaearctic eremial assessed ecological requirements of species. Here, very distinct species compositions were discovered at two sites representing almost maximally different biotopes within the North African arid zone. The semi-desert/erg ecotone sampled constitutes one of the climatically and ecologically most extreme habitats where myrmeleontids can be expected (although it has not been examined which species, if any, might still be found in vegetationless sandy or stony desert). In contrast, acacia savanna, in a less arid variant in pristine condition, may have constituted a transition to arboreal biotopes. The savannas and steppes found today in the Maghreb south of the Atlas mountains exhibit various, usually severe degrees of degradation and desertification. Compared to unspoiled habitats, an impoverished fauna might be expected with an introgression of species typical for less vegetated areas. The presence of a few individuals of several species in the Bou Hedma and Maknassy samples, which are common in the dwarf shrub semi-desert (see Figs 6, 8), may be interpreted in that light. A comparative sampling of degraded steppe habitats would be of considerable interest.

Obviously it would be an over-simplification to regard the two locations visited as representing extremes in a linear array of habitat types to be found in the Maghrebinian savanna and steppe belt. Many older samples from that region appear to include representatives from both the Bou Hedma and the Jbil species assemblage, though small sample sizes and uncertainties of the reported identifications make interpretation difficult. Biotopes with a mixture of ecological properties may well have been involved. On the other hand, different, and in some cases rather distant, habitats sampled could have been reported under the same locality, as collection data used to be recorded with little precision. Old collection data will thus be hard to evaluate in terms of ecological preferences of species. Many of the species recorded here at the erg/semi-desert ecotone have been cited rarely, or never before, for the Maghreb. Apparently, few previous excursions have touched this kind of habitat.

The comparison of results from the different light-trap locations at Bou Hedma reveal that some species detected are probably not associated with acacia savanna, occuring only at the oasis stations. *Myrmeleon fasciatus* can be connected with the presence of many cavelets along ravines at the foot of the mountain range where its larvae were found dwelling in considerable numbers. This may be true also for *Myrmeleon pseudofasciatus* even though the early stages of this species are not known. One of 11 specimens of *Creoleon* cf. *arenosus* was collected by day from grasses on the lower slopes of the mountains, possibly associating the species with that kind of habitat. The mountain grassland, typified by dense stands of halfa (*Stipa tenacissima* L.) differs considerably from the savanna plains where another esparto (*Lygeum spartum* LOEFL. ex L.) and sagebrush (*Artemisia herba-alba* ASSO) are more characteristic. The species *Delfimeus scriptus* and *Distoleon* sp. 1 may well be genuinely associated with oasis vegetation. There are a few records of the former from the Maghreb, all from the southern slope of the Saharian Atlas, which appears to be consistent with that presumption.

The most striking deviation of C. DUMONT's Maknassy sample from the present Bou Hedma material is the presence of some myrmeleontids which are to be regarded as Mediterranean rather than eremial faunal elements (see Fig. 8). Given the geographic location, this initially seems intriguing. The southern limit of distribution for Mediterranean fauna would ordinarily be expected in the south-eastern chain of the Atlas, the foothills of which are situated about 100 km to the northwest of Maknassy. Other data available from North Africa corroborate this. However, in the higher reaches of the Bou Hedma range, interspersed with halfa grasslands, one encounters tracts of very open juniper brush (Fig. 3), with some other shrubby vegetation of Mediterranean origin (e.g. *Pistacia* sp.) at the most sheltered spots. Surprisingly, two Mediterranean ascalaphids, *Libelloides ictericus* (DE CHARPENTIER, 1825) and *Deleproctophylla* sp. were observed flying here in early June. I suggest that DUMONT must have collected Mediterranean Myrmeleontidae on trips southward from Maknassy into the Bou Hedma chain. The collection data along with the high number of specimens indicate that DUMONT has been resident at Maknassy during the summer of 1927, making such excursions likely. For logistical reasons, I was unable to carry out black-lighting in the Bou Hedma mountains, which would be of special interest. The discovery of further Mediterranean faunal elements, which must be restricted to very isolated locations that far south, would still add to the already impressive diversity of Neuroptera at this protected area.

