

NEUROPTERA OF WALLACEA: A TRANSITIONAL FAUNA BETWEEN MAJOR GEOGRAPHICAL REGIONS

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The central regions of Malesia, Wallacea, are the meeting place of the biota of two major geographical regions: Australia and the Oriental Region. Knowledge of the lacewings of Wallacea is reviewed, as an aid to assessing this faunal overlap and to understanding the origins and affinities of the Australian fauna. The constitution of the Malesian fauna of about 420 described species in 12 families is outlined, and the interacting faunas are tentatively appraised and defined.

Key words: zoogeography, Australasia, Oriental region, Malesia, lacewings

INTRODUCTION

Malesia, the complex area linking the Oriental and Australian biotas, is one of the most intriguing biogeographical regions in the world. Many biologists have speculated on the existence and positions of boundaries delimiting floral and faunal elements there, and compromise between the distributions of numerous groups of animals – each with different biology, dispersal abilities and ecological needs – for any generalisation has been difficult to find (SIMPSON 1977). The central transitional zone, Wallacea (Fig. 1), is of particular interest in seeking to clarify faunal transitions, as it is in this region of essentially Asian flora that a mixture of Asian and Australian related fauna is most clear. However, the concept of ‘Wallacea’ as a distinct region is by no means universally accepted (WHITTEN *et al.* 1988), because of the great complexity of the area and the presence of numerous endemic animals and plants. Thus, in relatively well known groups of insects such as papilionid and danaine butterflies (COLLINS & MORRIS 1985, ACKERY & VANE-WRIGHT 1984) endemism is sufficiently high to render the regional fauna of major global significance. Discussion of additional groups of fauna, especially lesser known ones, has potential to contribute to interpreting the complex overall picture of faunal relationships in the region. In this paper, a preliminary appraisal of the Neuroptera of Wallacea is provided particularly to indicate the putative presences, absences and constitution of major groups, and how these may affect interpretation of the Oriental or Australian faunas. A more comprehensive appraisal of the Malesian Neuroptera by NEW (2001) forms the framework for the following overview.

