

# The HesperIIDae (Lepidoptera) of the Philippines

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All species and subspecies of the HesperIIDae known from the Philippines are listed and their distribution across the islands, preferred habitats and flight habits are indicated. By far the richest habitat is the primary lowland forest. In view of the high rate of deforestation it is estimated that 50% of the hesperiid species is endangered and may become extinct over the next 10 to 15 years. With 151 species the Philippines is considerably poorer than Borneo (214 species), but much richer than Sulawesi (84 species). In terms of endemism, however, the Philippines is with 35 endemic species (23.2%) relatively much richer than Borneo (12 species, 5.6%), and almost as rich as Sulawesi (20 species, 23.8%). The distribution and endemism of species and subspecies are analysed and compared with what is known of the geological history of the Philippines. It is concluded that the fauna is relatively young and essentially of Bornean derivation. The faunal connections with Sulawesi are ambiguous, and those with Taiwan very weak. The HesperIIDae do not provide patterns of vicariant speciation events in the Philippines, but there is a general north-south (Luzon-Mindanao) differentiation with an intermediate area of islands showing intricate and various biogeographic links. This agrees with the geological history: the islands of the Philippines are not the result of fragmentation of a single land mass (such a fragmentation could have been a vicariant speciation event), and most of the present-day islands apparently emerged from the sea and may have been much further apart rather than closer together in the geological past. Lowering of the sea level during the Ice Ages must have united the islands in a few clusters, but such clusters are not apparent in the distribution of the HesperIIDae, contrary to what has been reported for the Mammalia. Instead the islands between Luzon and Mindanao are seen as an area with repeatedly changing dispersal opportunities. Palawan does not fit in this picture; biogeographically it is best described as a northern extension of Sundaland (which geologically speaking its southern half actually is).

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## Introduction

### The Philippines

The Philippine Islands (fig. 1) are situated between latitude  $4.6^{\circ}$  and  $21.4^{\circ}$  north of the equator (1845 km) and between longitude  $116.5^{\circ}$ E and  $127^{\circ}$ E (1105 km). There are 7107 islands of which only around 2100 are said to be inhabited. About one third of the islands are not listed by name in the usual reference books or maps. Only about 500 islands have an area of over one km<sup>2</sup>. The eleven largest islands account for 96% of the land area of the Philippines. The largest three islands in order of size are Luzon, Mindanao and Palawan. The highest mountain is Mt. Apo (2954 m) in Southeast Mindanao. Seventeen active volcanoes are officially recognized with eruptions occurring quite frequently.

At this time there are 63 million inhabitants of whom approximately 89% are Christians with the remaining being Moslem and minority cultures. It is worth noting that there are 111 linguistic cultural and racial groups in the country. The national language is Tagalog, but a total of 70 languages and dialects are currently listed as being spoken within the boundaries of the country.

Whereas the Philippines is noted in reference books for its extensive forest coverage, this situation has certainly changed over the past 30 years. Space requirements for the explosive population increase coupled with the world demand for timber and the modern wood harvesting methods now used have resulted in substantially reducing the forest areas of the Philippines, particularly lowland forest. At this time it is believed that less than 10% of the original forest coverage of 30 years ago remains. Notwithstanding, reasonably large forested areas can still be found in such locations as Northeast Luzon and the Sierra Madre Mountain Range, parts of Palawan, South Mindanao, Central Mindanao (Bukidnon), North Negros, Central Leyte, North and Central Samar and East Tawitawi Islands. The higher mountains across the country tend to have forested slopes. Typical examples are Mt. Apo (Mindanao, 2954 m), Mt. Pulog (Luzon, 2934 m), Mt. Halcon (Mindoro, 2585 m), Mt. Canlaon (Negros, 2465 m), Mt. Isarog (Luzon, 1966 m), Mt. Guintinguintin (Sibuyan, 2057 m), Mt. Malindang (Mindanao, 2425 m), Mt. Mandalingajan (Palawan, 2085 m) and Mt. Katanlad (Mindanao, 2938 m). Further, there are in existence 61 national parks and protected areas. Nevertheless it has been forecasted that if the current rate of deforestation continues (525,000 acres per year, or more dramatically stated: one acre every minute) the Philippines will be without true forest shortly after the turn of the century. This will, of course, have a very strong impact on forest dwelling butterflies.

The Philippines experiences a tropical climate with generally speaking the cooler, drier period from December to February, the hot, drier period from March to May and a rainy season from June to November. In this latter period, strong typhoons can be quite destructive, especially in the East Visayan and North Luzon areas. Many of the larger islands of the Philippines can experience differing intensities of the general climatic conditions depending on the location of higher mountain ranges, the

amount of forest coverage existing and the prevailing winds. Such conditons can cause modest rainfall throughout the year (Southeast Mindanao, Sulu Archipelago) or with the heaviest rain from November to January (East Mindanao, East Samar) or with the heaviest rainfall from April to September (Southwest Mindanao).

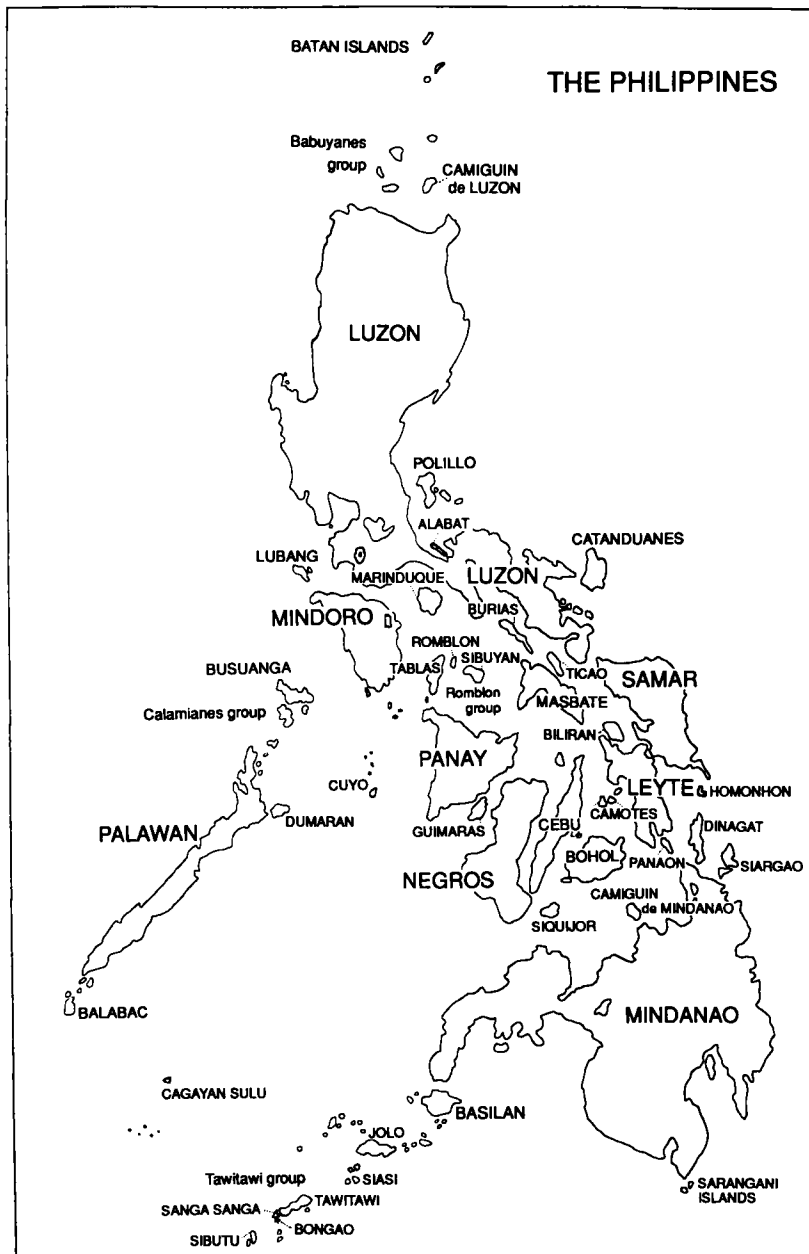


Fig. 1. The Philippines, with the names of the islands mentioned in the text.



Fig. 2. Mangrove and swamp area: Tawitawi Island (photo M. Gaulke). Six species:  
*Badamia exclamationis*, *Bibasis sena palawana*, *Halpe luteisquama*, *Hasora chromus chromus*, *Potanthus hetaerus hetaerus*, *Unkana ambasa batara*.



Fig. 3. Coastal coppice: Homonhon Island (photo C.G. Treadaway). 20 species:  
*Badamia exclamationis*, *Baoris oceia*, *Bibasis sena palawana*, *Caltoris cormasa*, *Erionota thrax mindana*, *Hasora caeruleostriata*, *Hasora moestissima moestissima*, *Hasora taminatus padma*, *Matapa aria*, *Oriens californica*, *Parnara kawazoei*, *Pelopidas agna agna*, *Pelopidas mathias mathias*, *Potanthus hetaerus hetaerus*, *Prusiana prusias matinus*, *Pyronneura liburnia minda*, *Sustus migreus*, *Telicota ancilla minda*, *Unkana ambasa mindanaensis*, *Zela zeus major*.



Fig. 4. In and around a small lowland village (gardens, rice paddies, wasteland etc.): Sibuyan Island (photo C.G. Treadaway). 16 species:  
*Baoris oceia*, *Cephrenes acalle chrysozona*, *Erionota thrax thrax*, *Gangara thrysis philippensis*, *Halpe luteisquama*, *Hasora mixta mixta*, *Hasora schoenherr saida*, *Notocrypta feisthamelii alinkara*, *Notocrypta paralysos volux*, *Odonoptilum leptogramma*, *Oriens californica*, *Parnara kawazoei*, *Pelopidas agna agna*, *Pelopidas conjuncta conjuncta*, *Potanthus pava lesbia*, *Taractrocera luzonensis luzonensis*.



### Habitats

The overall climatic conditions by and large do not lead to the development of noticeable wet and dry season forms for butterflies. However, considering the preceding data, it is not surprising that a number of differing butterfly biotopes are found across the Philippines. Figs. 2-10 are of a variety of localities in the Philippines together with examples of the typical HesperIIDae that can be found in the specific area. Note that such listings cannot be a 100% complete outline of all HesperIIDae that might possibly be encountered in each specific location, but rather a representative cross section of the HesperIIDae that have actually been recorded from the areas in question.

Bearing in mind that the species listings are for specific localities, then perhaps, as could be expected, primary (48 species) and secondary (24 species) forest areas under 1,000 metres yield the highest number of HesperIIDae species. Followed by the semi-cleared partly cultivated lowland area (22 species), coastal coppice (21 species), garden and cultivated areas around and in a small lowland village (16 species), primary forest over 1,000 metres (10 species), the mangrove and swamp area (6 species), mossy high altitude forest (5 species) and lastly high altitude meadow/ grassland (4 species).

### Distribution and threats

So far, 879 species of butterflies have been indentified as occurring in the Philippines. This number includes 151\* species of HesperIIDae of which 35 or 23.2% are endemic.

\* The exact identity of one further species, close to *Isma feralia* (Hewitson, 1868), is still under study.



Fig. 5. Semi-cleared lowland partly cultivated: Sibutu, Sulu Archipelago (photo M. Gaulke). 22 species:

*Badamia exclamationis*, *Bibasis harisa consobrina*, *Bibasis oedipodea oedipodea*, *Bibasis sena palawana*, *Borba cinnara*, *Caltoris cormasa*, *Caltoris philippina philippina*, *Cephrenes acalle kliana*, *Erionota thrax thrax*, *Halpe luteisquama*, *Hasora mixta prabha*, *Hasora taminatus padma*, *Notocrypta paralyos varians*, *Odontoptilum pygela*, *Pelopidas mathias mathias*, *Pelopidas conjuncta conjuncta*, *Polytremis lubricans lubricans*, *Potanthus serina*, *Psolos fuligo fuligo*, *Tagiades gana gana*, *Taructrocera luzonensis stella*, *Unkana ambasa batara*.

It may be of interest to provide a picture of how HesperIIDae species are spread across the Philippine Islands. Table 1 exhibits the total number of species and the number of species endemic to the Philippines occurring on each of 38 islands or island groups (listed alphabetically) for which we have experience.

Table 1. Number of species and (in brackets) of endemic species of HesperIIDae occurring on different islands. The three islands marked with an asterisk are considered together as they are only separated by a few hundred meters of sea.

Alabat	1 (1)	Marinduque	33 (9)
Babuyan Group	19 (2)	Masbate	23 (6)
Camiguin Island	16 (2)	Mindanao	89 (22)
Balabac	13 (1)	Mindoro	65 (15)
Basilan	21 (2)	Negros	55 (12)
Biliran	8 (1)	Palawan	85 (4)
Bohol	15 (1)	Panaon	15 (2)
Calamian Group	19 (1)	Panay	30 (9)
Busuanga Island	19 (1)	Polillo	17 (3)
Camiguin de Mindanao	21 (3)	Romblon Group	36 (6)
Camotes	11 (0)	Romblon Island	4 (1)
Cebu	2 (5)	Sibuyan Island	35 (6)
Dinagat	12 (1)	Samar	58 (14)
Guimaras	5 (0)	Siargao	3 (1)
Homonhon	25 (4)	Tawitawi Group	42 (6)
Jolo	9 (2)	* Bongao, Tawitawi &	
Leyte	70 (16)	Sanga Sanga islands	40 (6)
Lubang	2 (0)	Sibutu	21 (1)
Luzon	80 (22)	Ticao	9 (1)

Such a listing can only give a directional indication of the concentration of species on each of the listed islands. It has been compiled based on 28 years of experience of collecting and observing HesperIIDae in the Philippines. However, some islands, particularly the larger ones, were visited more often and at different times of the year. A number of the islands have had their forested areas drastically cut down. Several of the smaller islands are difficult to reach and through lack of transportation possibilities rather a challenge to cover effectively. The forested mountain areas of other islands tend to be closed to visitors due to the activities of insurgents, bandits and religious groups.