Obviously the significance of Bou Hedma National Park is greatest for the preservation of species directly dependent on acacia trees. Both *Centroclisis punctulata* and *Fadrina* sp. are lacking in DUMONT's material and are, respectively, rare and absent in all other collections from North Africa, whereas at least the former species is common at Bou Hedma (they are not in DUMONT's Bou Hedma sample, because he collected there to early in the year – May and June). These two species may hence be the most partial to true acacia savanna and some ecological dependence on the tree itself may be suspected. *C. punctulata* also occurs rather commonly in the sub-Saharan savanna zone where, according to the collection data in PROST (1998), it prefers the most arid part, also with *Acacia raddiana*. The few localities in Israel and the Sinai and Arabian Peninsulas recorded for *Fadrina formosa* (HÖLZEL, 1981), which may be identical to the Tunisian *Fadrina* sp. (see appendix), are generally well-watered areas, some protected, favouring both growth of trees including acacias and their preservation.

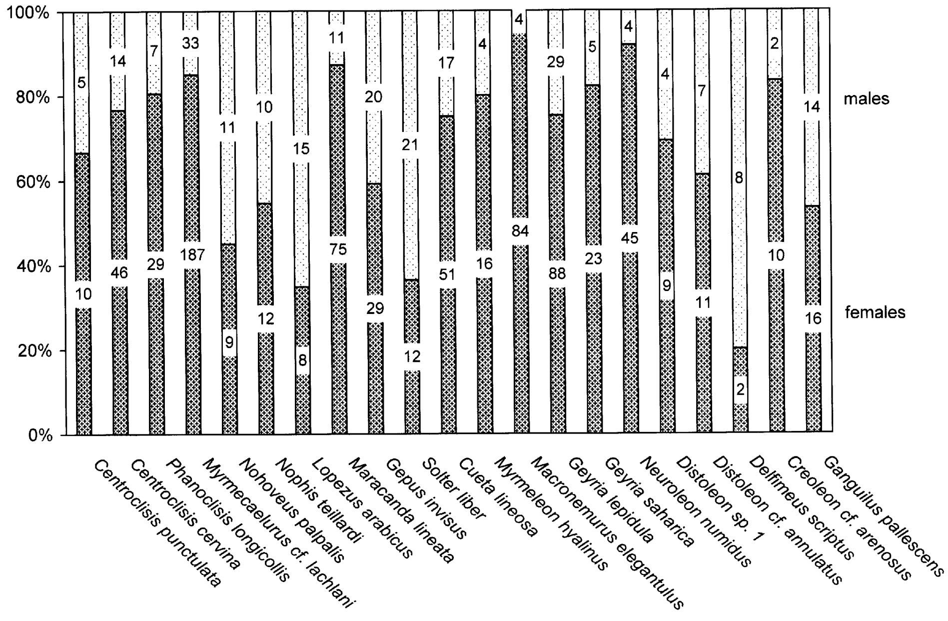


Fig. 9. Sex ratios encountered for antlion species at light traps in Tunisia. Species represented by less than 10 specimens in recent sampling omitted, DUMONT's material included for the presented species

Seasonality

A summary of the seasonal appearance of Palaearctic antlions by KRIVOKHATSKY (1998) shows adults of a majority of species to be encountered in August. While numbers of both species and individuals in the present study were clearly higher in August/September than in May/June, the seasonal seggregation proved considerable. About half of the species occurring in the early season were restricted to it, including the most numerous ones. KRIVOKHATSKY (1998) does not consider months beyond August in his summary. In the more temperate, arboreal regions of the Palearctic, records of antlions later than this month are rather sparse and virtually confined to September. They are more numerous in the eremial and there are indications from the material investigated here that adults of some species may be specialized for flying in September and October, possibly later. This pertains to *Distoleon* cf. *annulatus* as well as two species at Jbil probably assignable to *Quinemurus* (see appendix). Previous records of this genus are in line with this presumption (see HÖLZEL 1983, KRIVOKHATSKY 1992). As regards the mentioned *Distoleon* sp., it is noteworthy that *D. annulatus* is the only European antlion recorded as late as October according to ASPÖCK *et al.* (1980). At the savanna site, *Nohoveus lepidus* may be a late species, being present in Maknassy material from 1929, but not 1927 (see Fig. 8). In the earlier year, DUMONT discontinued collecting probably rather early in August, as concluded from the comparatively small overall number of specimens from that month. At the beginning of the season in the semi-desert, *Lopezus arabicus* was present as the only species in early April, but no longer found in late May. Previous, relatively numerous records of the species (as *L. fedtschenkoi* (MCLACHLAN, 1875)) from the Algerian Sahara date from February to May, with a single May citing from Nefta, Tunisia (NAVÁS 1930). Another species with a remarkable phenology is the ubiquitous pit-builder *Myrmeleon hyalinus*. It is the only antlion species in a small March sample from Bou Hedma, and DUMONT encountered one in November. In Arabia and the sub-Saharan steppe belt, adults of this species occur year-round (HÖLZEL 1987).

