

SOUTHERN AFRICAN BIOMES AND THE EVOLUTION OF
PALPARINI (INSECTA: NEUROPTERA: MYRMELEONTIDAE)

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Southern Africa harbours 42 of the 88 known species of Palparini (Insecta: Neuroptera: Myrmeleontidae). Twenty-nine of the 42 species are endemic to the western parts of the subregion, including Namibia, Botswana, the Western, Northern and Eastern Cape, and North-West Provinces of South Africa. Geographical Information Systems analyses and climate change models have been used to reveal possible reasons for the high diversity and levels of endemism of Palparini in southern Africa. The analyses have indicated that climate, and the consequent rich variety of vegetation and soil types, have been the driving forces behind southern Africa being a major evolutionary centre for palparines and other Neuroptera.

Key words: Neuroptera, Myrmeleontidae, Palparini, southern Africa, biomes, Geographical Information Systems

INTRODUCTION

The varied biomes of southern Africa have engendered a proliferation of lacewings (Insecta: Neuroptera). The subregion is a major evolutionary centre for Neuroptera, with many taxa being endemic to the countries south of the Cunene and Zambezi rivers. Twelve of the world's 17 families of lacewings are represented in South Africa, which has exceptionally rich faunas of the xerophilous Myrmeleontidae (antlions) and Nemopteridae (thread- and ribbon-winged lacewings). More than half of the world's known species of Nemopteridae occur in the Western and Northern Cape Provinces of South Africa, while the great antlion tribe Palparini attains its highest level of diversity in the subregion, with 42 species being present (Table 1). This represents 48% of the total number (88) of valid species in the tribe.

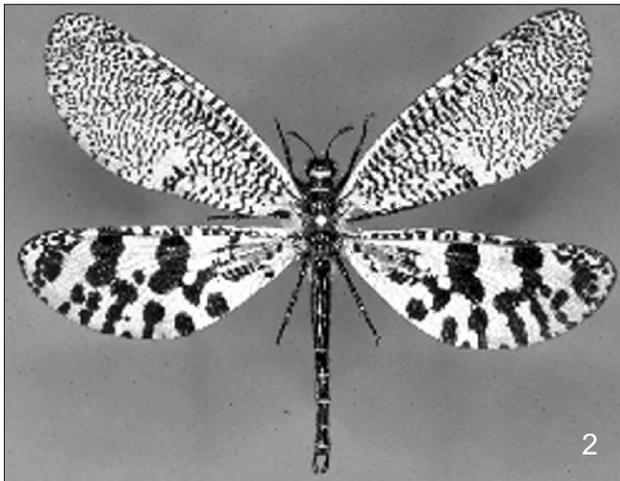
This rich variety, and the potentially detrimental effects of climate change on the fauna of southern Africa, is currently being investigated by Geographical Information Systems (GIS) analysis. In the process of modelling the known and potential distributions of Palparini in South Africa, it became evident that parameters other than climate also determined the distribution of species on the subcontinent. One of these is the influence of plant morphology on the morphology of adult

Palparini. This antlion tribe includes the largest species in the family and, consequently, the largest larvae (Fig. 1). A large larva enables these specialist predators to exploit a wide range of prey, but it also jeopardises the safety of the conspicuously large adults. Their great size renders them vulnerable to predators, and palparines have consequently evolved elaborately patterned wings to enhance their

Table 1. The Palparini of southern Africa, indicating their affiliation to the western or eastern faunal components of the subregion