The above points do interfere with a systematic evaluation of the distribution of HesperIIDae, but as could be expected, the larger islands such as Leyte (70), Luzon (80), Mindoro (65), Mindanao (89), Negros (55), Palawan (89) and Samar (58) yield the highest concentration of species. Disappointing results were obtained from Cebu (27), Masbate (23) and Panay (30). This is most likely due to the sparsity of forest. The same larger islands with the high numbers of individual species possess the highest concentrations of endemic species: Leyte (14), Luzon (21), Mindanao (21), Mindoro (13), Negros (12) and Samar (14). However, there is a notable exception as the island of Palawan, though home to the highest number of individual species, is one of the islands with the lowest count of endemic species. The endemism of the various islands is dealt with in more detail in the chapter on biogeography.

One is pleasantly surprised at the number of species on small island groups or small islands such as Basilan (21), Homonhon (25), Romblon Group (36) and the Tawitawi Group (42). Unfortunately, there is very little forest nowadays left on Basilan and Homonhon. It is highly possible that some years back, when these islands were for the most part forested, they were quite rich in species of Hesperidae. For the Romblon and Tawitawi groups of islands there is still some good primary and secondary forest existing on Sibuyan Island (Romblon Group) and Tawitawi Island, although even these forests are rapidly being reduced either for timber purposes or to provide cleared areas for farming.

Should the primary and secondary forests of the Philippines, as is expected, be totally cut down over the next 10 to 15 years, it must be accepted that many of those Hesperidae dependent on forest will have difficulty surviving. This could mean that roughly 50% of the currently known Hesperidae species in the Philippines will then no longer be found there.

#### **Annotated list of the Hesperidae**

Recently Baltazar (1991) published a list of the Hesperidae of the Philippines recorded in the literature. She came to a total of 92 species. Below we list 151 species and we are sure the list is not exhaustive, since new species (not only new to the Philippines but also to science) kept turning up until we had to close the manuscript.

The species have been arranged according to Evans (1949). Under "Geographic variation" the subspecies are mentioned that are relevant to the Philippines. Distinguishing characters have only been given, if more than one subspecies has been recorded from the Philippines. Generally no synonyms are given. For these, Evans (1949) should be consulted. The publication dates of original descriptions have been checked with Bridges (1988), and in cases of difference with Evans, Bridges has been followed. References to original descriptions have only been given for names not included in Bridges. If we deviate from Evans on other points, it is discussed under 'Remarks' and reference is given to the relevant literature. Unless otherwise stated the distribution in the Philippines is based on material examined by us. The islands have been listed alphabetically. Under "Status" four categories have been distinguished: very rare, rare, uncommon and common, to give a rough idea of the abundance of the species. The distinction is subjective, but based on the very extensive field experience of one of us (CGT). In some cases distinguishing characters of "difficult" species have been given under "Remarks". For genera with more than three "difficult" species in the Philippines keys are provided in the next chapter.

#### ***Bibasis* Moore, 1881**

A genus of 18 species covering the entire Oriental Region, extending east to the Lesser Sunda Islands and north to Japan and the Amur Region.

Normally fly during the day in lowland forest either primary or secondary up to 1,000 metres, but also seem equally at home in semi-cleared partially cultivated areas



Fig. 6. Secondary forest under 1,000 m: Culasi, Panay (photo C. G. Treadaway). 24 species:

*Aeromachus plumbeola*, *Ancistroides nigrifumatus*, *Baoris oceia*, *Bibasis gomata lorquini*, *Bibasis sena palawana*, *Caltoris bromus bromus*, *Caltoris philippina philippina*, *Erionota thrax thrax*, *Halpe luteisquama*, *Hasora mixta mixta*, *Hasora schoenherr saida*, *Hasora taminatus padma*, *Notocrypta feisthamelii alinkara*, *Notocrypta paralysos volux*, *Oriens californica*, *Parnara kawazoei*, *Pelopidas conjuncta conjuncta*, *Pelopidas mathias mathias*, *Potanthus mingo mingo*, *Prusiana prusias matinus*, *Tagiades japetus titus*, *Taractrocera luzonensis luzonensis*, *Unkana ambasa mindanaensis*, *Zographetus ogygioides*.

and coastal coppices (figs. 2-3, 5-7). Some species are attracted by *Lantana* blossom (*B. harisa*) as well as camp cooking areas in the middle of the day (*B. oedipodea*). They are found singly, in flight or at rest seldom above two metres.

***Bibasis oedipodea* (Swainson, 1820)**

General distribution.— Most of the Oriental Region, from NW Himalayas and Sri Lanka to China, Sulawesi, Sula Archipelago and Lesser Sunda Islands.

Geographic variation.— Six subspecies are recognized, two of which are found in the Philippines: ssp. *oedipodea* (Sundaland; type-locality: Java) and ssp. *paltra* Evans, 1949 (endemic; type-locality: Mindanao). They can be distinguished as follows. Vein 8 of hindwing in male relatively short and strongly diverging from vein 7, and as a consequence the straight part of the costa is quite short in ssp. *oedipodea*, while vein 8 is longer, not excessively far from vein 7, and the straight part of the costa is considerably longer in ssp. *paltra*. The orange scaling on the underside of the hindwing is usually not strong (but sometimes strong and fiery) and mainly restricted to the discal band in ssp. *oedipodea*, and restricted to internervular stripes and the basal wing area in ssp. *paltra*. Moreover, in the latter there are orange stripes on both sides of vein 7 (not vein 8, as stated by Evans, 1949) on the underside of the hindwing, which are absent in ssp. *oedipodea*.

Distribution in the Philippines (fig. 87).— Ssp. *oedipodea*: Balabac, Palawan, Sibutu, Tawitawi. Ssp. *paltra*: Cebu, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros.

Status.— Rare.



Fig. 7. Primary forest under 1,000 m: Mt. Balocaue, Central Leyte (photo C.G. Treadaway). 48 species: *Acerbas anthea anthea*, *Acerbas duris duris*, *Ancistroides nigrita fumatus*, *Badamia exclamationis*, *Baoris oceia*, *Bibasis gomata lorquini*, *Bibasis oedipodea paltra*, *Caltores cormasa*, *Caltores philippina philippina*, *Cephrenes acalle chrysozona*, *Choaspes estrella pallens*, *Choaspes plateni visaya*, *Coladenia ochracea*, *Erionota hiraca apex*, *Erionota surprisa*, *Gangara lebadea janlourensi*, *Gangara thyrus philippensis*, *Halpe sulphurifera*, *Halpe dante tilia*, *Halpe luteisquama*, *Hasora borneensis luzu*, *Hasora caeruleostriata*, *Hasora chromus chromus*, *Hasora khoda minsona*, *Hasora leucospila leucospila*, *Hasora mixta mixta*, *Hasora moestissima moestissima*, *Hasora proxissima proxissima*, *Hasora taminatus padma*, *Mooreana princeps*, *Notocrypta feisthamelii alinkara*, *Notocrypta paralyos volux*, *Oerane microthyrus microthyrus*, *Odina hieroglyphica cuneiformis*, *Parnara kawazoei*, *Pelopidas conjuncta conjuncta*, *Pelopidas mathias mathias*, *Plastingia naga*, *Potanthus hetaerus hetaerus*, *Prusiana prusias martinus*, *Psolos fuligo fuligo*, *Pyroneura liburnia minda*, *Tagiades gana elegans*, *Telicota augias pythias*, *Unkana ambas mindanaensis*, *Xanthoneura telesinus*, *Zela zeus major*, *Zographetus ogygia durga*.

***Bibasis etelka*** (Hewitson, [1867])

General distribution.— Sundaland, north to Peninsular Thailand and S Burma.

Distribution in the Philippines (fig. 87).— Mindanao, Palawan.

Status.— Very rare.

***Bibasis harisa*** (Moore, 1865)

General distribution.— From Sikkim and Assam through Sundaland to Sulawesi and Sula Archipelago.

Geographic variation.— Five subspecies are recognized, three of which occur in the Philippines: ssp. *consobrina* (Plötz, 1884) (Sundaland; type-locality: Java), ssp. *pala* de Jong & Treadaway, 1993 (endemic; type-locality: Palawan) and ssp. *grandis* de Jong & Treadaway, 1993 (endemic; type-locality: Dinagat). They can be distinguished by the antennae (black in ssp. *grandis*, ochreous on upperside of shaft and club in the other two), size (ssp. *grandis* being larger than the other two), colouration and male genitalia (shape of cucullus). See de Jong & Treadaway (1993a) for details.



Distribution in the Philippines (fig. 87).— *Ssp. consobrina*: Sibutu Island (Tawitawi group). *Ssp. pala*: Palawan. *Ssp. grandis*: Dinagat, Samar.

Status.— *Ssp. consobrina* and *ssp. pala* rare; *ssp. grandis* very rare.

***Bibasis gomata* (Moore, 1865)**

General distribution.— Most of the Oriental Region, north to W China and Yunnan, east to Sulawesi and Banggai Archipelago.

Geographic variation.— Six subspecies are recognized, one of which occurs in the Philippines (endemic): *ssp. lorquini* (Mabille, 1876) (type-locality: Luzon).

Distribution in the Philippines (fig. 88).— Calamian Islands, Camiguin de Luzon, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Palawan, Panay, Polillo.

Status.— Common.

***Bibasis sena* (Moore, 1865)**

General distribution.— Most of Oriental Region, east to Sulawesi and Lesser Sunda Islands.

Geographic variation.— Four subspecies are recognized, one of which occurs in the Philippines (endemic): *ssp. palawana* (Staudinger, 1889) (type-locality: Palawan).

Distribution in the Philippines (fig. 88).— Calamian Islands, Cebu, Homonhon, Leyte, Luzon, Marinduque, Mindanao, Negros, Palawan, Panay, Polillo, Sibutu, Sibuyan, Tawitawi.

Status.— Common.

***Hasora* Moore, 1881**

A large genus of 30 or more species, occurring throughout the Oriental Region, penetrating southern China to Omeishan, extending north to Ryukyu Islands, east to Fiji and south to E Australia (New South Wales). A key to the thirteen Philippine species is given on pages 74-75.

Males are more often encountered hilltopping early morning at sunrise or around huts and cooking areas early evening at sunset. Females are more retiring but are to be seen during the day. Both sexes fly in primary and secondary forest as well as partially cultivated areas in and around small villages, coastal coppices and even swamp areas (figs. 2-8). Though more frequently encountered under 1,000 metres, some species (*H. borneensis luza* and *H. leucospila*) are equally at home at altitudes up to 1,700 metres. *H. borneensis luza* is a noted fast flying hilltopper between 5 to 5.30 a.m., but with a seemingly fixed flight pattern making observation relatively easy. Usual flight height 2 to 4 metres.

***Hasora proxissima* Elwes & Edwards, 1897**

General distribution.— Very widely distributed, from Thailand to the Solomon Islands, but known from very few localities only.

Geographic variation.— Five subspecies are recognized, differing in the width of the white band and the colour of the basal part of the underside of the hindwing. See de Jong (1982) for details. Two subspecies are found in the Philippines: *ssp. proxissima* (endemic; type-locality: Mindoro) and *ssp. siva* Evans, 1932 (Borneo, Palawan;



type-locality: Borneo). In ssp. *proxissima* the white band is 4.2 mm wide and the basal area is dull green, in ssp. *siva* the band is 2 mm and the basal area is bluish violet.

Distribution in the Philippines (fig. 89).— Ssp. *proxissima*: Leyte, Mindoro, Mindanao. Ssp. *siva*: Palawan.

Status.— Ssp. *proxissima* is local, ssp. *siva* is rare.

***Hasora borneensis* Elwes & Edwards, 1897**

General distribution.— Perak, Borneo, Java and the Philippines.

Geographic variation.— The geographic variation was discussed by de Jong (1982) who concluded that the recognition of three subspecies (Evans, 1949; Eliot, 1978) does not find much justification in the material at hand. The Philippine form was distinguished as ssp. *luza* by Evans (1949) (type-locality: N Luzon).

Distribution in the Philippines (fig. 89).— Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Panaon, Samar.

Status.— Local.

Remarks.— Recently Maruyama (1991) separated ssp. *mavis* Evans, 1934 (type-locality: Perak) as a separate species, distributed in Thailand, the Malay Peninsula, Talaud and the Philippines, restricting *Hasora borneensis* to Borneo and the Philippines. This action was not explained, and since for *mavis* as conceived by Maruyama no males are known, a decision must await further material and study.

***Hasora chromus* (Cramer, [1780])**

General distribution.— Oriental Region (also Ryukyu Islands), and through New Guinea to N Australia and east to Vanuatu and Fiji.

Geographic variation.— Three subspecies are recognized of which ssp. *chromus* (type-locality: Coromandel) occupies almost all of the distribution area of the species, including the Philippines.

Distribution in the Philippines (fig. 89).— Leyte, Marinduque, Negros, Tawitawi, Ticao.

Status.— Rare.

***Hasora taminatus* (Hübner, 1818)**

General distribution.— Throughout the Oriental Region, north to W China and east through the Moluccas to Waigeo.