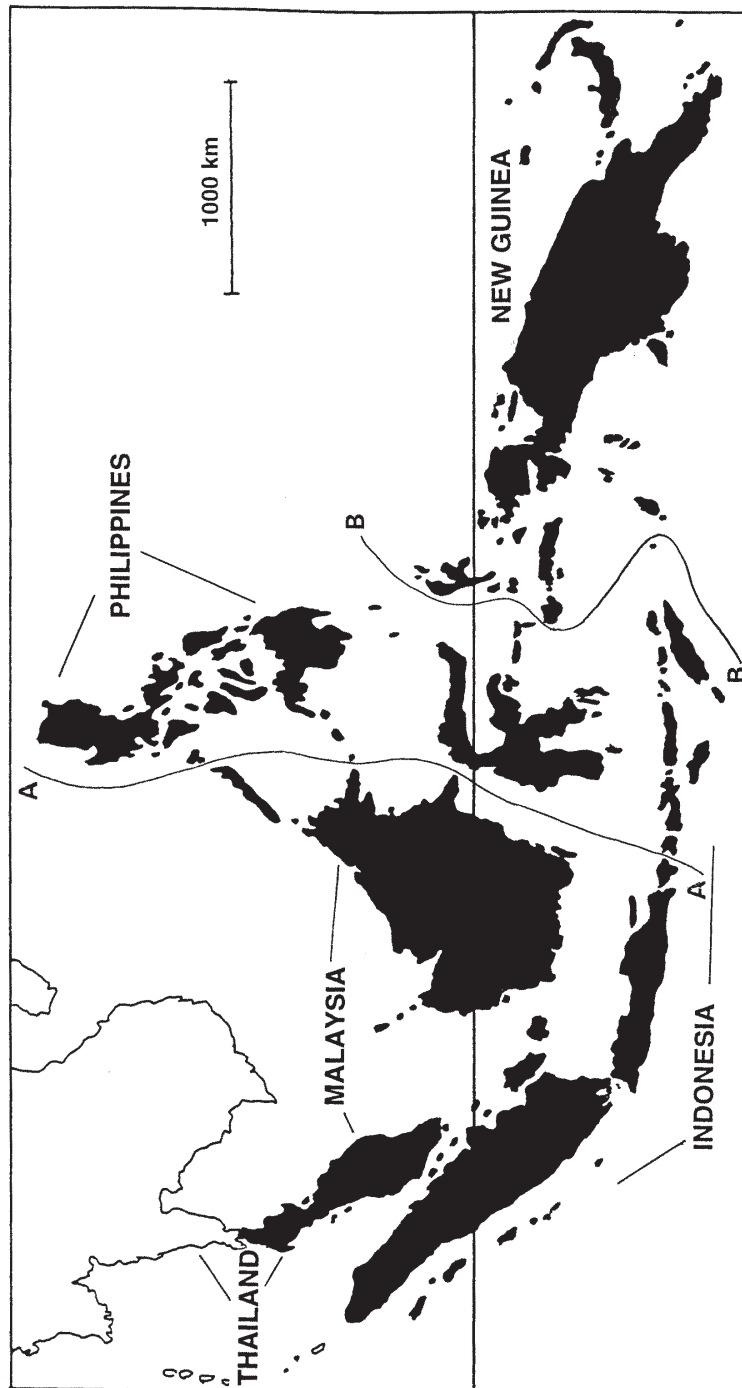


Fig. 1. Outline map of Malesia (black) with central region, Wallacea, delimited by WALLACE's line (A-A) and WEBER's line (B-B)

As with many other groups of insects, there are clear limitations to the reliability of information available. VAN DER WEELE's (1909) account remains the most comprehensive overview of the fauna of parts of Indonesia but the more limited region of Wallacea has not hosted resident neuropterists for any extended periods, and most of the few records of lacewings from the region are of material collected sporadically by non-specialists and described, with varying degrees of accuracy, by workers far distant from the region. Many of the early generic attributions have never been verified, and some assessments of distributions are compounded by labelling ambiguities: 'E. Ind.', for example has the ambiguity of "East Indies" or "East India". However, in recent years, I have tried to examine most of the species reported from the region, augmented by my own collections from parts of Papua New Guinea, Indonesia and Malaysia, with the primary focus of seeking to clarify the affinities of the diverse Australian fauna, and its transitions to the Oriental region.

The main features of the documented fauna are summarised in Table 1, which is based on published records and descriptions. For some groups, the perspective is likely to change considerably at the species diversity level. However, much of the Malesian region has been subject to massive environmental changes over the last century (MACKINNON 1997), predominantly through clearing of native vegetation for support of a burgeoning human population. MACKINNON (1997) claimed that more than 90% of the natural vegetation of the Philippines has

Table 1. Summary of recorded richness of families of Neuroptera in Wallacea, compared with Malesia

Family	No of species recorded from	
	Malesia	Wallacea
Rapismatidae	11	0
Coniopterygidae	59	7
Sisyridae	3	1
Osmylidae	56	8
Mantispidae	63	27
Berothidae	6	1
Dilaridae	3	0
Hemerobiidae	50	19
Chrysopidae	105	34
Nymphidae	9	1
Ascalaphidae	25	7
Myrmeleontidae	60	16

now been cleared for agriculture, logging and mining, for example, although figures for some parts of Indonesia are much less than this. Many of the elusive ecologically specialised taxa of lacewings and other insects have probably become even rarer than the few records suggest. It is perhaps doubtful that some of them are still extant, and anomalies in interpretation will inevitably persist for the foreseeable future. For some families, some of the nominal genera are apparently widely distributed in the region. For others, there is some evidence of 'skewed' incidence which may reflect attenuation from an area of origin to one or other side of Wallacea. However, knowledge of the source areas is itself uneven. A substantial framework is available for appraisal of the Australian fauna (NEW 1997), but many parts of western Malesia, continental south east Asia, and the Indian subcontinent are still relatively poorly documented. The extent of lacewing evolution on the complex archipelagos of Wallacea (essentially, southern and parts of eastern Indonesia, with Sulawesi the largest island, and the Philippines, excluding Palawan (note that many recent authorities now restrict the definition of Wallacea to exclude the Philippines [see COATES *et al.* 1997]) needs further investigation, together with elucidation of the dispersal powers of many taxa. Thus, for a related example, the lacewings recorded on the Krakatau Islands include several not normally considered to be competent dispersers (NEW & SUDARMAN 1988) or to occur in non-forested environments. A record of *Isoscelipteron nicobaricum* (NAVÁS) there was not only unexpected, but marked a considerable extension from the species' known range in Malaysia and the Nicobar Islands. A coniopterygid, *Heteroconis axeli* NEW, from the small patch of early successional *Casuarina* woodland on Anak Krakatau remains unknown elsewhere in Indonesia, despite the predominance of the genus in the regional fauna. Likewise, MONSERRAT's (1982) records of Coniopterygidae from Indonesia included some notable range extensions. Although the gross distributions of families and some major segregates of Neuroptera in the region are reasonably well understood, any synthesis at finer levels must remain tentative.