Light-trap performance

It is the usual perception that nearly all Myrmeleontidae – excepting some diurnal Palparini (e.g. *Pamexis* spp., MANSELL 1992*a*) – are attracted to light. Nonetheless, as in all studies envolving black-lighting or, in fact, other trapping methods, the trap responses cannot be taken as fully reliable representations of actual abundance of the species concerned. Light-trap responses of different species of Myrmeleontidae may differ for a multitude of reasons, possibly widely, so that even relative catch rates of species in a given locality have to be viewed with care. The clearest indication for this is the very different sex ratios recorded for antlion species at light-traps in the present (Fig. 9) as well as previous studies, although this finding has rarely been stressed. It is deemed highly unlikely that distinct female preponderance of up to 95% represents the true sex ratio present in the population. While there is almost no information on life histories for most species, mating systems as described by YASSERI (1994) and YASSERI and PARZEFALL (1996) for the European *Euroleon nostras* (GEOFFROY, 1785) would predict sex ratios close to 1:1. However, trap responses are deemed associated with flight activity, as individuals are probably not attracted to light while inactive. Highly female-skewed sex ratios at light traps may thus be associated with stationary males attracting females as is the case in *Euroleon nostras*. Flight activity can also be linked to feeding or oviposition, the latter also promoting higher trap yields for females. Whatever the reason, there is strong indication that trap responses of the sexes differ distinctly in some species – so, therefore, may trap responses of different species, which is only harder to demonstrate. As there exists presently no alternative trapping method for myrmeleontids which would yield a sufficient catch to allow a meaningful comparison with black-lighting, this issue will be difficult to elucidate. There is circumstantial evidence that some species may – at least during certain periods – not have been attracted to the light source employed here. A single male of *Pseudoformicaleo gracilis* was caught out of a number of antlions hovering around the canopy of an acacia, possibly in mating activities. It appeared that they were all this species. Clearly they were not attracted to the light-trap in operation about 30 m distant. The single male of *Neuroleon dumontinus* was netted hovering around low bushes close to the light source, without showing orientation towards it.

Another issue touching the representation of population densities in the catch is the interpretation of the very high number of individuals encountered at the trap at Jbil, particularly of the dominant species *Maracanda lineata* early in the season and *Geyria lepidula* later. This may be caused either by a much greater radius of influence for the trap compared to the situation at Bou Hedma, by exceptionally high trap response of the species concerned under the given circumstances, or by genuinely high population densities. While the open landscape of the semi-desert in fact allowed the fluorescent lamps at Jbil to be seen from over 10 km distance by the human eye, it appears unlikely that the radius of influence was nearly that large, nor a lot larger than in the acacia savanna. For example, a 125 W mercury vapour bulb was calculated to show an effective radius – defined as the area in which the light-trap surpassed background light intensity – of just over 500 m maximally (*i.e.* under new moon conditions) in light-trapping campaigns in tropical Africa (BOWDEN

& MORRIS 1975). Hence, while the more structured vegetation at Bou Hedma may have accounted for a somewhat lower effective radius than at Jbil, all other factors deemed equal, it is unlikely that this has effected the trap performance severely. There is, further, no indication that the climatic and moon cycle conditions would have favored large turnouts particularly during the trapping days at Jbil. Successful trapping nights were characterized throughout by low winds and usually little moonlight. In fact, trapping at Jbil rather than at Bou Hedma was impared by an almost constant slight breeze. I can see no reason why *Maracanda lineata* and *Geyria lepidula* should show much higher trap responses than the other antlion species encountered. Both are very small species, so neither large areas of activity, nor above-average flight performance under somewhat unfavourable wind conditions would be expected (the latter may be true for the large *Centroclisis cervina*, also very numerous at Jbil). Possibly, species with more even sex ratios at light-traps – probably with mating systems not characterized by female attraction – may have higher trap responses overall if both sexes instead of only females show high flight activity. However, *Geyria lepidula* and *Maracanda lineata* showed strongly female-skewed sex ratios at the trap (see Fig. 9). It has thus to be concluded that the large numbers caught of these, and to a lesser extent some other species at Jbil, indeed represent, to a significant part at least, high population densities.