Western species	Eastern species
1. <i>Crambomorphus sinuatus</i> (OLIVIER, 1811)	1. <i>Lachlathetes moestus</i> (HAGEN, 1853)
2. <i>C. sp. n. 1</i> (Kalahari)	2. <i>Palpares caffer</i> (BURMEISTER, 1839)
3. <i>C. sp. n. 2</i> (Namibia)	3. <i>P. cataractae</i> PÉRINGUEY, 1910
4. <i>Golafrus oneili</i> (PÉRINGUEY, 1911)	4. <i>P. inclemens</i> (WALKER, 1853)
5. <i>Palpares annulatus</i> STITZ, 1912	5. <i>P. kalahariensis</i> STITZ, 1912
6. <i>P. campanai</i> NAVÁS, 1915	6. <i>P. lentus</i> NAVÁS, 1912
7. <i>P. elegantulus</i> PÉRINGUEY, 1910	7. <i>P. sobrinus</i> PÉRINGUEY, 1911
8. <i>P. gratiosus</i> NAVÁS, 1929	8. <i>P. sparsus</i> MCLACHLAN, 1867
9. <i>P. immensus</i> MCLACHLAN, 1867	9. <i>P. torridus</i> NAVÁS, 1912
10. <i>P. karrooanus</i> PÉRINGUEY, 1910	10. <i>P. tristis</i> HAGEN, 1853
11. <i>P. speciosus</i> (LINNAEUS, 1758)	11. <i>Palparellus nyassanus</i> (NAVÁS, 1911)
12. <i>P. sp. n. 1</i> (Gobabeb)	12. <i>P. festivus</i> (GERSTAECKER, 1894)
13. <i>P. sp. n. 2</i> (Pofadder)	13. <i>Tomatares citrinus</i> (HAGEN, 1853)
14. <i>P. sp. n. 3</i> (Elefantenberg)	
15. <i>Palparellus damarensis</i> (MCLACHLAN, 1867)	
16. <i>P. dubiosus</i> (PÉRINGUEY, 1910)	
17. <i>P. flavofasciatus</i> (MCLACHLAN, 1867)	
18. <i>P. ovampoanus</i> (PÉRINGUEY, 1910)	
19. <i>P. pulchellus</i> (ESBEN-PETERSEN, 1922)	
20. <i>P. ulrike</i> MANSELL, 1996	
21. <i>Pamares damarus</i> MANSELL, 1990	
22. <i>P. deru</i> MANSELL, 1990	
23. <i>P. nephele</i> MANSELL, 1990	
24. <i>P. parvus</i> MANSELL, 1990	
25. <i>Pamexis bifasciatus</i> (OLIVIER, 1811)	
26. <i>P. contaminatus</i> (HAGEN, 1887)	
27. <i>P. karoo</i> MANSELL, 1992	
28. <i>P. luteus</i> (THUNBERG, 1784)	
29. <i>P. namaqua</i> MANSELL, 1992	

camouflage. In many species these patterns mimic the dominant plant species within the biomes in which the antlions occur. This in turn restricts Palparini to the biomes that influenced their evolutionary adaptations. Each palparine species in southern Africa has a closely related sister-species that occurs in a different biome, and they are seldom sympatric. Examples of these species complexes and their morphological adaptations are discussed here to support the camouflage hypothesis, and to explain the high diversity of Palparini in southern Africa.



Figs 1–3. 1 = Larva of *Golafrus oneili* (PÉRINGUEY), length 35 mm; 2 = *Pamexis luteus* (THUNBERG), wing length 30 mm; 3 = *P. karoo* MANSELL, length 32 mm. (Photographs – 1: A. S. SCHOEMAN; others: M. W. MANSELL)

MATERIAL AND METHODS

The geo-referenced locality data upon which the GIS analyses are based, were drawn from the "Palpares Relational Database" (MANSELL & KENYON 2002). This database includes locality data from specimens in the South African National Collection, Pretoria (SANC) and other collections world-wide. The analyses were carried out by means of a model that provides a spatially explicit set of probabilities of occurrence values for each species (ERASMUS *et al.* 2000). This model was used to derive predicted distributions of antlion species based on validated records, and to generate climate-effected distribution patterns for these species under a possible climate change scenario of increasing temperatures. Recorded distributions were plotted to quarter degree grid cells (approx. 25×25 km), to which the model interpolated potential records based on climate data. These data were the mean minimum temperature of the coldest month and the mean maximum temperature of the warmest month for each grid cell, as well as the mean annual rainfall and precipitation seasonality. The latter is a joint measure reflecting when precipitation occurs, as well as the amount recorded (ERASMUS *et al.* 2000).

In addition to the climate modelling procedure, recorded distributions were also superimposed on a map of the biomes of South Africa to determine whether biotic as well as climatic factors influenced the distribution of Palparini. Data derived from such models are ultimately used to highlight areas of endemism, species richness and to identify rare and endangered taxa with a view to providing objective criteria for selection of conservation areas and land-use planning.