FAMILY REPRESENTATION AND RELATIVE DIVERSITY

The following families of Neuroptera have not been recorded from Wallacea or greater Malesia: Ithonidae, Rhachiberthidae, Nevrorthidae, Psychopsidae and Nemopteridae. Most of these are unambiguously absent, with the fauna clearly centred on other parts of the world, but two merit further investigation. Nevrorthidae and Psychopsidae are both known from Australia and regions to the north or west of Malesia, so that their known distributions are inexplicably disjunct. It is

possible that they occur in intervening zones, and the characteristic larvae of nevrorthids should be sought in running waters in the region. Nymphidae might also be found in Wallacea, as an attenuation from New Guinea, but it would indeed be surprising if such large and conspicuous insects as these and Psychopsidae have escaped notice until now.

Some other families are represented in Malesia by very few described species or other records, but are globally widespread. Few taxa of Sisyridae, Berothidae and Dilaridae have been described, with the last of these absent from Australia.

The remaining eight families are all well represented, and more diverse. They are thus the core taxa for more detailed faunal appraisal. The following notes refer to the Malesian fauna, as a basis for appraising the centre of this region.

DISTRIBUTION AND DIVERSITY OF MAJOR FAMILIES OF NEUROPTERA IN MALESIA

RAPISMATIDAE

The archaic Rapismatidae extend from northern India and Nepal, through Myanmar and West Malaysia to Borneo (BARNARD 1981), but their biology is unknown. Most species are known from very few individuals, and from single localities, and the family does not extend to the Australian Region. Their greatest richness is in West Malaysia. Not recorded from Wallacea, rapismatids are apparently restricted to the regions west of this. The Malesian species are clearly related to taxa from the Indian subcontinent and mainland south east Asia, and the family is absent from New Guinea and Australia. The narrowly endemic family is highly characteristic of the region and apparently limited to natural habitats, mainly at higher altitudes.

CONIOPTERYGIDAE

Most of the genera present in Malesia are widespread. *Heteroconis* ENDERLEIN is by far the most diverse genus, as it is in Australia. The suggestion by MEINANDER (1972) that Australian taxa might be generically distinct from Asian forms is not supported by the variety of species now known. Many *Heteroconis* species appear to have very restricted distributions in the region. The great diversity of *Heteroconis* is the most striking feature of the regional fauna, and this dominance is shared with Australia. *Heteroconis* occurs also in parts of Africa, but not

in the Palaearctic and much of south east Asia. It is most speciose in Indonesia, Papua New Guinea and Australia.

Paraconis MEINANDER is known only from Sabah, and may be an endemic Malesian genus, and should be sought in Wallacea. Most other genera are widespread, but the apparent lack of *Neosemidalis* ENDERLEIN, diverse in Australia and represented also in Papua New Guinea, emphasises the affinities of the genus as Australian. Likewise, *Cryptoscenea* ENDERLEIN is relatively poorly represented in Malesia (one record from Bali: MONSERRAT 1982) and more diverse in Australia. It may occur in Wallacea. *Coniocompsa* ENDERLEIN has not been reported from Australia and is more diverse elsewhere, including Africa.

OSMYLIDAE

Osmylidae of Malesia are characterised by massive radiation of Spilosmylinae and the absence or paucity of other subfamilies found in Australia and the eastern Palaearctic. *Spilosmylus* KOLBE is particularly diverse in Indonesia, the Philippines and Papua New Guinea, and it is likely that many further species await discovery there. The genus is scarcely represented in Australia. *Thaumatomylus* KRÜGER appears to be restricted to western parts of Malesia, and has not been recorded from New Guinea.