Geographic variation.— Ten subspecies are recognized, two of which occur in the Philippines: ssp. *malayana* (Felder, 1860) (Sundaland, north to S Burma and Hong Kong, and east to Sumbawa; type-locality: Malacca), and ssp. *padma* Fruhstorfer, 1911 (type-locality: Basilan). The two differ in the colour of the basal area of the underside of the hindwing (shining steely blue in ssp. *malayana*, greener in ssp. *padma*) and the width of the white band (very narrow, 1 mm or less in ssp. *malayana*, about 1.5 mm in ssp. *padma*).

Distribution in the Philippines (fig. 90).— Ssp. *malayana*: Balabac, S Palawan. Ssp. *padma*: Basilan, Cebu, Homonhon, Leyte, Luzon, Marinduque, Masbate, Mindoro, Mindanao, Negros, C and N Palawan, Panay, Panaon, Romblon, Sibuyan, Tawitawi, Ticao.

Status.— Common.



Fig. 8. Primary forest over 1,000 m: Mt. Amuyao area, North Luzon (photo C.G. Treadaway). Ten species: *Celaenorrhinus nigricans mindanus*, *Choaspes estrella estrella*, *Erionota thrax alexandra*, *Hasora borneensis luzu*, *Hasora leucospila*, *Odontoptilum angulatum sinka*, *Potanthus niobe hyugai*, *Tagiades trebellius martinus*, *Thoressa justini*, *Xanthoneura telesinus*.

Remarks.— According to Evans (1949) *ssp. padma* should occur in the Philippines and two of the Lesser Sunda Islands, viz. Sumba and Timor, whereas in the area in between (Sulawesi) the Sulawesi endemic *ssp. attenuata* (Staudinger, 1889) occurs. Moreover, *ssp. malayana* is mentioned from as far east as Sumbawa. It seems rather unlikely that the Sumba and Timor populations really belong to *ssp. padma*.

***Hasora schoenherr* (Latreille, 1828)**

General distribution.— From Assam to Vietnam and through Sundaland to the Philippines.

Geographic variation.— Five subspecies are recognized, two of which occur in the Philippines: *ssp. chuza* (Hewitson, [1867]) (Sundaland; type-locality: Sarawak) and *ssp. saida* (Hewitson, [1867]) (Philippines only; type-locality: Philippines). In the male the yellow spots of the forewing are hyaline in *ssp. chuza* and opaque in *ssp. saida*, while on the upperside of the forewing the base of cell is brown in *ssp. chuza* and yellow in *ssp. saida*. In the female there is an elongate yellow patch across vein 1 on the upperside of the forewing in *ssp. saida*, which is absent in *ssp. chuza*. Male and female of *ssp. saida* differ conspicuously from both sexes of *ssp. chuza* by the completely yellow base of the hindwing upperside, while this area is always dark brown in *ssp. chuza*.

Distribution in the Philippines (fig. 90).— *Ssp. chuza*: Balabac, Palawan. *Ssp. saida*: Babuyan, Bohol, Camiguin de Luzon, Camiguin de Mindanao, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Panaon, Panay, Samar, Sibuyan.

Status.— Common.

Fig. 9 (right). Mossy forest: Mt. Parker Range, Mindanao (photo C.G. Treadaway). Five species:  
*Celaenorrhinus treadawayi treadawayi*,  
*Halpe luteisquama*, *Isma binotatus*, *No-  
tocrypta feisthamelii alinkara*, *Xantho-  
neura telesinus*.

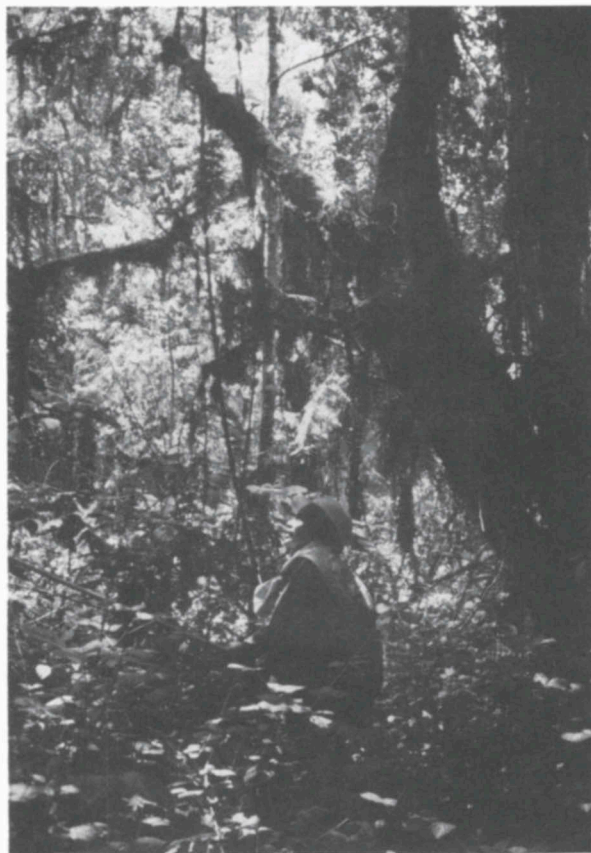


Fig. 10 (below). High altitude meadow and grassland: Mt. Apo National Park, Mindanao (photo C.G. Treadaway). Four species:  
*Aeromachus musca*, *Caltoris philippina philippina*, *Halpe luteisquama*, *Oriens fons*.



Remark.— Hayashi (1976) separated the Palawan population as *ssp. hondai*, but we agree with Maruyama (1991) that this name is synonymous with *ssp. chuza*.

***Hasora mixta* (Mabille, 1876)**

General distribution.— From S Burma through Sundaland to the Moluccas.

Geographic variation.— Four subspecies are recognized, two of which occur in the Philippines: *ssp. prabha* Fruhstorfer, 1911 (from S Burma through Sundaland; type-locality: Palawan) and *ssp. mixta* (endemic to the Philippines; type-locality: Manila, Luzon). They differ in the colour of the underside of the hindwing, predominantly brown in *ssp. prabha* and with a purple wash in *ssp. mixta*; the female has well-developed apical spots in *ssp. prabha* and no apical spots in *ssp. mixta*.

Distribution in the Philippines (fig. 91).— *Ssp. prabha*: Palawan, Tawitawi. *Ssp. mixta*: Basilan, Biliran, Cebu, Camiguin de Luzon, Leyte, Luzon, Marinduque, Masbate, Mindanao, Mindoro, Negros, Panaon, Panay, Samar, Sibuyan.

Status.— *Ssp. prabha* uncommon, *ssp. mixta* common.

***Hasora badra* (Moore, 1857)**

General distribution.— Throughout the Oriental Region, east to Sulawesi and Flores.

Geographic variation.— Two subspecies are recognized, one of which occurs in the Philippines: *ssp. badra* (whole distribution area of the species except Sri Lanka; type-locality: Java).

Distribution in the Philippines (fig. 91).— Balabac, Calamian, Palawan.

Status.— Uncommon.

***Hasora quadripunctata* (Mabille, 1876)**

General distribution.— Sundaland, Philippines, Sulawesi, N Moluccas.

Geographic variation.— Three subspecies are recognized, one of which occurs in the Philippines: *ssp. gnaeus* (Plötz, 1884) (Sundaland, Philippines; type-locality: Philippines).

Distribution in the Philippines (fig. 91).— Camiguin de Mindanao, Dinagat, Leyte, Mindanao, Mindoro, Samar.

Status.— Uncommon.

***Hasora vitta* (Butler, 1870)**

General distribution.— From S India and W China to New Guinea.

Geographic variation.— Six subspecies are recognized, one of which is restricted to the Philippines: *ssp. proximata* (Staudinger, 1889) (type-locality: Palawan).

Distribution in the Philippines (fig. 92).— Luzon, Mindanao, Mindoro, Palawan.

Status.— Uncommon.

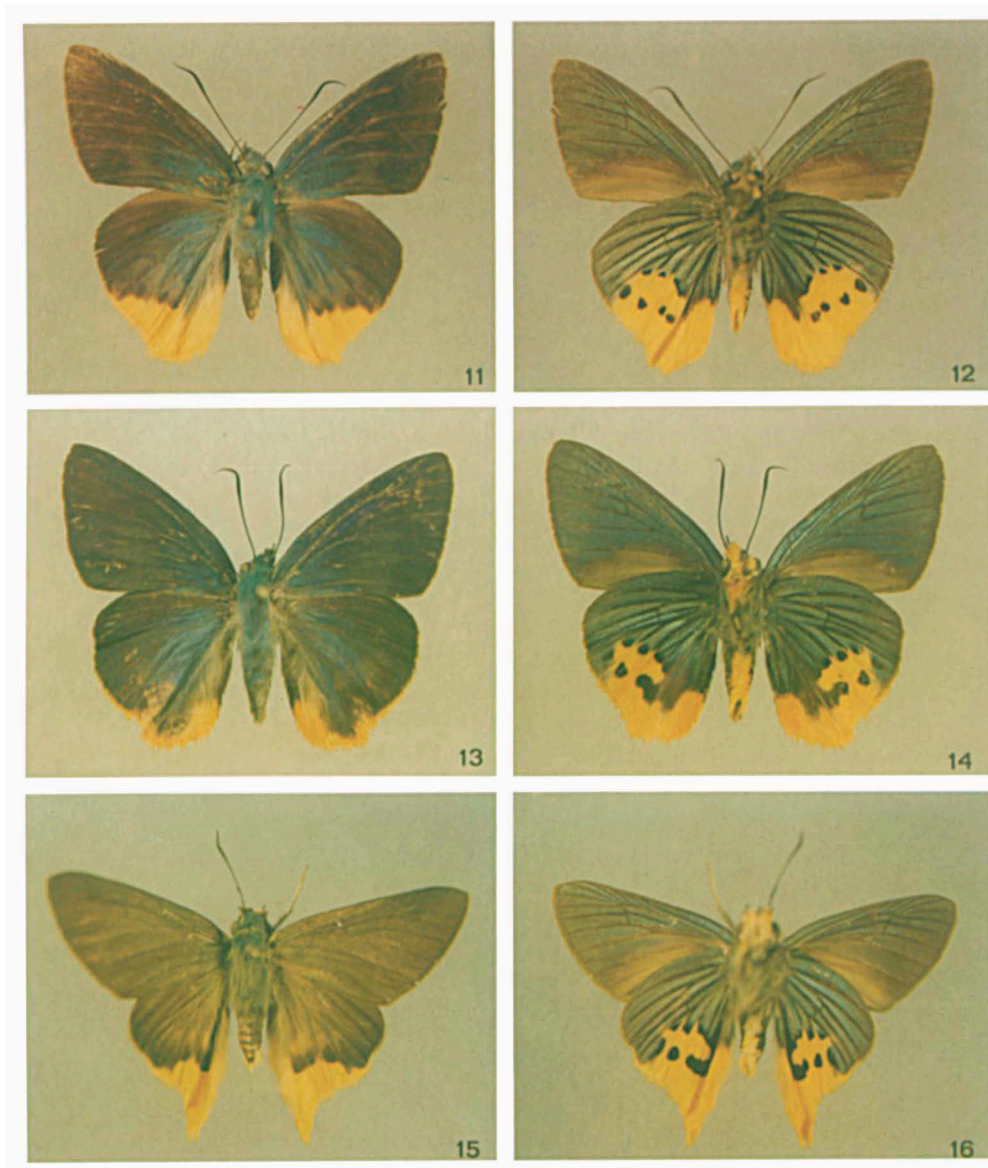
***Hasora moestissima* (Mabille, 1876)**

General distribution.— Philippines, Sulawesi and Aru (?).

Geographic variation.— Two subspecies are recognized, with the nominotypical one in the Philippines and Sulawesi (type-locality: Sulawesi).

Distribution in the Philippines (fig. 92).— Camiguin de Mindanao, Homonhon, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Samar.

Status.— Common.



Figs. 11-16. Endemic taxa of *Choaspes*. 11-12, *C. plateni boreus*, Luzon. 13-14, *C. plateni visaya*, Leyte. 15-16, *C. estrella estrella*, Luzon. All specimens natural size.

***Hasora caeruleostriata* de Jong, 1982 (figs. 17, 18)**

General distribution.— Endemic to the Philippines (type-locality: Quezon Park, Luzon).

Distribution in the Philippines (fig. 92).— Homonhon, Leyte, Luzon, Masbate, Negros, Palawan, Panay, Samar.

Status.— Common.

Remarks.— The species was originally described as a subspecies of *H. moestis-*



*sima*, differing in the blue instead of white colour of the band on the underside of the hindwing and a few other features, see de Jong (1982).

***Hasora khoda* (Mabille, 1876)**

General distribution.— From Assam to Queensland and Pacific islands (New Caledonia, Lifu, Sandwich Is.).

Geographic variation.— Evans (1949) recognized ten subspecies, but one of them, *ssp. mavis* Evans, 1934, originally described as a subspecies of *Hasora borneensis*, but for unknown reasons listed as a subspecies of *Hasora khoda* by Evans (1949) was moved back to *Hasora borneensis* by Eliot (1967). This action was followed by de Jong (1982). The latter author added a new subspecies, bringing the total number again to ten. Recently Maruyama (1991) raised *mavis* to species rank; see under *Hasora borneensis*. In the Philippines *ssp. minsona* Swinhoe, 1907, flies; outside the Philippines it occurs in Malaya and Borneo (type-locality: Borneo).

Distribution in the Philippines (fig. 93).— Leyte, Luzon, Marinduque, Negros, Palawan, Samar, Tawitawi.