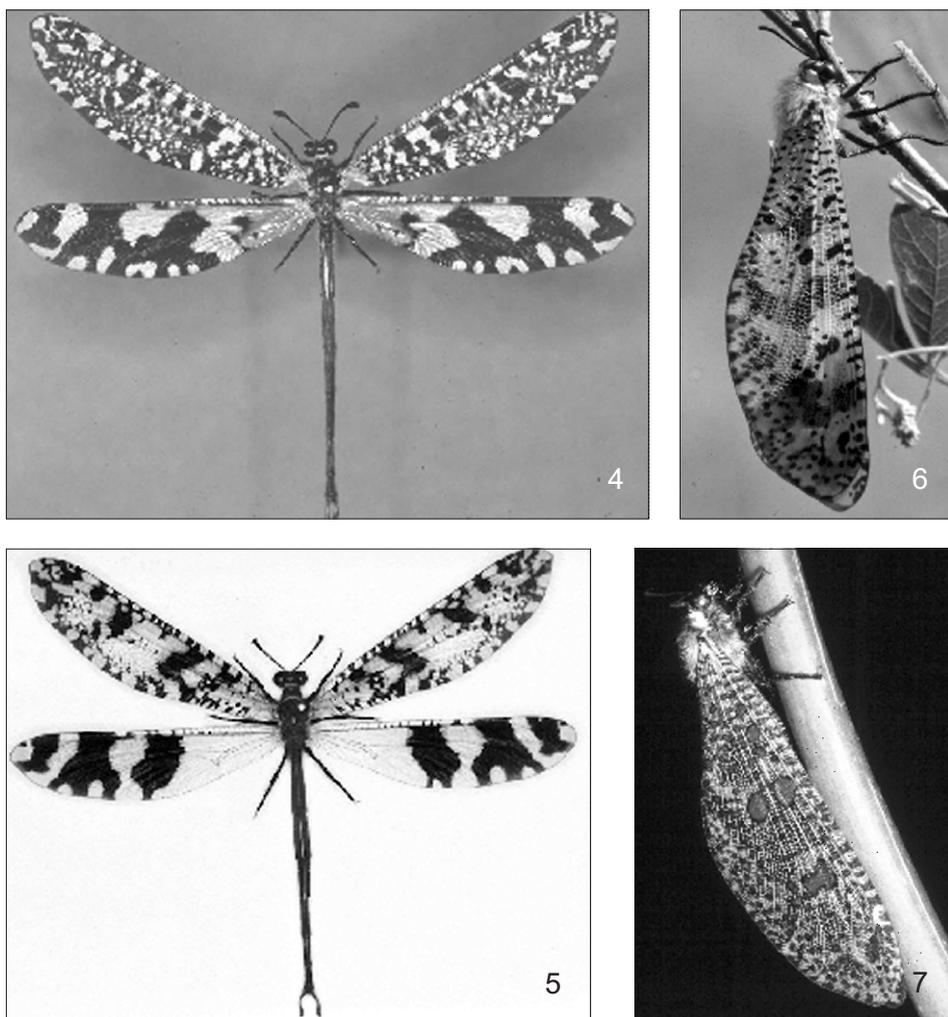
Three species-pairs were selected for comparison: *Pamexis luteus* (THUNBERG) and *Pamexis karoo* MANSELL, *Palparellus pulchellus* (ESBEN-PETERSEN) and *Palparellus ulrike* MANSELL, and *Palpares caffer* (BURMEISTER) and *Palpares speciosus* (LINNAEUS). They were identified as their distributions are well known, and because each species is restricted to a specific biome.