Larval niches

It is hard to reconcile the failure to discern larvae at the semi-desert/desert biotope with the postulated abundance of several species. The methods to detect non-pit-building antlion larvae employed at Jbil, all fruitless, were sieving sand from the bases of chamaephytes and grass tussocks as well as looking for tracks in the sand at night, and digging out clumps of vegetation during the day. It must be emphasized that the climate extremeties prevalent during the investigation period may have been particularly unfavorable for the detection of antlion larvae. Daily sand surface temperature approached 70°C both in early June and late August, so that arthropods needed to be hidden several decimeters deep. Even nocturnal activity periods may have been shortened and the possibility that some antlion larvae undergo a summer diapause under this climatic regime cannot be ruled out, even if such a case has yet to be demonstrated. Other workers at Jbil, though not specifically in search of antlions, have procured 3 larvae by digging out grass tussocks and a further one from its track at the sand surface in March and October. The difficulties of detecting non-pit-builders at Bou Hedma were less unexpected because of the hard soil surface of most tracts of open ground, even though it had been hoped that sifting litter under acacias would produce some results. Season may again have been a factor. In a previous study of ground-dwelling arthropods at Bou Hedma, some myrmeleontid larvae were encountered in soil traps (MOLDRZYK pers. comm.).

It was quite obvious in the field that surface structure at Jbil does not support the construction of pitfall traps by antlions due to extremely fine-grained, movable dune sand. The sand-free tracts are characterized by an exceedingly solidified and stony surface. *Cueta lineosa* does occur in similar soil, e.g. around Cairo, but no pits were found at Jbil. The array of species collected at light seems to confirm the absence of pit-builders. Larvae of only two of the species have been described – *Phanoclisis longicollis* (STANGE & MILLER 1985) and *Nophis teillardi* (SIMON 1986) –, but the two genera of the region in which all species construct pits as far as known, *Myrmeleon* and *Cueta*, are conspicuously absent at Jbil. The tribe Myrmecaelurini, some species of which are known as facultative pit-builders, is represented by *Nophis teillardi*, which does not construct pits (SIMON 1986), by the virtually unknown *Myrmecaelurus medius* and by *Nohoveus palpalis*. Two larvae from Egypt from which *N. palpalis* could be reared were described by the collector as having been extracted from round shallow depressions reminiscent of, but not quite conforming to, typical antlion pits. The absence of pit-builders will probably be found a local phenomenon, not extending to every biotope influenced by dune sand. At the oasis of Douz, 50 km north of Jbil, adults of *Myrmecaelurus* cf. *lachlani* and *Myrmeleon hyalinus* were collected. In a semi-desert habitat nearby, similar to Jbil but deviating somewhat in surface structure and vegetation composition, pits of *Myrmecaelurus* sp. were detected in very sheltered spots under dense, low shrubs. At the acacia savanna at Bou Hedma, species of *Myrmeleon*, *Cueta* and *Myrmecaelurus* featured prominently in the adult trap yields (42% of specimens, see Fig. 6), and pits of all three genera were encountered.

Obviously, detecting larvae and describing feeding habits, connection to specific substrates and other ecological requirements will be paramount to understand the syntopic occurrence of so many species of Myrmeleontidae as demonstrated here as well as in other studies. While the adults of antlions may well show specific demands on the habitat (*e.g.* YASSERI 1994), the main differences between ecological niches will concern the life histories of larvae. MANSELL (1996) has reviewed the different habitats used by myrmeleontid larvae, but there is little information how non-pit-building psammophilous species, which is by far the largest group, differ in their specific niches. STEFFAN (1971) has demonstrated such differences for several species at the French Mediterranean coast. As regards the species treated here, there are a few laboratory observations on larvae of *Centroclisis punctulata* and *Phanoclisis longicollis* along with other Acanthaclisini by STANGE and MILLER (1985) that revealed differences of feeding behaviour, though very few individuals were involved.