Status.— Local.

***Hasora leucospila* (Mabille, 1891)**

General distribution.— From S Burma through Sundaland to the Moluccas.

Geographic variation.— Two subspecies are recognized. The nominotypical subspecies occurs throughout the area of the species except the Moluccas (type-locality: N Sulawesi).

Distribution in the Philippines (fig. 93).— Basilan, Homonhon, Leyte, Luzon, Mindanao, Mindoro, Negros, Samar.

Status.— Local.

***Badamia* Moore, 1881**

Only two species make up this genus, one restricted to a number of Pacific islands, the other very widely distributed, from Pakistan to the Pacific islands and SE Australia.

Can be encountered almost anywhere in the countryside during the day under 1,000 metres (figs. 2-3, 5-7). Usually pitches under a leaf with wings closed and is loath to move. Is extraordinarily abundant in some areas. Normal flight level 1 to 3 metres. Has been caught at night at an ultraviolet light trap.

***Badamia exclamationis* (Fabricius, 1775)**

General distribution.— Throughout the Oriental Region and east to Australia and the Pacific islands as far as Samoa.

Distribution in the Philippines (fig. 93).— Basilan, Homonhon, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Palawan, Sibutu, Tawitawi, Ticao.

Status.— Common.

Remarks.— The species is known to migrate in vast flights, which may explain their geographic uniformity. Locally the species can be so numerous that its food plants (*Terminalia*) are completely defoliated (Common & Waterhouse, 1981).



*Choaspes* Moore, 1881

Eight or nine species, together covering most of the Oriental Region, extending north to Japan and east to New Guinea. Recently, Igarashi (1992) distinguished two larval types with different pattern, suggesting a bipartition of the genus. (\*)

Primary and advanced secondary forest butterflies (figs. 7-8). *C. plateni* and *C. subcaudatus* are found under 1,000 metres while *C. estrella* can be found up to 1,700 metres. *C. plateni* flies sluggishly during the daytime inside the forest at about 1 to 2 metres moving rather slowly, but is more active at sunset, when it can be found hill-topping 5.30 to 6.30 p.m. between 2 to 4 metres using a short repetitive flight path. In general, the flight of *Choaspes* is considerably slower than *Hasora*. *C. subcaudatus* seems to be particularly fond of flying up and down shaded forest trails midday at about 1 to 1.5 metres.

*Choaspes plateni* (Staudinger, 1888) (figs. 13-16)

General distribution.— From Sikkim and Assam to Hainan, and through Sundaland to the Philippines and Sulawesi.

Geographical variation.— Eight subspecies are recognized (\*), five of which occur in the Philippines: ssp. *caudatus* Evans, 1932 (Sundaland; type-locality: Mergui, Burma), ssp. *adhara* Fruhstorfer, 1911, ssp. *visaya* de Jong, 1980, ssp. *negrosa* de Jong & Treadaway, 1993, and ssp. *boreus* de Jong & Treadaway, 1993 (all endemic to the Philippines). The subspecies mainly differ in the extent of the yellow tornal area of the hindwing. For details, see de Jong & Treadaway (1993a).

Distribution in the Philippines (fig. 94).— Ssp. *caudatus*: Palawan; ssp. *adhara*: Mindanao; ssp. *visaya*: Biliran, Bohol, Leyte, Panaon, Samar; ssp. *negrosa*: Negros; ssp. *boreus*: Luzon, Mindoro.

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(\*) Just before this paper was sent to press we obtained a copy of the second issue of the journal *Butterflies*, published by The Butterfly Association of Japan, containing two interesting articles relating to *Choaspes* (Chiba, 1992; Tsukiyama, 1992). These authors propose a new arrangement of species and subspecies. *C. plateni* is split into three species, *C. stigmatus* (continental Asia, the large Sunda islands and Palawan), *C. plateni* (Sulawesi) and *C. adhara* (Philippines outside Palawan). The geographic variation of *C. adhara* is considered clinal. *C. estrella* is downgraded to a subspecies of the largely continental Asian *C. xanthopogon* (Kollar, 1844), and its subspecies *pallens* is sunk into synonymy. Since the text is in Japanese and our understanding of this language is very poor, it is possible that we do not fully rate the conclusions at their true value, but it seems that they are based on the fully subjective criterium of the degree of differentiation of island populations. This criterium is not applied consistently. Thus, *C. pallidus* Evans, 1932, from Sumatra, originally described as a subspecies of *C. benjamini* (Guérin, 1843) from continental Asia, Taiwan and Japan, is raised to species rank, although the genitalia are rather similar and the two seem connected by an undescribed subspecies of *C. benjamini* from West Malaysia. On the other hand, *C. estrella*, although (subjectively) at least as distinct from *C. xanthopogon*, as *C. pallidus* is from *C. benjamini*, is downgraded. We cannot accept the denomination of the variation found in *C. adhara* as clinal. It is an oversimplification of a complex situation and the claim is not substantiated. We applaud new insights in the interrelationships of the taxa involved, but the new arrangement does not seem to contribute much in this respect. A phylogenetic analysis of the genus should be helpful in revealing interrelationships, but even then the taxonomic rank of island populations can only be decided upon subjectively.

Finally, we regret that Tsukiyama (1992: 30) deals with *C. hemixanthus cora* Evans, 1934, in the original combination, while six pages later it is transferred to *C. xanthopogon* (by Tsukiyama himself, or by Chiba who, again six pages later, deals with this subspecies?). Such actions do not promote stability.

Status.— *Ssp. caudatus*: very rare; *ssp. adhara*: local; *ssp. visaya*: common; *ssp. negrosa*: local; *ssp. boreus*: rare.

Remark.— In a recent publication on the different larval forms found in the genus Igarashi (1992) listed *caudatus* as a subspecies of *C. stigmatus*. The latter taxon was considered a subspecies of *C. plateni* by Evans (1949). Igarashi's action suggests that *plateni* and *caudatus* are not conspecific. If correct, it remains to be seen if the Philippine populations outside Palawan belong to *C. stigmatus* (E India east to Line of Wallace) or to *C. plateni* (Sulawesi). Photos taken by Mr Hyuga of *C. plateni* larvae from Mindoro show a larval form similar to Igarashi's *C. stigmatus*. However, since Igarashi did not deal with *C. plateni* at all, it does not follow that the Philippine populations belong to *C. stigmatus* and not to *C. plateni*. Until the question has been settled, we follow Evans' (1949) arrangement. (\*)

***Choaspes estrella* de Jong, 1980 (\*)**

General distribution.— Restricted to the Philippines (type-locality: Baguio, Luzon).

Geographic variation.— Two subspecies are recognized: *ssp. estrella* and *ssp. pallens* Schröder & Treadaway, 1986. They can be distinguished by the extent and colour of the yellow/orange ternal area of the hindwing

Distribution in the Philippines (fig. 94).— *Ssp. estrella*: Luzon, Negros, Panay. *Ssp. pallens*: Leyte, Samar.

Status.— Local.

***Choaspes subcaudatus* (Felder, 1867)**

General distribution.— S Burma, Thailand and Sundaland.

Geographic variation.— The nominotypical form is from Java. In the rest of the distribution area of the species *ssp. crawfurdii* Distant, 1886 (type-locality: Malaya), occurs.

Distribution in the Philippines (fig. 94).— Tawitawi.

Status.— Rare.

***Celaenorrhinus* Hübner, 1819**

One of the largest genera of the Hesperidae and the only pantropical one, with about 80 species. Almost half of the species occur in the Oriental Region. The genus does not extend east of the Moluccas.

Normally primary, but also secondary forest up to 1,700 metres (figs. 8-9). This genus is usually found during the day inside the forest in the shade, but early morning or late afternoon can be found in sunny patches in the forest. Flies between 1 to 3 metres above ground.

***Celaenorrhinus nigricans* (de Nicéville, 1885)**

General distribution.— From Sikkim and Assam to Burma and W Thailand; Borneo; Philippines.

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(\*) See footnote on page 19.

Geographic variation.— Four subspecies are recognized, of which two (*balukinus* Elwes & Edwards, 1897, and *orbiferus* Elwes & Edwards, 1897) undoubtedly relate to the same population (i.e. the names are synonymous), since they are both from Kinabalu (Sabah). The Philippine material was described as a separate subspecies, *mindanus* de Jong, 1981 (type-locality: Bukidnon, Mindanao).

Distribution in the Philippines (fig. 95).— Luzon, Mindanao.

Status.— Rare.

***Celaenorrhinus treadawayi* de Jong, 1981 (figs. 19,20)**

General distribution.— Restricted to the Philippines (type-locality: Mindanao).

Geographic variation.— The two island populations have been distinguished as two subspecies, ssp. *treadawayi* and ssp. *samarensis* de Jong, 1981. They differ as follows: On the forewing the spot in space 3 completely fills the base of space 3, and it is conjoined to the spots in space 2 and cell in ssp. *treadawayi*, while the spot in space 3 not completely fills the base of space 3, and is not conjoined to the cell spot in ssp. *samarensis*. There are also differences in the male genitalia, see de Jong (1981).

Distribution in the Philippines (fig. 95).— Ssp. *treadawayi*: Mindanao. Ssp. *samarensis*: Samar.

Status.— Ssp. *treadawayi* is rare, ssp. *samarensis* is very rare.

***Celaenorrhinus halconis* de Jong & Treadaway, 1993 (figs. 21-22)**

Only known from Mt. Halcon on Mindoro (fig. 95). Apparently very local. See de Jong & Treadaway (1993c) for details and possible relationship.

***Celaenorrhinus asmara* (Butler, 1877)**

General distribution.— From Assam to Indo-China and throughout Sundaland.

Geographic variation.— Three subspecies are recognized. In the Philippines only ssp. *palajava* (Staudinger, 1889) (Borneo, Palawan, Sulawesi; type-locality: Palawan) occurs.

Distribution in the Philippines (fig. 95).— Palawan.

Status.— Uncommon.

***Celaenorrhinus bazilanus* (Fruhstorfer, 1909)**

General distribution.— Borneo and the Philippines.

Geographic variation.— Two subspecies are recognized. The nominotypical form is restricted to the Philippines (type-locality: Basilan).

Distribution in the Philippines (fig. 95).— Basilan, Mindanao.

Status.— No experience.

***Tapena* Moore, 1881**

A monotypic genus restricted to the Oriental Region.

Found during the day in lowland (under 1,000 metres) primary forest, but appears to seek out sunny patches. Can be seen on the edge of primary forest pitched with wings flat on the leaf basking in the sunshine between 2 to 5 metres above ground.

*Tapena thwaitesi* Moore, 1881

General distribution.— From Sri Lanka and India to Sumatra and Borneo.

Geographic variation.— Three subspecies are recognized, of which ssp. *bornea* Evans, 1931, occurs in Malaya, Sumatra, Borneo and Palawan (type-locality: Perak).

Distribution in the Philippines (fig. 96).— Palawan.

Status.— Uncommon.

*Darpa* Moore, 1865

The genus consists of only three Oriental species, two of which occur in Sundaland.

Another lowland (up to 350 metres) dayflying primary forest butterfly that seeks sunny clearings in the forest. A fairly fast flier which tends to keep to a given area. Can be found from ground level up to 2 metres.

*Darpa pteria* (Hewitson, 1868)

General distribution.— From Assam through Sundaland to the Philippines.

Geographic variation.— Two subspecies are recognized, both occurring in the Philippine: the nominotypical form is restricted to the Philippines (type-locality: Philippines), ssp. *dealbata* Distant, 1886 (with a more extended white tornal area) from Assam through Sundaland (type-locality: Malacca).

Distribution in the Philippines (fig. 96).— Ssp. *pteria*: Luzon, Mindanao; ssp. *dealbata*: Palawan.

Status.— Rare.

*Odina* Mabille, 1891

Two species, one of which is restricted to the mainland, from Sikkim to Indo-China.

Lowland (up to 650 metres) dayflying butterfly which seems equally at home in sunny clearings in primary forest (fig. 7), secondary forest or even semi-cleared partly cultivated areas. It pitches with wings flat arranging its position to receive the most direct sunshine on its wings. Ground level to 2 metres. Has a fast flight, but tends to stay more or less in the same area.

*Odina hieroglyphica* (Butler, 1870)

General distribution.— From Burma through Sundaland to the Philippines, Sulawesi and the Sula Archipelago.

Geographic variation.— Five subspecies are recognized. The Philippine populations belong to ssp. *cuneiformis* (Semper, 1892), which is restricted to the Philippines (type-locality: Mindoro).

Distribution in the Philippines (fig. 96).— Camiguin de Luzon, Leyte, Luzon, Marinduque, Mindoro, Palawan.

Status.— Uncommon.

*Coladenia* Moore, 1881

Fifteen species, through most of the Oriental Region, with four species restricted to China. With five endemic species (of which three were described recently, see Chiba et al., 1991, and de Jong & Treadaway, 1992b) the Philippines show a remarkable development of this genus. For a revision of the Philippine species, with synonymy and details of the male genitalia, see de Jong & Treadaway (1992b).

Dayflying forest loving butterfly found in lowland (up to 650 metres) primary forest (fig. 7) and well developed secondary forest. Flies rapidly and when disturbed tends to seek a new area. Can be seen from 1 metre to 5 metres above the ground in sunny clearings or along sunny trails through the forest.

*Coladenia igna* (Semper, 1892) (figs. 23, 24)

General distribution.— Philippines.

Geographic variation.— Two subspecies can be distinguished: ssp. *igna* and ssp. *marinda* de Jong & Treadaway, 1992, the latter with larger hyaline spots.