RESULTS AND DISCUSSION

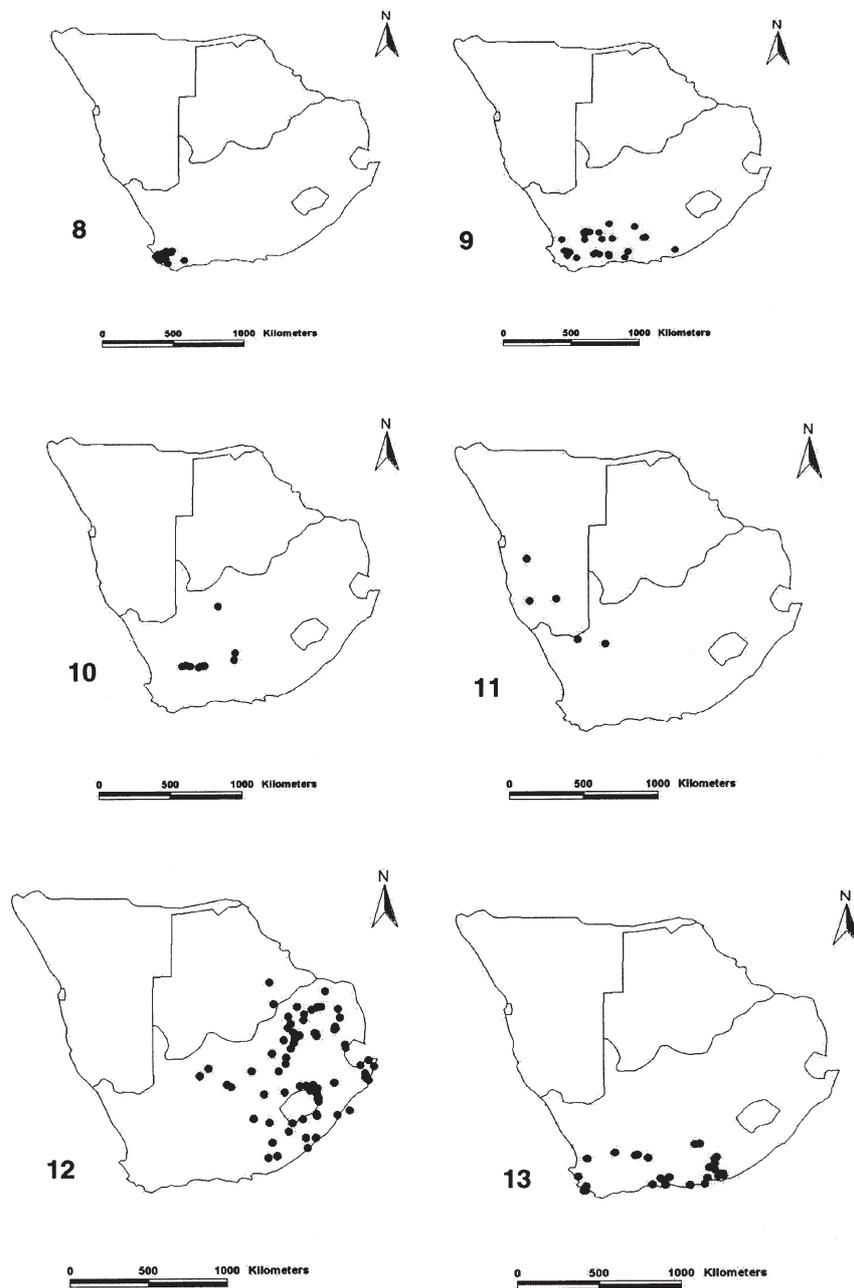
Pamexis luteus (Figs 2, 8) – This species is limited to the Fynbos biome (see REBELO 1996) in the south of the Western Cape Province. In living specimens the forewings are yellowish-green (fading to yellow in preserved material) with fine dense brown maculation.

Pamexis karoo (Figs 3, 9) – Is the sister-species of *P. luteus* and their distributions abut in the Hex River Valley area (33.29°S 19.36°E) of the Western Cape Province. *Pamexis karoo* inhabits the Nama Karoo biome (see HOFFMAN 1996), extending from Ceres (33.22°S 19.19°E) in the west to Fort Brown (33.08°S 26.38°E) in the east. It is similar to *P. luteus*, but the brown maculation in the forewings is larger and less dense than in *P. luteus*. Both *P. luteus* and *P. karoo* are diurnal and are not attracted to light. When flushed, they fly rapidly and use wind currents as an evasion strategy. The short broad wings are an adaptation to rapid and erratic flight in these day-flying species. When inactive they rest in vegetation where the patterns on the closed wings provide camouflage in the dappled shade afforded by the small-leafed fynbos or karoo (*Pentzia* sp.) vegetation.

Palparellus pulchellus (Figs 4, 10) – This species is endemic to the Upper and Great Nama Karoo biomes (see HOFFMAN 1996) and is sympatric with *Pamexis karoo* for much of its range. The wing coloration and patterns are similar in the two species, and they frequently occur in the same habitat in association with *Pentzia* bushes.