It will be a time-consuming task to describe niche seggregation of the numerous syntopic species through the habitat use of larvae, given the difficulties of studying them. Meanwhile, sampling of more localities for adults could shed some light on associations of species with certain ecological features of habitats and certain seasons. A revision of the North African Myrmeleontidae is desirable so as to be able to assign valid names to the investigated species.

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APPENDIX

In the following, some taxonomic notes are given regarding those species which have not yet been identified with certainty and thus were assigned provisional names in the present paper. Also, comments are added for some species of *Neuroleon* and *Creoleon* which could be identified to species described by NAVÁS (1928, 1930, 1933, 1934) from the vicinity, but for which probably older synonyms will surface upon revision. Generally, names could not be assigned to the majority of *Neuroleon*, *Distoleon* and *Creoleon* species due to the deficient state of knowledge of the systematics of these nemoleontine genera. I also mention new records for Tunisia. Note that some of the 42 species recorded here are not new for the country even though uncited by ASPÖCK *et al.* (2001); records have been detected and verified for these (*Phanoclisis longicollis*, *Nohoveus lepidus*, *Lopezus arabicus*, *Geyria lepidula*) in NAVÁS (1921*b*, 1930).

"*Palpares*" *germaini* NAVÁS, 1921 (Fig. 5) – The Palparini species found at the semi-desert locality could be securely identified as *Palpares germaini* NAVÁS, 1921, described from Béchar at the border of the Grand Erg Occidental in western Algeria. NAVÁS' description, for once extensive, matches to the detail, and M. W. MANSELL (Pretoria) kindly compared specimens from Tunisia with the holotype and previously single known specimen. Both this species and "*Palpares*" *angustus* are not longer regarded as belonging to *Palpares* RAMBUR, 1842 – their generic placement will be determined in the ongoing revision of the Palparini by M. W. MANSELL (see MANSELL 1992*b*).

Fadrina sp. – Antlions of this genus have not hitherto been reported from Northern Africa. The present specimens are not referable to *F. rufa* NAVÁS, 1912 which is rather common in the sub-Saharan savanna belt (PROST 1998), though apparently inhabiting rather southerly, more humid parts. However, it is very similar, possibly identical, to *Fadrina formosa* (HÖLZEL, 1981) from Israel, Sinai, the Arabian Peninsula and Sudan. The relation to *F. nigra* NAVÁS, 1912 from Yemen and East Africa also needs reinvestigation.

Centroclisis cervina (GERSTAECKER, 1863) – New for Tunisia.

Myrmecaelurus cf. *lachlani* NAVÁS, 1912 – All specimens of *Myrmecaelurus* s. str. are here subsumed under one species, in the absence of compelling evidence to the contrary. A few females from Bou Hedma appear distinctly aberrant, more material will have to be studied to determine if they may represent other species. The many specimens collected by DUMONT have been attributed to no less than 5 species by NAVÁS (1930): *M. lachlani* (predominantly), *M. trigrammus* PALLAS, 1771, *M. laetus* (KLUG, 1834), *M. tabarinus* NAVÁS, 1913 and *M. quedenfeldti* (KOLBE, 1884), the latter in fact belonging to *Macronemurus*. Viewing the material, there are no criteria discernible on which this distinction may have been based. Recently, a specimen of *Myrmecaelurus* s. str. from the Moroccan desert has been attributed to *M. lachlani* (MONSERRAT *et al.* 1990), though there seems to be doubt as the type was collected in the Moroccan Atlas mountains.

Myrmecaelurus medius NAVÁS, 1913 – The only specimen hitherto reported has been the female holotype from east of Ghardaia, Algeria, which is clearly conspecific with one male from Jbil. Male genitalic features place the species in the genus *Nohoveus* as presently conceived.

Nohoveus palpalis (KLAPÁLEK, 1914) – New for Tunisia.