Distribution in the Philippines (fig. 97).— Ssp. *igna*: Luzon, Samar; ssp. *marinda*: Marinduque.

Status.— Rare to very rare.

*Coladenia ochracea* de Jong & Treadaway, 1992 (figs. 25, 26)

General distribution.— Philippines (type-locality: Leyte).

Distribution in the Philippines (fig. 97).— Leyte, Mindanao.

Status.— Very rare.

*Coladenia semperi* Elwes & Edwards, 1897 (figs. 27-28)

General distribution.— Philippines type-locality: Camiguin de Mindanao).

Distribution in the Philippines (fig. 97).— Camiguin de Mindanao, Leyte.

Status.— Very rare.

*Coladenia minor* Chiba, Nakanishi, Fukuda & Yata, 1991 (figs. 29, 30)

General distribution.— Philippines (type-locality: Luzon).

Distribution in the Philippines (fig. 97).— Luzon, Marinduque.

Status.— Rare.

*Coladenia similis* de Jong & Treadaway, 1992 (figs. 31, 32)

General distribution.— Philippines (type-locality: Marinduque).

Distribution in the Philippines (fig. 97).— Camiguin de Mindanao, Luzon, Marinduque, Mindanao.

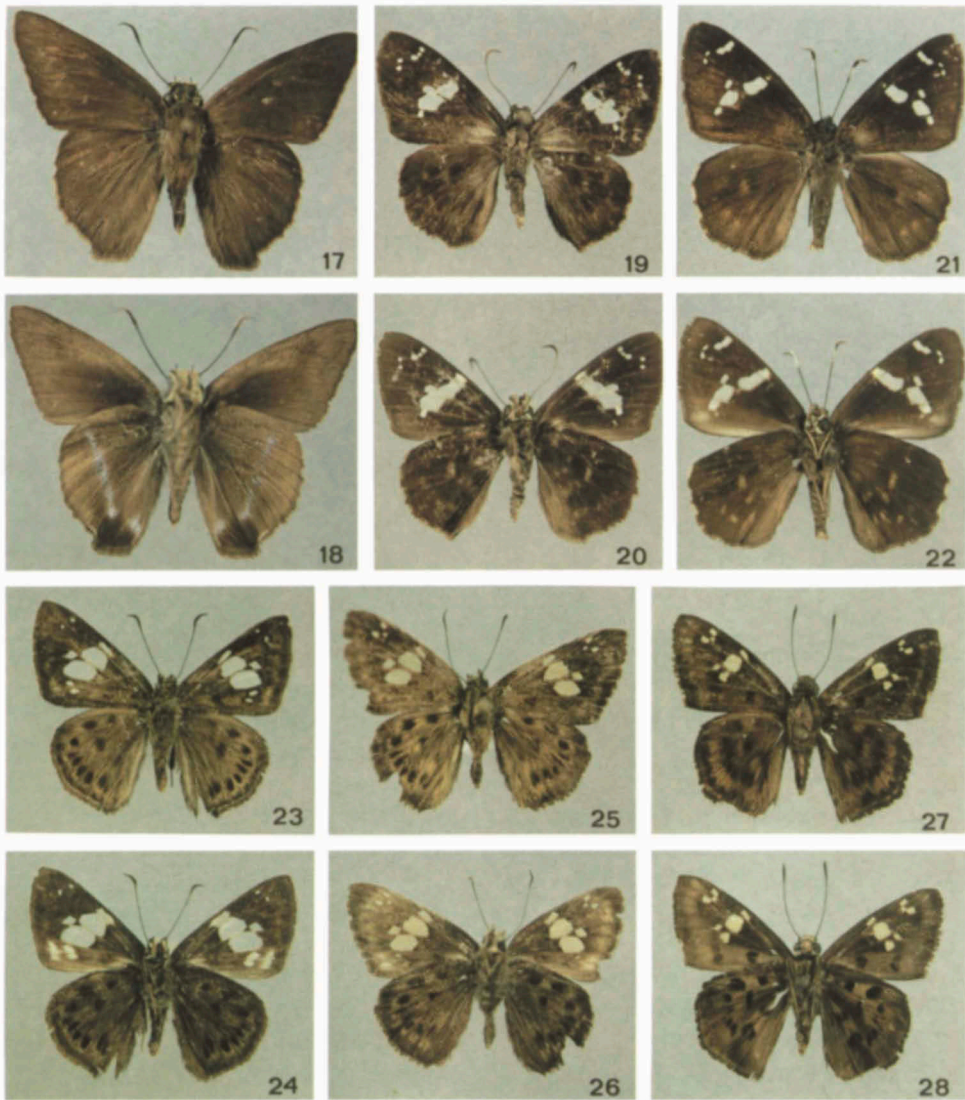
Status.— Rare.

*Coladenia palawana* (Staudinger, 1889)

General distribution.— Sundaland (reported from Bali, Maruyama, 1991, but unknown from Java), Philippines.

Distribution in the Philippines (fig. 97).— Palawan.

Status.— Rare.



Figs. 17-28. Endemic species and subspecies of *Hasora*, *Celaenorrhinus* and *Coladenia*. 17-18, *H. caeruleostriata*, Luzon. 19-20, *Cel. treadawayi treadawayi*, Mindanao. 21-22, *Cel. halconis*, Mindoro. 23-24, *Col. igna marinda*, Marinduque. 25-26, *Col. ochracea*, Leyte. 27-28, *Col. semperi*, Leyte. All specimens natural size.

#### *Gerosis* Mabille, 1903

Six species, from China and NE India to Java and the Sula Archipelago east of Sulawesi.

Dayflying lowland (650 metres) forest (primary or advanced secondary) butterfly which seeks sunny areas, but can be encountered in the shade (females). Usually seen between 1 to 4 metres above ground.





Figs. 29-40. Endemic species of *Coladenia*, *Mooreana*, *Gerosis* and *Odontoptilum*. 29-30, *C. minor*, Luzon. 31-32, *C. similis*, Marinduque. 33-34, *M. princeps*, Samar. 35-36, *G. corona* ♂, Leyte. 37-38, *G. corona* ♀, Luzon. 39-40, *O. leptogramma*, Samar. All specimens natural size.

***Gerosis limax* (Plötz, 1884)**

General distribution.— Sundaland, north to S Burma and Thailand.

Geographic variation.— Four subspecies are recognized, one of which, *philippina* Evans, 1932, occurs in the Philippines (endemic; type-locality: Palawan).

Distribution in the Philippines (fig. 98).— Palawan.

Status.— Rare.

*Gerosis corona* (Semper, 1892) (figs. 35-38)

General distribution.— Restricted to the Philippines (type-locality: Mindoro).

Distribution in the Philippines (fig. 98).— Alabat, Camiguin de Mindanao, Leyte, Luzon, Masbate, Mindanao, Mindoro, Samar.

Status.— Uncommon.

*Tagiades* Hübner, 1819

An Indo-African genus, with three species in the Afrotropical Region and 13 species from India and Sri Lanka to NE Australia and the Pacific islands.

For the identification of the five Philippine *Tagiades* species, see p. 75.

A dayflying up to 1,300 metres primary and secondary forest butterfly, but can also be encountered occasionally in semicleared partly cultivated areas (figs. 5-8). Flies quite fast but keeps to a preferred area often returning to the same leaf. Tends to pitch under a leaf and is not easily disturbed. Flight height between 2 and 6 metres.

*Tagiades japetus* (Stoll, 1782)

General distribution.— Throughout the Oriental Region and further east to NE Australia and the Pacific islands.

Geographic variation.— Twenty-four subspecies are recognized. In spite of the proliferation of local forms, the Philippines harbours only one, endemic subspecies: *titus* (Plötz, 1884) (type-locality: Philippines).

Distribution in the Philippines (fig. 99).— Basilan, Biliran, Bohol, group), Calamian, Camiguin de Luzon, Camiguin de Mindanao, Camotes, Cebu, Guimaras, Leyte, Lubang, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Polillo, Samar, Siargao, Sibuyan, Sibutu, Tawitawi.

Status.— Common.

*Tagiades gana* (Moore, 1865)

General distribution.— Most of the Oriental Region.

Geographic variation.— Ten subspecies are recognized, of which three occur in the Philippines: ssp. *gana* (Sundaland; type-locality: Java), ssp. *elegans* Mabilis, 1877 (endemic to the Philippines; type-locality: Mindoro), and ssp. *semperi* Fruhstorfer, 1910 (endemic to the Philippines; type-locality: Camiguin de Luzon). The three subspecies can be distinguished as follows: the white tornal area on the upperside of the hindwing is bordered by two black spots in ssp. *gana*, and by three black spots in the ssp. *elegans* (more or less united to a continuous band), and by a continuous broad dark border in ssp. *semperi*; the white hyaline discal dots in spaces 4 and 5 on the forewing are missing in ssp. *elegans*, present in ssp. *semperi*.

Distribution in the Philippines (fig. 99).— Ssp. *gana*: Palawan, Tawitawi. Ssp. *elegans*: Basilan, Biliran, Bohol, Camiguin de Mindanao, Camotes, Dinagat, Leyte, Luzon, Marinduque, Masbate, Mindanao, Mindoro, Negros, Panaon, Polillo, Samar, Siargao, Sibuyan. Ssp. *semperi*: Camiguin de Luzon.

Status.— Ssp. *gana* is uncommon; ssp. *elegans* is common; with ssp. *semperi* we have no experience.

*Tagiades parra* Fruhstorfer, 1910

General distribution.— From Sikkim and Assam to Indo-China, and throughout Sundaland.

Geographic variation.— Four subspecies are recognized. The nominotypical form (type-locality: N Borneo) flies in Sumatra, Borneo and Java, and the Philippines.

Distribution in the Philippines (fig. 100).—Leyte, Palawan.

Status.— Rare.

*Tagiades ultra* Evans, 1932

General distribution.— S Burma, Thailand, Sundaland.

Geographic variation.— Three subspecies are recognized, of which the nominotypical form (type-locality: S Burma) occurs from S Burma to Borneo and Palawan.

Distribution in the Philippines (fig. 100).— Palawan.

Status.— Rare.

Remark.— The species was listed as a subspecies of *Tagiades litigiosa* Möscher, 1878, by Evans (1949), but it was separated by Eliot (1978) because of differences in the genitalia and distributional overlap.

*Tagiades trebellius* (Hopffer, 1874)

General distribution.— From Borneo and the Philippines through Sulawesi, the Moluccas and New Guinea to the Solomon Islands.

Geographic variation.— Eleven subspecies are recognized. In the Philippines only the endemic ssp. *martinus* (Plötz, 1884) (type-locality: Philippines) occurs.

Distribution in the Philippines (fig. 100).— Babuyan, Basilan, Bohol, Cebu, Camiguin de Mindanao, Dinagat, Homonhon, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Palawan, Polillo, Samar, Sibuyan, Tawitawi, Ticao.

Status.— Common.

*Mooreana* Evans, 1926

Two species, from N India to Java, Borneo and the Philippines.

Encountered up to 1,000 metres during the daytime in and around primary (fig. 7) and secondary forest. Flies quite fast but keeps between 1 to 3 metres - 1 to 2 metres in repose. Usually single specimens are encountered.

*Mooreana trichoneura* (Felder & Felder, 1860)

General distribution.— N India to Indo-China, and throughout Sundaland.

Geographic variation.— Six subspecies are recognized; ssp. *trichoneuroides* (Elwes & Edwards, 1897) (type-locality: N Borneo) flies in Borneo and Palawan.

Distribution in the Philippines (fig. 101).— Palawan.

Status.— Rare.

*Mooreana princeps* (Semper, 1892) (figs. 33- 34)

General distribution.— Restricted to the Philippines (type series is from Panaon, E and SE Mindanao).



Figs. 41-58. Endemic species of *Thoressa* and *Halpe*. 41-42, *T. justini*, Luzon. 43-44, *H. palawea*, Busuanga Is. (Calamian group). 45-46, *H. luteisquama*, Mindoro. 47-48, *H. latipinna*, Mindoro. 49-50, *H. dante dante*, Negros. 51-52, *H. dante luzona*, Luzon. 53-54, *H. sulphurifera*, Leyte. 55-56, *H. purpurascens*, Masbate. 57-58, *H. inconspicua*, Leyte. All specimens natural size.





Figs. 59-80. Endemic species and subspecies. 59-60, *Suada albina*, Mindanao. 61-62, *Suastus gremius*, Cebu. 63-64, *Zographetus pallens*, holotype, Marinduque. 65-66, *Pyroneura liburnia liburnia*, Luzon. 67-68 *Pyroneura liburnia minda*, Homonhon. 69-70, *Oriens californica*, Mindanao. 71-72, *Aeromachus musca*, Cebu. 73-74, *Xanthoneura telesinus*, Luzon. 75-76, *Potanthus niobe hyugai*, paratype, Mindoro. 77-78, *Oriens fons*, Mindanao. 79-80, *Aeromachus plumbeola*, Luzon. All specimens natural size.

Distribution in the Philippines (fig. 101).— Leyte, Mindanao, Panaon, Samar.  
Status.— Uncommon.

*Odontoptilum* de Nicéville, 1890

Three species, throughout the Oriental Region, from Sri Lanka and N India to the Lesser Sunda Islands, Sulawesi and the Philippines.

Dayflying in sunny clearings of primary and secondary forest up to 1,000 metres as well as semicleared areas (figs. 4-5, 8). Occasionally found around small villages. Often seen on flowers along trails and in village gardens. Is certainly a sun loving butterfly which pitches with wings flat. It is seen most often between ground level to 2 metres. Flies rather fast but not great distances.