Figs 4–7. 4 = *Palparellus pulchellus* (ESBEN-PETERSEN), wing length 52 mm; 5 = *P. ulrike* MANSELL, wing length 55 mm; 6 = *Palpares caffer* (BURMEISTER), length 65 mm; 7 = *P. speciosus* (LINNAEUS), length 66 mm. (Photographs – 6: M. J. SAMWAYS; others: M. W. MANSELL)



Figs 8–13. Recorded distributions of Palparini in southern Africa: 8 = *Pamexis luteus* (THUNBERG); 9 = *P. karoo* MANSELL; 10 = *Palparellus pulchellus* (ESBEN- PETERSEN); 11 = *P. ulrike* MANSELL; 12 = *Palpares caffer* (BURMEISTER); 13 = *P. speciosus* (LINNAEUS)

Palparellus ulrike (Figs 5, 11) – This species is similar to *Palparellus pulchellus* (see MANSELL 1996), and the two are clearly sister species. The forewings of *Palparellus ulrike* are, however more sparsely marked than those of *P. pulchellus*. It occurs in the Bushman Nama Karoo biome (HOFFMAN 1996) and northwards into Namibia. Both *P. pulchellus* and *P. ulrike* are attracted to light and rest concealed amongst vegetation during the day.

Palpares caffer (Figs 6, 12) – This species is widespread in the eastern parts of southern Africa, and is essentially a species of the Grassland biome (see LUBKE *et al.* 1996), although it also occurs in grassland of the Savanna biome. *P. caffer* has sparsely marked forewings and is nocturnal, resting in long grass during the day. This is the only palparine that inhabits the high altitude grasslands of southern Africa.

Palpares speciosus (Figs 7, 13) – Was the first palparine to be described from Africa, and it replaces *P. caffer* in the Fynbos and Nama Karoo biomes (see REBELO 1996, HOFFMAN 1996), from approximately Grahamstown (33.18°S 26.32°E) westwards. As in the *Pamexis* species and *Palparellus pulchellus* the forewings are maculate, an adaptation to the dappled shade provided by the fine-leaved plants of the Fynbos and Nama Karoo biomes.

Distribution of Myrmeleontidae

The climate of southern Africa is characterised by increasing aridity from east to west on the subcontinent (Fig. 14), and this has a profound influence on the distribution of Neuroptera and other insects in the subregion. Southern African Myrmeleontidae manifest three main distributional trends (MANSELL 1990). There is an eastern faunal component, a western fauna, and a third component comprising a limited number of widespread species. The eastern component is dominated by species that are widespread in Africa, while there is a rich xerophilous element that inhabits the drier western parts of the subregion, where the annual rainfall is generally less than 500 millimetres per annum. This western fauna is characterised by a high level of endemism, and inhabits Botswana, Namibia and the Western Cape, Northern Cape, Eastern Cape, and North-West Provinces of South Africa. Of the 42 species of Palparini in southern Africa, 29 occur in the west, while only 13 inhabit the eastern side of the subcontinent (Table 1), and all but four of the western species are endemic to the subregion. *Palparellus flavofasciatus* (MCLACHLAN), *P. ovampoanus* (PÉRINGUEY), *P. damarensis* (MCLACHLAN) and *Palpares immensus* MCLACHLAN, also extend into southern Angola.

During GIS analyses a model was developed (ERASMUS *et al.* 2000) to indicate potential areas of distribution based on the climatic conditions in which the

various species were known to occur. This revealed several areas where the climate was suitable for colonisation by a particular species, but in which that species did not occur. It consequently became apparent that, although climate was important, it was not the only parameter that determined species distribution. When the recorded distributions of endemic species were superimposed on a map of the biomes of South Africa (LOW & REBELO 1996) it became apparent that most species were associated with specific areas and vegetation types. This trend is clearly manifest in the six species considered here. The general similarity in wing patterns of four species, *Pamexis luteus*, *P. karoo*, *Palparellus pulchellus* and *Palpares speciosus*, also show a striking convergence in adapting to life in the Fynbos and Nama Karoo biomes.

The increasing aridity in the west of the subregion results in the availability of large tracts of sand and exposed soil that are conducive to the large sand-dwelling larvae of Palparini. The western regions of southern Africa also include widely dif-