The southern subfamilies predominant in the Australian fauna are absent. Spilosmylinae occur from Africa (TJEDER 1957) and India to northern Australia, where they are represented very poorly. Most of the species in the region appear to have rather narrow distributions, and Malesia is clearly a major centre for diversification of *Spilosmylus*. The two Australian species are known only from northern tropical Queensland, and represent attenuation from the diverse Malesian fauna.

MANTISPIDAE

The precise generic allocation of many of the complex array of taxa in this family remains uncertain. A few distinctive genera of large, wasp-like mantispids (*Campanacella* HANDSCHIN, *Mimetispa* HANDSCHIN) are known only from Malaysia and Indonesia, and others (such as *Eumantispa* OKAMOTO and *Euclimacia* ENDERLEIN) are distributed more widely in and around the region. Details of distribution of most taxa are unclear.

Three subfamilies are represented in Australia, but only Mantispinae are known from Wallacea. Many of the putative genera in Malesia do not occur in

Australia, and Australia and New Guinea share several genera which are unknown elsewhere. Some other Australian genera are apparently endemic (NEW 1998).

HEMEROBIIDAE

Few species of Hemerobiidae are common or widespread in the region, other than the very widely distributed *Micromus timidus* HAGEN. Broad-winged species of *Notiobiella* BANKS and *Psectra* HAGEN occur throughout the region, but are usually not common. *Hemerobius* L. is very poorly represented (except in the Philippines), and *Zachobiella* BANKS may be more diverse than presently documented.

Most genera found in Malesia are widespread, but several genera from Australia do not extend northward to the region. These are either confined to Australia (*Carobius* BANKS), where they may be Bassian (*Notherobius* NEW), or occur also in New Guinea. Others, such as *Wesmaelius* KRÜGER occur also in the eastern Palaearctic but have not been reported in Malesia. *Hemerobius* is also predominantly from the north, as evidenced by its apparently greatest regional diversity in the Philippines. The most characteristic genus in the region is *Zachobiella*, which ranges from south east Asia and New Guinea to Australia.

CHRYSOPIDAE

The large Apochrysinæ are represented by three genera (*Joguina* NAVÁS, *Nobilinus* NAVÁS, *Synthochrysa* NEEDHAM) in Indonesia, but Chrysopinae is by far the more diverse subfamily. A number of regional species have not been attributed firmly to genus (BROOKS & BARNARD 1990), but *Glenochrysa* ESBEN-PETERSEN and *Kostka* NAVÁS are both characteristic taxa for the region. *Ankylopteryx* BRAUER s. l. is widely distributed, with some species rather variable (*A. octomaculata* (F.) and its 'forms'). *Italochrysa* PRINCIPI is also diverse. Nothochrysinæ are absent, but represented by two genera in Australia. Two genera of Apochrysinæ (*Joguina*, *Nobilinus*) are predominantly Malesian, with most described species of the latter from Indonesia. *Synthochrysa* is distributed more widely in the western Pacific. Affinities of most taxa of Chrysopinae are still confusing, as many of the genera are widely distributed to both 'sides' of Wallacea. *Kostka* is probably endemic to Malesia, and *Glenochrysa* (with several species undescribed) and sections of *Ankylopteryx* s. l. more diverse than elsewhere and shared with northern Australia.

ASCALAPHIDAE

Haplogleniinae are far less diverse in Malesia than are Ascalaphinae, in which the predominant genera appear to be *Ascalohybris* SZIRÁKI, *Suhpalacsa* LEFÈBVRE and *Suphalomitus* VAN DER WEELE. *Ascalohybris* occurs also in India, China and Taiwan, but is absent from Australia. The predominance of *Suhpalacsa* is a clear affinity with the Australian fauna, as all the Australian species belong to this tribe. However, many of the Australian genera are not known from nearby countries and may be endemic. *Suhpalacsa* and *Suphalomitus* are widespread in the region. The Haplogleniinae, a relatively minor component of the Malesian fauna (as *Idricerus* MCLACHLAN and *Protidricerus* VAN DER WEELE) show greater affinities with the Palearctic fauna. *Helicomitus* MCLACHLAN (if a valid genus) is widespread in south east Asia.

MYRMELEONTIDAE

Some early records of Myrmeleontidae from Malesia are anomalous, and remain tantalising. Palparini (if present) and Acanthaclisinae are very poorly known, and most knowledge of antlions in the region is based on Myrmeleontinae. Myrmeleontini include the widely distributed group of species allied to *Myrmeleon acer* WALKER and several species of *Hagenomyia* BANKS. Protoplectrini is represented only by *Pseudoformicaleo* VAN DER WEELE. Distoleontini and Dendroleontini are the predominant tribes, with several genera of each widely distributed.