*Odontoptilum angulatum* (Felder, 1862)

General distribution.— Oriental Region.

Geographic variation.— Five subspecies are recognized. In the Philippines two subspecies occur, both endemic: ssp. *helisa* (Semper, 1892) (type-locality: Mindanao) and ssp. *sinka* Evans, 1949 (type-locality: Los Baños, Luzon). In the first subspecies the upperside of the hindwing is covered with pale blue scales, which are absent in the other subspecies.

Distribution in the Philippines (fig. 101).— Ssp. *helisa*: Basilan, Bohol, Cebu, Mindanao, Mindoro, Negros, Samar. Ssp. *sinka*: Luzon, Marinduque, Polillo.

Status.— Ssp. *helisa* is uncommon, ssp. *sinka* is rare.

*Odontoptilum pygela* (Hewitson, 1868)

General distribution.— Sundaland, north to S Burma and Thailand.

Geographic variation.— Two subspecies are recognized, of which one is restricted to Java, while the nominotypical subspecies (type-locality: Malacca) just reaches the Philippines.

Distribution in the Philippines (fig. 101).— Palawan, Tawitawi.

Status.— Uncommon.

*Odontoptilum leptogramma* (Hewitson, 1868) (figs. 39, 40)

General distribution.— Restricted to the Philippines (type-locality: Philippines).

Distribution in the Philippines (fig. 101).— Cebu, Leyte, Luzon, Mindanao, Mindoro, Samar, Sibuyan.

Status.— Uncommon.

*Aeromachus* de Nicéville, 1890

Eleven small and inconspicuous species, occurring throughout the Oriental Region and extending northwards to the Amur region and Japan.

Dayflying with a strong preference for gardens and meadows from sea level to 2,000 metres. Seems equally at home in a garden in Manila or a mountain meadow. Usually flies not more than 1 metre above the ground. Can be found on flowers. Has



a rather weak flight for a HesperIIDae. Likes sunshine and pitches with forewings closed and hindwings flat.

*Aeromachus musca* (Mabille, 1876) (figs. 71-72)

General distribution.— Restricted to the Philippines (type-locality: Luzon).

Distribution in the Philippines (fig. 102).— Cebu, Luzon, Mindanao, Negros, Siargao.

Status.— Uncommon.

*Aeromachus plumbeola* (Felder, 1867) (figs. 79-80)

General distribution.— Restricted to the Philippines (type-locality: Luzon).

Distribution in the Philippines (fig. 102).— Biliran, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Panay, Samar.

Status.— Common.

*Thoressa* Swinhoe, 1913

Twenty species, mainly in India and China; one species occurs in Taiwan and one other species goes as far north as Japan and the Kurile Islands; absent from Sundaland. In SE Asia it was only known from three species occurring in Indo-China, until Inoue & Kawazoé (1969) described it from the Philippines.

Dayflying high altitude butterfly found in stunted primary forest, in clearings and along the roadside at 1,300 to 2,000 metres (fig. 8). Flies fast between 1 to 4 metres in sunny or clouded conditions. Usually single specimens encountered.

*Thoressa justini* Inoue & Kawazoé, 1969 (figs. 41, 42)

General distribution.— Only known from N Luzon (fig. 102).

Status.— Very rare.

Remark.— Murayama & Okamura (1973) described the same species under the name *Halpe nuydai*, see Kawazoé (1973).

*Halpe* Moore, 1878

About 35 species, throughout the Oriental Region, northwards extending into China; contrary to the previous genus, *Halpe* is well represented in Sundaland. Eleven species are known from the Philippines. For identification, see p. 76.

The species are not always easy to identify; the key in the next chapter may be helpful, but examination of the genitalia is indispensable in some cases.

Dayflying with some species occurring from sea level to high altitude (2,500 metres) meadows. Found in primary and secondary forest as well as semicultivated small village gardens, coastal coppices and swamp areas (figs. 2, 4, 6, 7, 9, 10). Flies fast in a limited area with usually a number of specimens being found in any given location. Likes sunshine and goes to flowers. More often seen between ground level and 2 metres, but sometimes flies up to 5 metres. Pitches either with wings closed or with forewings closed and hindwings at an angle.



Figs. 81-86. Endemic species and subspecies. 81-82, *Gangara thyrsis magnificens*, holotype, Negros. 83-84, *Pirdana fusca*, paratype, Samar. 85-86, *Erionota surprisa*, paratype, Marinduque. All specimens natural size, but *G. thyrsis magnificens* 0.86X.

***Halpe zema* (Hewitson, 1877)**

General distribution.— Sikkim to Indo-China and Malaya, Borneo and the Philippines.

Geographic variation.— Four subspecies can be recognized, one of which, *mahapara* Fruhstorfer, 1911, is endemic to the Philippines (type-locality: Palawan).

Distribution in the Philippines (fig. 103).— Calamian, Palawan.

Status.— Uncommon.

Remark.— Eliot (1959) revised some of the *Halpe* species that were mixed up by Evans (1949). As a consequence he restricted *H. zema* to the area from Sikkim to Indo-China and Malaya. Later, Maruyama (1991) recorded the species from Borneo, so the occurrence of the species in the Philippines does not come as a surprise. The Philippine form was already described by Fruhstorfer in 1911 (as a distinct species), but the name was sunk as a junior synonym of *ormenes* Plötz (see below) by Evans (1949), who considered *ormenes* a subspecies of *H. zema*.

***Halpe ormenes* (Plötz, 1886)**

General distribution.— Sundaland and north to Burma.

Geographic variation.— Two subspecies are recognized, ssp. *ormenes* (the area of the species minus Borneo) and ssp. *vistula* Evans, 1937 (type-locality: Borneo). The latter subspecies also occurs in the Philippines.

Distribution in the Philippines (fig. 103).— Palawan.

Status.— Rare.

***Halpe palawea* (Staudinger, 1889) (figs. 43, 44)**

General distribution.— Restricted to the Philippines (type-locality: Palawan).

Distribution in the Philippines (fig. 103).— Calamian, Palawan.

Status.— Uncommon.

***Halpe luteisquama* (Mabille, 1876) (figs. 45, 46)**

General distribution.— Restricted to the Philippines (type-locality: "Himalayas").

Distribution in the Philippines (fig. 103).— Basilan, Camiguin de Luzon, Cebu, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Palawan, Panay, Samar, Sibutu, Sibuyan, Tawitawi.

Status.— Common.

***Halpe latipinna* de Jong & Treadaway, 1993 (figs. 47, 48)**

General distribution.— Restricted to the Philippines (type-locality: Mindoro).

Distribution in the Philippines (fig. 103).— Only known from two males from Mt. Halcon (Mindoro).

Status.— Very rare.

Remark.— Although externally very different this species is in the genitalia similar to *H. luteisquama*, which also occurs on Mt. Halcon (de Jong & Treadaway, 1993f).

***Halpe dante* Evans, 1949 (figs. 49-52)**

General distribution.— Restricted to the Philippines.

Geographic variation.— Three subspecies are recognized: ssp. *dante* (type-locality: Negros), ssp. *luzona* Evans, 1949 (type-locality: Palali, Benguet, Luzon), and ssp. *tilia* Evans, 1949 (type-locality: Mindanao). They differ in size, ssp. *luzona* being the smallest form and ssp. *dante* the largest one; ssp. *tilia* is very dark, while ssp. *dante* has a conspicuous clothing of pale greenish yellow scales on the upperside.

Distribution in the Philippines (fig. 104).— Ssp. *dante*: Negros. Ssp. *luzona*: Luzon. Ssp. *tilia*: Leyte, Mindanao.

Status.— Rare to very rare.

Remark.— The three subspecies not only differ strongly in external characters,

they also have dissimilar genitalia (see figures in Evans, 1949). Actually it is only the broadly and deeply indented uncus that unites the three forms and a taxonomic reevaluation may be appropriate.

***Halpe sulphurifera*** (Herrich-Schäffer, 1869) (figs. 53, 54)

General distribution.— Restricted to the Philippines (type-locality: "Philippines", fixed by Plötz, 1884).

Distribution in the Philippines (fig. 104).— Jolo, Leyte, Luzon, Marinduque, Masbate, Mindanao, Mindoro, Negros, Sibuyan, Tawitawi.

Status.— Common.

Remark.— The present species was considered a subspecies of *H. beturia* (Hewitson, 1868) by Evans (1949), although clearly different in external characters and the shape of the cucullus. The discovery of *H. purpurascens* (next species) made the association of *H. sulphurifera* with *H. beturia* even more uncertain and for the time being the three taxa are considered separate species (de Jong & Treadaway, 1993f).

***Halpe purpurascens*** de Jong & Treadaway, 1993 (figs. 55, 56)

General distribution.— Restricted to the Philippines (type-locality: Negros).

Distribution in the Philippines (fig. 104).— Only known from the West Visayan islands: Negros, Panay and Masbate.

Status.— Uncommon.

***Halpe toxopea*** Evans, 1932

General distribution.— Sundaland.

Distribution in the Philippines (fig. 104).— Calamian, Palawan.

Status.— Rare.

Remarks.— Evans (1949) considered it a subspecies of *Halpe auriferus* (Elwes & Edwards, 1897), but the area of the latter completely falls within the area of *H. toxopea*, and Eliot (1978) correctly separated the two specifically.

***Halpe pelethronix*** Fruhstorfer, 1910

General distribution.— Burma, Sundaland.

Geographic variation.— Three subspecies are recognized. The nominotypical subspecies (Sundaland; type-locality: Java) also occurs in the Philippines.

Distribution in the Philippines (fig. 104).— Palawan.

Status.— Rare.

***Halpe inconspicua*** de Jong & Treadaway, 1993 (figs. 57, 58)

General distribution.— Restricted to the Philippines (type-locality: Leyte).

Distribution in the Philippines (fig. 104).— Leyte, Panaon.

Status.— Very rare.

***Koruthaialos*** Watson, 1893

Five species, mainly Sundaland, but extending to N India and the Philippines.

Dayflying primary and secondary forest butterfly. Found up to 1,000 metres but more often under 350 metres. Loves sunshine. Flight is not strong, but when dis-

turbed, butterfly tends to disappear in the undergrowth. When pitching in the sunshine, tends initially to shift position on the leaf alternatively opening and closing its wings revealing the bright orange yellow patches. Seems most at home between 1 and 2 metres above the ground in forest clearings or sunny trails.

***Koruthaialos rubecula* (Plötz, 1882)**

General distribution.— From Assam to Indo-China, and through Sundaland to the Philippines.

Geographic variation.— A very variable species, geographically and otherwise, especially in the extent of the red on the upperside of the forewing. Eleven subspecies are recognized, three of which occur in and are restricted to the Philippines: ssp. *luzonensis* Fruhstorfer, 1910 (type-locality: Luzon), with a very broad, bright orange yellow band; ssp. *atra* Evans, 1949 (type-locality: Mindanao), without a band; and ssp. *ponta* Evans, 1949 (type-locality: Palawan), with a weakly developed band. See also the next species.

Distribution in the Philippines (fig. 105).— Ssp. *luzonensis*: Luzon, Marinduque. Ssp. *atra*: Cebu, Leyte, Mindanao, Negros, Samar. Ssp. *ponta*: Calamian, Palawan.

Status.—Common.

***Koruthaialos sindu* (Felder, 1860)**

General distribution.— As for *Koruthaialos rubecula*.

Geographic variation.— Six subspecies are recognized; one occurs in and is restricted to the Philippines: *palawites* (Staudinger, 1889) (type-locality: Palawan).

Distribution in the Philippines (fig. 105).— Palawan.

Status.— Uncommon.

Remarks.— The subspecies is very much like *Koruthaialos rubecula ponta*. It can be recognized by the groove below the radius on the underside of the forewing in the male, which is filled with a double row of white shining scales in *K. sindu* and without special scales in *K. rubecula*.

***Psolos* Staudinger, 1889**

Monotypic genus, found through most of the Oriental Region.

A dayflying lowland (under 1,000 metres) primary and secondary forest butterfly. Seems equally at home in the shade of a forest or in sunny clearings or trails within the forest. A rather slow-flying butterfly which resorts to the undergrowth when disturbed. Can be found between 1 to 2 metres above ground.

***Psolos fuligo* (Mabille, 1876)**

General distribution.— Oriental Region.

Geographic variation.— Three subspecies are recognized. The nominotypical subspecies (type-locality: Java) occurs in Sundaland as well as in the Philippines.

Distribution in the Philippines (fig. 105).— Basilan, Bohol, Cebu, Camiguin de Mindanao, Camotes, Jolo, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Samar, Sibutu, Sibuyan, Tawitawi.

Status.— Common.

*Ancistroides* Butler, 1874

Six Oriental, mainly Sundaland, species.

A dayflying lowland (under 650 metres) primary and secondary forest butterfly (figs. 6-7). More often found within the shade of the forest but will come to clearings and trails dappled with sunshine. Seems to prefer to exist between ground level and 2 metres.

*Ancistroides nigrata* (Latreille, 1824)

General distribution.— From Sikkim and Assam to the Philippines, Java and Borneo.

Geographic variation.— Four subspecies are recognized. In the Philippines the endemic ssp. *fumatus* (Mabille, 1876) (type-locality: Philippines) is found.

Distribution in the Philippines (fig. 105).— Babuyan, Balabac, Basilan, Biliran, Bohol, Camiguin de Mindanao, Cebu, Guimaras, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Samar, Sibuyan.

Status.— Common.