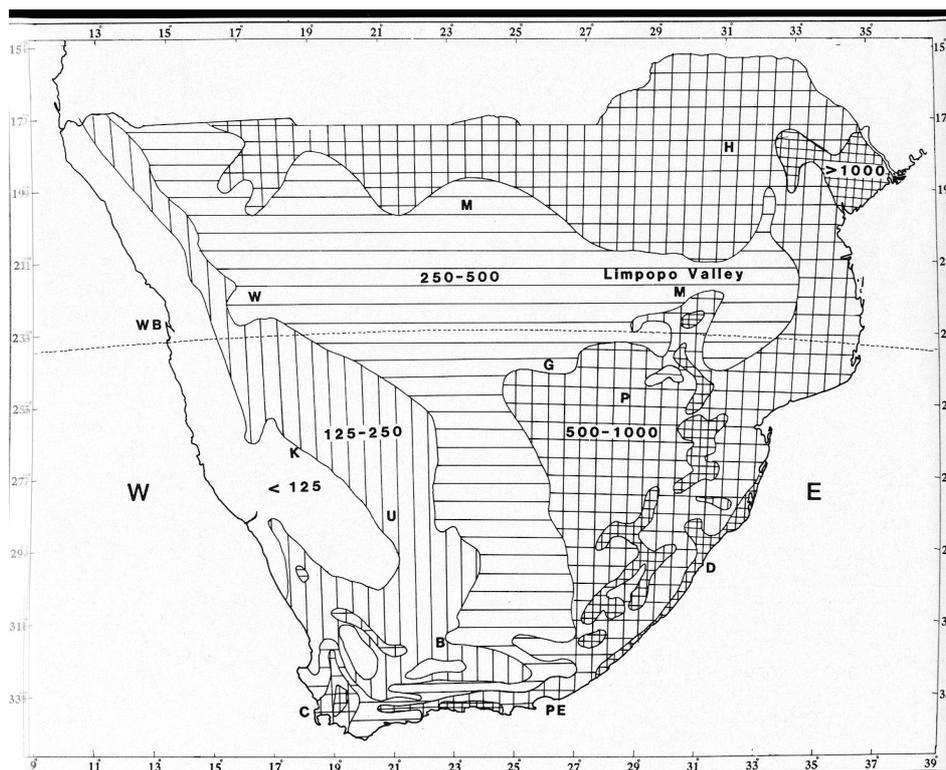


Fig. 14. Southern Africa with average rainfall pattern in mm. Abbreviations: B = Beaufort West, C = Cape Town, D = Durban, G = Gaborone; H = Harare, K = Keetmanshoop, MA = Maun, M = Messina, PE = Port Elizabeth, P = Pretoria, U = Upington, WB = Walvis Bay, W = Windhoek

fering biomes, including Desert, Nama Karoo, Succulent Karoo, Savanna and Fynbos (LOW & REBELLO 1996). The combination of these physical and biotic features, together with their associated topography and related floras, has provided numerous niches in which Palparini could evolve.

Southern Africa is also dominated by “open” biomes including Savanna, Grassland, Nama and Succulent Karoo and Desert, where trees and shrubs are either absent, sparse or low-growing. Only a very small part of South Africa is covered by Forest or Thicket biomes, which are not favoured by Myrmeleontidae, and Palparini in particular. There are consequently vast areas of southern Africa that are conducive to habitation by Palparini.

CONCLUSIONS

Southern Africa has a rich fauna of Neuroptera, with high levels of endemism. It is also the area with the world’s greatest numbers of Palparini (Myrmeleontidae) and Nemopteridae. Reasons for this richness are continually being sought, especially with regard to identifying objective criteria for conservation measures and reserve selection. Modern computer technology and advanced software programmes have placed powerful database and analytical tools in the hands of biologists. These enable scientists to gather, collate and analyse data, and to apply the products in sustainable environmental planning and innovative research.

The comprehensive data set generated by the Southern African Lacewing Monitoring Programme (MANSELL 2002) has been especially valuable in contributing to the development of analytical procedures and the database model (FREITAG & MANSELL 1997, ERASMUS *et al.* 2000, MANSELL & KENYON 2002). These procedures also hold inherent heuristic value, as they frequently reveal reasons for phenomena other than those they are modelled to analyse. In the present study, climate alone could not account for the distributions of Palparini, which led to the notion that vegetation and soil types could also be a major influence. The striking congruence between recognised plant biomes and palparine distributions strongly support this hypothesis.

In the case of Nemopteridae, whose adults are specialised pollinators, such an association is obvious, but in Palparini where both larvae and adults are predacious the explanation was not as clear. The present contribution highlights another aspect of insect/plant relationships, camouflage, which is quite independent of the usual pollination or host dependence. It emphasises the close evolutionary association between insects and plants in the western regions of southern Africa, and the need for a holistic approach to ecosystem study and conservation.

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