The few records of Palparini and Acanthaclisinae from Malesia are difficult to evaluate because of doubts over correct generic attributions. *Echthromyrmex* MCLACHLAN, although rare, is a clear affinity with the north and western fauna (such as the Indian subcontinent). Other palparines, if records of their incidence are indeed valid, represent attenuation from the African fauna. Palparines are absent from Australia.

The major groups of interest for zoogeographical appraisal are Dendroleontini and Distoleontini, the predominant tribes of antlions in Australia. Both are much more diverse in Australia than in neighbouring countries, but several genera are widespread, and correct placement of some Malesian taxa must await critical re-examination of the types. Some major species radiations, such as proliferation in the genera *Austrogymnocnemia* ESBEN-PETERSEN and *Glenoleon* BANKS are apparently confined to Australia. Some Australian genera (such as *Periclystus* GERSTAECKER) shared with New Guinea do not occur elsewhere. Both major genera of Myrmeleontini are widespread, with *Hagenomyia* limited to the far north in

Australia; *Callistoleon* BANKS is apparently absent from Malesia. The sole Malesian genus of Protoplectrini (*Pseudoformicaleo*) is widespread in the area, and shared with northern Australia; it has been recorded from Timor (HANDSCHIN 1937), and probably reflects an Australian lineage.

ENDEMISM AND FAUNAL DEFINITION

The above summaries indicate the overlap of the distinctive Australian fauna with that of south east Asia, and the differing extents to which this occurs in various lacewing families. However, the Neuroptera of central Malesia, Wallacea, are extremely poorly documented. The region is geographically complex, with considerable discussion since DICKERSEN *et al.*'s (1928) definition of the area to include the Philippines. At present, only about 15 species of Neuroptera are known from both southern Indonesia and the Philippines, and most of these occur more widely in Malesia. Three major groups of islands form Indonesian Wallacea and form the basis of distinctive subregions as (a) Sulawesi and its neighbours, (b) the Moluccas and (c) the Lesser Sunda Islands. The overall regional complexity is manifest by VAN STEENIS' (1972) appraisal of the putative origins of Sulawesi's allochthonous mountain flora, with three main tracks of (a) Luzonian, southward from the Asian mainland through the Philippines, (b) Sumatran, eastward from Malaysia through Sumatra and Java, and extending through the Lesser Sundas, and (c) Papuan, westward from Melanesia through New Guinea. Faunal origins are similarly complex, with each contributing to development of endemic (or autochthonous) taxa after establishment. Some broad parallels between Neuroptera and plant tracks could be suggested; the apparent diversity of *Hemerobius* in the Philippines, for example, may represent their southward extension from Asia that has not reached Sulawesi. However, even for Sulawesi, few recent records of lacewings exist, and knowledge of the complex Philippines fauna has scarcely been augmented since the descriptive accounts by BANKS (1916, 1937, 1939). Many of the Indonesian islands lack records of Neuroptera, and the most recent synoptic publications are by HANDSCHIN (1935, 1937). Table 1 reveals records for only about 120 species (of a Malesian total of about 420) in 10 families (of 12 in Malesia). The Philippines total of 80 species considerably exceeds the 54 notional species reported from Wallacean Indonesia, and the latter region has been substantially undersampled in relation to Irian Jaya and the main western islands of Indonesia. In particular, the apparent paucity of *Heteroconis* and *Spilosmylus* in relation to other parts of Malesia is unlikely to be realistic.

Neuroptera of Wallacea do not appear to constitute a distinctive faunal unit above the species level, but include elements that are (a) widely distributed in Malesia, (b) predominantly Australian in relationships, a trend evident particularly for areas close to Australia, such as Timor, or (c) more clearly aligned with the south east Asian fauna. The broader regional fauna is more distinctive, but the extent to which this picture is realistic – or can be augmented meaningfully – is clearly open to doubt. Overall, Sulawesi is not as biologically diverse as Borneo, but both it and the Philippines have high levels of species endemism. It is reasonable to suppose that further endemic lacewings await discovery in the remaining less disturbed parts of Wallacea.

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