*Notocrypta* de Nicéville, 1889

Twelve species, distributed from Sri Lanka and N India to NE Australia and Fiji; five species do not occur west of the Moluccas.

Since the identification of the species may be difficult, the four Philippine species are keyed in the next chapter.

Flies during the day around and in primary/secondary forest as well as semi-cleared partly cultivated areas near to small villages and also in meadows (figs. 4-7, 9). Can be found most often up to 1,000 metres usually during the middle of the day in shaded areas amongst trees, but early morning and late afternoon can be seen in clearings, trails and meadows in sunny areas. Pitches between 1 to 3 metres above ground with wings closed.

*Notocrypta parálysos* (Wood-Mason & de Nicéville, 1881)

General distribution.— Oriental Region.

Geographic variation.— Eleven subspecies are recognized. Three subspecies occur in the Philippines: ssp. *varians* (Plötz, 1882) (Sundaland; type-locality: S Asia), ssp. *chunda* Fruhstorfer, 1911 (endemic, type-locality: Palawan), and ssp. *volux* (Mabille, 1883), (endemic, type-locality: Philippines). In ssp. *chunda* the white band is more strongly elbowed than usual and there is no dot in space 4 of the forewing; in the other subspecies the band is broad and rather straight; in ssp. *varians* the dot in space 4 of the forewing is usually absent in the male; in ssp. *volux* there is conspicuous violet scaling on the underside before termen of hindwing and at apex of forewing (may also be found to some extent in the other subspecies).

Distribution in the Philippines (fig. 106).— Ssp. *varians*: Sibutu. Ssp. *chunda*: Balabac, Calamian, Palawan. Ssp. *volux*: Basilan, Biliran, Cebu, Dinagat, Homorhon, Leyte, Luzon, Marinduque, Masbate, Mindanao, Mindoro, Negros, Panay, Polillo, Samar, Sibuyan, Tawitawi group excluding Sibutu.

Status.— The species is common in the Philippines.



***Notocrypta clavata*** (Staudinger, 1889)

General distribution.— Sundaland (but without Java) and north to Burma, Thailand and Indo-China.

Geographic variation.— Four subspecies are recognized. In the Philippines the nominotypical form (Sundaland; type-locality: Palawan) occurs.

Distribution in the Philippines (fig. 106).— Palawan.

Status.— Very rare.

***Notocrypta feisthamelii*** (Boisduval, 1832)

General distribution.— From NW Himalayas and W Sechuan to the Moluccas.

Geographic variation.— Eight subspecies are recognized. In the Philippines only the endemic ssp. *alinkara* Fruhstorfer, 1911 (type-locality: Mindanao) occurs.

Distribution in the Philippines (fig. 106).— Babuyan, Calamian, Cebu, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Palawan, Panaon, Panay, Polillo, Samar, Sibuyan.

Status.— Common.

***Notocrypta howarthi*** Hayashi, 1980

General distribution.— Restricted to the Philippines (type-locality: Mindanao).

Distribution in the Philippines (fig. 106).— Mindanao.

Status.— Very rare.

***Suada*** de Nicéville, 1895

Three species, from Sikkim and Assam to Java, Borneo and the Philippines. Since the three species are allopatric, they could as well be regarded subspecies of a single species according to Evans (1949), but because of differences in genitalia and facies he hesitated to take this step. As it turns out, two species occur together on Mindanao.

Dayflying in primary and secondary forest up to 650 metres and sometimes in semi-cleared partly cultivated lowland areas. Can be seen most often in the shade of trees flying 0.5 to 1.5 metres above ground.

***Suada cataleucos*** (Staudinger, 1889)

General distribution.— Borneo, Philippines.

Distribution in the Philippines (fig. 107).— Mindanao, Palawan (type-locality).

Status.— Uncommon.

Remarks.— Hayashi (1980) described *S. c. treadawayi* from Mindanao, but our material does not warrant such a distinction, and we consider the latter name a synonym of *S. cataleucos* (**syn. nov.**).

***Suada albina*** (Semper, 1892) (figs. 59-60)

General distribution.— Restricted to the Philippines (type-locality: SW Mindanao).

Distribution in the Philippines (fig. 107).— Basilan, Luzon, Mindanao.

Status.— Uncommon.

*Suastus* Moore, 1881

Four small, inconspicuous species. Throughout the Oriental Region, not extending beyond Java and Borneo.

Dayflying in lowland (up to 350 metres) shaded areas either in forested or partly cultivated regions (fig. 3). Most often encountered under the shade of a young tree along a sunny trail. Flight difficult to follow as it is very fast for such a small butterfly. Can be most often seen pitched between 0.5 to 2 metres above the ground. Is a quite nervous butterfly prone to resort to flight at the slightest unusual movement.

*Suastus minutus* (Moore, 1877)

General distribution.— Widely distributed on the mainland, from Sri Lanka and S India to Thailand and Hainan, further in Andamans, Coco Island, Java and Palawan, suggesting that it became extinct in the intervening areas.

Geographic variation.— Six subspecies are distinguished, two of which are endemic to the Philippines: ssp. *scopas* (Staudinger, 1889) (type-locality: Palawan), and ssp. *compactus* subsp. nov.

Distribution in the Philippines (fig. 107).— Only known from Calamian group and Palawan.

Status.— Uncommon.

Description of *Suastus minutus compactus* subspecies nova.— Smaller than ssp. *scopas*, length of forewing ♂ 12.5 mm, ♀ 13.4 mm (♂ and ♀ ssp. *scopas* 13-14.9 mm). Spots on forewing larger and closer together, spot in space 2 rectangular, wider than high, overlapping lower cell spot completely and spot in space 3 just (♂) or for  $\frac{1}{3}$  (♀) (in ssp. *scopas* the spot in space 2 is not wider than high and is well separated from the spot in space 3).

Material.— Holotype (♂) and paratype (♀) from Busuanga Island (Calamian group), 8.v.1991. In coll. C.G. Treadaway.

*Suastus migreus* Semper, 1892 (figs. 61-62)

General distribution.— Restricted to the Philippines (type-locality: Luzon).

Distribution in the Philippines (fig. 107).— Babuyan, Cebu, Homonhon, Luzon, Marinduque, Mindanao, Mindoro, Sibuyan, Tawitawi.

Status.— Uncommon.

*Cupitha* Moore, 1884

A monotypic genus with an Oriental distribution.

Dayflying within and at the edge of lowland primary forest (up to 350 metres). Seems to prefer sunny trails or openings in the forest. Rests up to 3 metres above ground.

*Cupitha purreea* (Moore, 1877)

General distribution.— Oriental Region.

Distribution in the Philippines (fig. 107).— Palawan.  
Status.— Rare.

*Zographetus* Watson, 1893

Eight species, from NE India to Sulawesi and the Lesser Sunda Islands. With five species the Philippines take a good share. In view of the often highly discontinuous distributions of the species it seems that geographically the genus is insufficiently known. The taxonomic heterogeneity of the genus was discussed by de Jong & Treadaway (1993e).

The key in the next chapter (p. 77) may help identify the species.

Dayflying in lowland (up to 650 metres but more often under 150 metres) primary and secondary forest (figs. 6-7) as well as occasionally in coastal coppices. Seeks sunny clearings or sun dappled trees within the forest. Rather fast flier existing between 1 to 5 metres above ground.

*Zographetus ogygia* (Hewitson, 1866)

General distribution.— From Sikkim and NE India through Sundaland to the Lesser Sunda Islands and the Philippines.

Geographic variation.— Three subspecies are recognized. In the Philippines ssp. *durga* (Plötz, 1884) is found (type-locality: Philippines). According to Evans (1949) the same subspecies occurs in the Lesser Sunda Islands. This seems unlikely in view of the absence of the species from Sulawesi and the presence of another subspecies in Java.

Distribution in the Philippines (fig. 108).— Camiguin de Mindanao, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Polillo, Samar.

Status.— Uncommon.

*Zographetus ogygioides* (Elwes & Edwards, 1897)

General distribution.— Sundaland (but not in Java), Philippines.

Distribution in the Philippines (fig. 108).— Masbate, Panay, Sibuyan, Tawitawi.

Status.— Uncommon.

*Zographetus abima* (Hewitson, 1877)

General distribution.— Sulawesi, Palawan.

Distribution in the Philippines (fig. 108).— Only recorded from Palawan (Strand, 1921, as "*Gehenna palawanica*"; synonymy according to Evans, 1949).

Status.— No experience.

*Zographetus rama* (Mabille, 1876)

General distribution.— Burma, Malaya, Sumatra, Sulawesi, Philippines.

Distribution in the Philippines (fig. 108).— Mindoro, Samar.

Status.— Very rare.

*Zographetus pallens* de Jong & Treadaway, 1993 (figs. 63-64)

General distribution.— Only known from the Philippines (type-locality: Marinduque).

Distribution in the Philippines (fig. 108).— Camiguin de Luzon, Marinduque.  
Status.— Very rare.

*Oerane* Elwes & Edwards, 1897

Monotypic genus distributed from Burma to Java, Borneo and the Philippines.

Dayflying in primary to broken secondary forest; in our experience only up to 150 metres. Pitches on thickly leaved bushes and trees in open sunny areas or at the edge of the forest in the sunshine. Fairly fast flier which rests with wings closed 1.5 to 3 metres above ground.

*Oerane microthyrus* (Mabille, 1883)

General distribution.— Sundaland, Burma, Thailand, Philippines.

Geographic variation.— Two subspecies are recognized. The nominotypical subspecies flies in, and is restricted to the Philippines (type-locality: Philippines).

Distribution in the Philippines (fig. 109).— Leyte, Luzon, Marinduque, Mindanao, Mindoro, Samar.

Status.— Uncommon.

*Hyarotis* Moore, 1881

Three species, occurring through most of the Oriental Region. All three are found in the Philippines.

Normally dayflying but will come to ultraviolet light around sunset or shortly after. Flies from sea level to 1,000 metres, more often under 350 metres, in primary forest. Is equally at home in the shade or in sunny clearings. Has been found on *Lantana* blossom. Rather fast flier existing between 0.5 to 6 metres above ground.

*Hyarotis adrastus* (Stoll, 1782)

General distribution.— Oriental Region.

Geographic variation.— Three subspecies are recognized, with ssp. *praba* (Moore, 1866) (type-locality: Sri Lanka) occupying most of the range of the species including the Philippines.

Distribution in the Philippines (fig. 109).— Calamian, Mindanao, Palawan.

Status.— Common.

*Hyarotis microsticta* (Wood-Mason & de Nicéville, 1887)

General distribution.— From India to Sumatra and Borneo.

Geographic variation.— Two subspecies are recognized, with the nominotypical subspecies (type-locality: Cachar) occupying most of the range of the species including the Philippines.

Distribution in the Philippines (fig. 109).— Luzon, Mindoro.

Status.— Rare.

*Hyarotis iadera* de Nicéville, 1895

General distribution.— Sundaland.

Distribution in the Philippines (fig. 109).— Palawan.

Status.— very rare.

*Quedara* Swinhoe, 1919

Five Oriental species, but only one has a reasonably large distribution area and is found in the Philippines.

Dayflying in and at the edge of lowland (up to 150 metres) primary to broken secondary forest. Found in our experience in the sunshine pitched 2 to 3 metres above the ground. When disturbed flies rather fast to a new location.

*Quedara monteithi* (Wood-Mason & de Nicéville, 1887)

General distribution.— Sundaland, S Burma, S Thailand, Philippines.

Geographic variation.— Three subspecies are recognized, one of which occurs in and is restricted to the Philippines: ssp. *noctis* (Staudinger, 1889) (type-locality: Palawan).

Distribution in the Philippines (fig. 110).— Balabac, Calamian, Leyte, Mindanao, Palawan, Samar.

Status.— Rare.

*Isma* Distant, 1886

About 17 species, mainly occurring in Sundaland with slight extensions to Burma, Indo-China and the Philippines.

Dayflying in primary forest both mossy and regular up to 2,000 metres basking in the sunshine. Is usually found settled 1 to 3 metres above ground.

*Isma binotatus* (Elwes & Edwards, 1897)

General distribution.— Borneo, Philippines.

Distribution in the Philippines (fig. 110).— Mindanao.

Status.— Very rare.

*Isma bononia* (Hewitson, [1868])

General distribution.— Sundaland, north to S Burma and Thailand.

Geographic variation.— Three subspecies are recognized. In the Philippines only the endemic ssp. *bipunctata* (Elwes & Edwards, 1897) (type-locality: Palawan) occurs.

Distribution in the Philippines (fig. 110).— Mindanao, Palawan.

Status.— Very rare.

Remarks.— Ssp. *bipunctata* differs from the other subspecies in the absence of a brand over the basal part of vein 1 on the upperside of the forewing in the male. Possibly because of this Maruyama (1991), in his treatise of the HesperIIDae of Borneo, did not mention the Philippines as part of the distribution area of the species, thus excluding *bipunctata* and implying that the latter is a species on its own. We do not consider the absence of the brand enough reason for this action.

*Pyroneura* Eliot, 1978

About 15 species. Most species occur in Sundaland, but one occurs from NE India to Indo-China and Hainan, and one other is endemic to the Philippines.

For the identification of the six species occurring in the Philippines, see next chapter (p. 78).

Dayflying in primary to broken secondary forest up to 650 metres (more common under 150 metres) (figs. 3, 7). Flies fast, but once pitched is not easily disturbed. Seems equally at home in sunshine or shade. Visits white flowers along trails and in clearings in the forest. Will remain for hours in such locations. Usually several specimens are found in any given area. Normal height when observed at rest with wings closed is between 1.5 to 2.5 metres.