Cueta sp. 3 – A few specimens from Bou Hedma differ clearly from the other two *Cueta* species recorded, showing the following combination of characters: wings narrow and unmarked as in *C. pallens* with pale unmarked venation, much smaller than that species (size as in small *C. lineosa*), male ectoprocts intermediate in length. It remains to be studied whether NAVÁS has hit this species among the wealth of new names he has supplied for North African *Cueta*. Most of these will probably prove to be synonyms of *C. lineosa* even though I suspect that the North African material assigned to the latter may contain a second, very similar species.

Myrmeleon pseudofasciatus HÖLZEL, 1981 – New for Tunisia and North Africa, hitherto known only from the Middle East.

Neuroleon dumontinus (NAVÁS, 1930) – One male from Bou Hedma can be unequivocally associated with a female in DUMONT's Maknassy material, the holotype of *Afroclimacius dumontinus* NAVÁS, 1930. The species recalls *Noaleon limbatellus* (NAVÁS, 1913) described from Algeria, especially as regards the very slender elongated legs, but wing structure and pattern differ.

Neuroleon sp. 3 – Differs from *N. dumontinus* very little, mainly in more heavily marked wings. The Bou Hedma and Jbil populations are being provisionally kept separate here.

Neuroleon numidus NAVÁS, 1928 – The species, common at Jbil, has been known before from the lone holotype from El Kantara in the Aurès range in eastern Algeria. That locality may be imprecisely reported: areas of sandy desert rather occur farther south near Biskra. The swelling of the male abdominal segments III and IV strongly suggests that the species be placed in the genus *Quinemurus* (compare figure in KRIVOKHATSKY 1992) though ectoproct and leg structure would appear not to be in accordance.

Quinemurus cf. *cinereus* KIMMINS, 1943 – Based on the structure of the cubital field in the hindwing this species seems also to belong to *Quinemurus*, and the similarity to *Q. cinereus* from Arabia is great. However, males have unfortunately not been found yet at Jbil.

Distoleon sp. 1 – It appears that this species is not identical with any described *Distoleon*. It is smaller than any other Palearctic species currently assigned to the genus with the exception of *D. gafsanus* (Navás, 1921). The latter originates from the Tunisia steppe zone and is apparently again smaller, but only parts of the body without wings remain of the type. A character which should make *D.* sp. 1 easily recognizable are numerous strongly elongated setae on the male hind tibiae (some more than half the length of the tibia itself).

Distoleon cf. annulatus (KLUG, 1834) – Both the Jbil and the Bou Hedma specimens are a lot paler and less extensively marked than any *D. annulatus* specimens I have seen, but there is no obvious structural difference.

Delfimeus scriptus NAVÁS, 1912 – New for Tunisia.

Creoleon cf. *arenosus* NAVÁS, 1934 – Being the only *Creoleon* represented here by more than one specimen, its similarity is greatest to *C. arenosus* described from Maknassy, but the identification is not certain as the latter is only known from a single discoulored type. In any case, it seems possible that a revision will turn up an older synonym.

Creoleon alternus NAVÁS, 1933 – There is one specimen each of *C. alternus* in DUMONT's material from Bou Hedma (type) and Maknassy , along with a further one in the recent sample. The species appears identical to one from the Middle East, Arabia and East Africa referred to as *C. irroratus* (KLUG, 1834) and *C. parallelus* (KLAPÁLEK, 1911) in recent publications (HÖLZEL 1972, 1983). These names are preoccupied and the valid name of this species will have to be determined. Numerous other described species are suspected to be the same.

Creoleon sp. 3 – A few specimens present among DUMONT's Myrmeleontidae and identical with one from Bou Hedma were determined by NAVÁS as *C. surcoufi* (NAVÁS, 1912) known from Algeria. I have not seen the type, but it is considered by HÖLZEL (1983) to be synonymous with *C. parallelus*. This suggests that it may be the same species as the previous one, and Arabian examples indeed show transitions. The obvious differential characters are size and falcation of wings which are of little taxonomic value. The fact that the (admittedly few) specimens from North Africa discretely form two groups suggests that they should be kept separate for the time being.

Creoleon sp. 4 – A single specimen from Jbil, August 1998, not assignable to species.

Creoleon sp. 5 – A single specimen from Jbil, October 1999, not assignable to species.

Ganguilus pallescens NAVÁS, 1912 – New for Tunisia.