*Pyroneura flavia* (Staudinger, 1889)

General distribution.— Sundaland.

Geographic variation.— Two subspecies are recognized. The nominotypical subspecies flies in, and is restricted to the Philippines (type-locality: Palawan).

Distribution in the Philippines (fig. 111).— Palawan.

Status.— Rare.

*Pyroneura agnesia* (Eliot, 1967)

General distribution.— Sundaland, but absent from Java.

Geographic variation.— Two subspecies are recognized. In the Philippines ssp. *limbanga* Eliot, 1967 (type-locality: Borneo, Limbang), occurs.

Distribution in the Philippines.— Palawan (not plotted as exact location on Palawan is not known).

Status.— Very rare.

*Pyroneura liburnia* (Hewitson, 1868) (figs. 65-68)

General distribution.— Endemic to the Philippines.

Geographic variation.— Six subspecies are recognized, ssp. *liburnia* (type-locality: Philippines), ssp. *divinae* Schröder & Treadaway, 1987 (type-locality: Sibuyan), ssp. *minda* (Evans, 1941) (type-locality: Mindanao), ssp. *rosa* de Jong & Treadaway, 1993 (type-locality: Negros), ssp. *dora* de Jong & Treadaway, 1993 (type-locality: Mindoro), and ssp. *wita* de Jong & Treadaway, 1993 (type-locality: Tawitawi). They differ mainly in the extent of the yellow scaling and the development of the hyaline spots. Generally the females are darker (i.e. with less extensive yellow scaling) than the males. In ssp. *liburnia* the males and females are similar, the basal yellow area in space 1bc of the forewing hardly reaches the hyaline spot in space 2 and the yellow area on the hindwing is narrower than its distance from the wing margin. In ssp. *divinae* the yellow spot in space 1bc of the forewing overlaps the basal third of the hyaline spot in space 2, particularly in the male. The extent of the yellow colouring is progressively larger in the males ssp. *dora*, ssp. *rosa* and ssp. *minda*. In these three subspecies the yellow area on the hindwing is much wider than its distance from the wing margin; in ssp. *minda* the basal yellow area in space 1bc of the forewing not only extends to the end of the hyaline spot in space 2, but is continued across the latter spot (rendering it opaque for the greater part) and the cell to touch the basal yel-



low subcostal streak. *Ssp. wita* has a less extensive yellow colouring and it is smaller than the other subspecies. For more details, see de Jong & Treadaway (1993b).

Distribution in the Philippines (fig. 111).— *Ssp. liburnia*: Luzon, Marinduque, Polillo. *Ssp. divinae*: Panay, Romblon, Sibuyan. *Ssp. minda*: Homonhon, Leyte, Mindanao. *Ssp. rosa*: Negros. *Ssp. dora*: Mindoro. *Ssp. wita*: Tawitawi.

Status.— *Ssp. liburnia* is common; *divinae*, *minda* and *rosa* are uncommon; *dora* is rare; *wita* is very rare.

***Pyroneura derna* (Evans, 1941)**

General distribution.— Sundaland, but absent from Java.

Distribution in the Philippines (fig. 111).— Palawan.

Status.— Very rare.

***Pyroneura niasana* (Fruhstorfer, 1909)**

General distribution.— From Assam to Sumatra and Borneo.

Geographic variation.— Two subspecies are recognized. The nominotypical subspecies is restricted to Nias, *ssp. burmana* (Evans, 1926) (type-locality: Dawnas, Burma) covers the rest of the range of the species.

Distribution in the Philippines (fig. 112).— Palawan.

Status.— Uncommon.

***Pyroneura toshikoeae* Hayashi, 1980**

General distribution.— Endemic to the Philippines (type-locality: Mindanao).

Distribution in the Philippines (fig. 112).— Only known from East Mindanao.

Status.— Very rare.

***Plastingia* Butler, 1870**

Six species, from NE India to Java, Bali, Sulawesi and the Philippines.

Dayflying up to 1,000 metres (more usually under 350 metres) in primary (fig. 7) and secondary forest. Has its wings closed when at rest. Most often seen between 1 to 3 metres above ground either in sunny or shaded locations.

***Plastingia naga* (de Nicéville, 1884)**

General distribution.— As for the genus.

Distribution in the Philippines (fig. 112).— Camiguin de Luzon, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Palawan, Panaon.

Status.— Common.

***Plastingia pellonia* Fruhstorfer, 1909**

General distribution.— Sundaland, north to Burma.

Distribution in the Philippines (fig. 112).— Palawan.

Status.— Very rare.

***Plastingia viburnia* (Semper, 1892)**

General distribution.— Endemic to the Philippines (type-locality: Mindoro).

Distribution in the Philippines (fig. 112).— Luzon, Mindanao, Mindoro, Negros, Palawan, Samar.

Status.— Rare.

*Salanoemia* Eliot, 1978

Five species, occurring in Burma, Thailand, Malaya and Borneo, but one species also in S India, and one other species restricted to Sikkim and Assam.

Dayflying in lowland (under 1,000 metres) primary and good secondary forest.

*Salanoemia sala* (Hewitson, 1866)

General distribution.— From S India, and from Burma through Thailand and Malaya to Borneo.

Distribution in the Philippines (fig. 112).— Palawan.

Status.— Very rare.

*Salanoemia similis* (Elwes & Edwards, 1897)

General distribution.— So far only known from Borneo and the Malay Peninsula.

Distribution in the Philippines (fig. 112).— Dumaran (east of the northern half of Palawan).

Status.— Very rare.

*Xanthoneura* Eliot, 1978

Three species: one in Sundaland and north to N Thailand and Burma, one endemic to N Borneo, and the third endemic to the Philippines.

Dayflying in primary and mossy forest as well as secondary forest between 350 and 1,700 metres (figs. 7-9). Is most often seen in the forest or along trails within the forest pitched on a leaf dappled with sunshine between 1 to 3 metres above the ground. Is rather easily observed as it seems loath to fly and usually several occur in the same location.

*Xanthoneura telesinus* (Mabille, 1878) (figs. 73-74)

General distribution.— Endemic to the Philippines (type-locality: E Philippines).

Distribution in the Philippines (fig. 112).— Bohol, Leyte, Luzon, Mindanao, Mindoro, Negros, Samar.

Status.— Common.

Remark.— There are two forms differing in the colour of the underside of the hindwing, one light yellow brown, the other dark reddish brown. Apparently the fly together, and since we did not notice differences in the genitalia, we consider them forms of the same species.

*Lotongus* Distant, 1886

Three species; form NE India through Sundaland to Sechuan, Sulawesi and the

Philippines.

Reported as dayflying on the edge of or in clearings within a primary forest below 1,000 metres.

*Lotongus calathus* (Hewitson, 1876)

General distribution.— From Burma to Tonkin, and through Sundaland to Sulawesi.

Geographic variation.— Five subspecies are recognized. The nominotypical subspecies (type-locality: Sumatra) occurs in Sundaland, including Palawan.

Distribution in the Philippines.— Palawan (not plotted as exact location on Palawan is not known).

Status.— No experience.

*Zela* de Nicéville, 1895

Eight species, all occurring in Sundaland, with one species extending to Assam.

Dayflying around the edges of or in clearings of lowland primary and secondary forest as well as coastal coppices (figs. 3, 7). Usually found under 650 metres either in the shade of the forest or in sunny patches within the forest. Is a rather fast flier encountered between 2 to 6 metres above the ground.

*Zela excellens* (Staudinger, 1889)

General distribution.— Sundaland, north to S Thailand.

Distribution in the Philippines.— Palawan (not plotted as exact location on Palawan is not known).

Status.— No experience.

Remark.— See Maruyama (1991) for synonymy.

*Zela zeus* de Nicéville, 1895

General distribution.— From Assam through Sundaland (excluding Java) to the Philippines.

Geographic variation.— Three subspecies are recognized. The nominotypical subspecies (type-locality: Pulo Laut) occurs in Malaya, Sumatra and Borneo, and just penetrates the Philippines, but the majority of the Philippine populations belong to the endemic ssp. *major* Evans, 1932 (type-locality: Mindoro). According to Evans (1949) the latter is larger than ssp. *zeus*, length of forewing 24 mm as against 21 mm, but in the nine males of ssp. *major* checked the length of the forewing varied from 20 to 24 mm, with an average of 21.67 mm, while in the single male of ssp. *zeus* checked the length of the forewing was 23 mm. Though on the average the spots in ssp. *major* are larger than in ssp. *zeus*, there is much variation, also in the shade of the apex of the forewing and the development of the brand on the underside of the forewing.

Distribution in the Philippines (fig. 113).— Ssp. *zeus*: Tawitawi. Ssp. *major*: Homonhon, Leyte, Luzon, Mindanao, Mindoro, Samar, Sibuyan.

Status.— Ssp. *zeus* is rare, ssp. *major* is uncommon.

*Zela zenon* de Nicéville, 1895

General distribution.— Malaya, Siberut, Borneo, Palawan.

Distribution in the Philippines (fig. 113).— Palawan.

Status.— Rare.

Remarks.— Evans(1949) distinguished two subspecies, but his subspecies *cowani* Evans, 1939, was raised to species rank by Maruyama (1991). Both species occur in Malaya and Borneo.

*Gangara* Moore, 1881

Four species, together covering most of the Oriental Region. For a recent summary, see de Jong (1992).

Normally dayflying, but can be seen at sunset and early evening in and around small villages. Is also attracted to ultraviolet light. Ranges from sea level to 650 metres in and around primary and secondary forest as well as in semi-cleared partly cultivated lowlands and, as mentioned above, small villages (figs. 4, 7). At rest, its wings are closed. Perhaps because it is usually found on the underside of a leaf it seems loath to move when disturbed, often only flying a few metres before pitching again. It can be seen between 1 to 10 metres above the ground.

*Gangara thyrsis* (Fabricius, 1775)

General distribution.— Oriental Region.

Geographic variation.— Five subspecies are recognized. Three subspecies occur in the Philippines, of which two are restricted to these islands: ssp. *thyrsis* (India to Sulawesi, excluding Java; type-locality: "America"), ssp. *philippensis* Fruhstorfer, 1911 (type-locality: Philippines), and ssp. *magnificens* subspecies nova. Ssp. *philippensis* and ssp. *magnificens* can be distinguished by the presence of a spot in space 1b on the upperside of the forewing; this spot is absent in ssp. *thyrsis*. For the difference between ssp. *philippensis* and ssp. *magnificens*, see description below.

Distribution in the Philippines (fig. 114).— Ssp. *thyrsis*: Palawan. Ssp. *philippensis*: Camiguin de Luzon, Leyte, Luzon, Mindanao, Mindoro, Panaon, Samar, Sibuyan. Ssp. *magnificens*: Negros.

Status.— Ssp. *thyrsis* and ssp. *philippensis* uncommon, ssp. *magnificens* very rare.

Description of *Gangara thyrsis magnificens* subspecies nova (figs. 81-82). Characterized by very large forewing spots, the spots in space 2 and cell subequal, the spot in space 3 very large, filling basal  $\frac{3}{4}$  of space 3, the spots in spaces 1bc, 2 and 3, and in cell only separated by dark veins. In all other subspecies the spots are much smaller; the spot in space 3 is far from the spot in space 2, it does not fill the base of space 3 and it is closer to the termen than to the origin of vein 3. Very large, length of forewing 42 mm (wingspan 75 mm).

Material.— Holotype,  $\sigma$ , Negros, Mt. Canlaon, 27.vii.1991. In coll. C.G. Treadaway.

*Gangara lebadea* (Hewitson, 1868)

General distribution.— Sri Lanka, and from Sikkim and Assam to Indo-China

and Sundaland (Evans, 1949, did not list the species from Sumatra, but there is material from that island in the National Museum of Natural History, Leiden).

Geographic variation.— Four subspecies are recognized, two of which are found within the boundaries of the Philippines: ssp. *lebadea* (from Sikkim to Indo-China and Sundaland; type-locality: Borneo) and ssp. *janlouremsi* Schröder & Treadaway, 1987 (endemic; type-locality: Leyte). The latter differs from the nominotypical form in the conspicuous pale pink colour on the underside of the forewing along costa from apex to vein 12 with extension near cell end, a similarly coloured spot in the distal half of the cell, and the wide, distally not sharply outlined, pale pink band on the underside of the hindwing.

Distribution in the Philippines (fig. 114).— Ssp. *lebadea*: Palawan. Ssp. *janlouremsi*: Leyte.

Status.— Ssp. *lebadea* is rare, ssp. *janlouremsi* is very rare.

#### *Erionota* Mabille, 1878

Eight species, from N India to C China (Szechuan), the Moluccas and Lesser Sunda Islands.

*Erionota thrax* can be readily observed between sea level to 1,300 metres in secondary forest, semicleared lowland as well as in and around villages, towns and cities - anywhere banana grows. It flies by day as well as in the evening up to midnight, when it comes readily to ultraviolet light, especially subspecies *alexandra*, which additionally seems to prefer higher altitudes (650 to 1,700 metres) and a more wooded habitat. *E. torus*, although found in similar habitat to *E. thrax*, also has a preference for more wooded areas while *E. hiraca apex*, *E. surprisa* and *E. sybirita* are lowland primary and secondary forest butterflies (figs. 3-8). All species seem secretive by nature. They are not easily disturbed and are usually found resting under leaves with their wings closed between 2 to 6 metres above ground.

#### *Erionota torus* Evans, 1941

General distribution.— So far thought to be restricted to continental Asia, but widespread in the Philippines.

Distribution in the Philippines (fig. 115).— Cebu, Dinagat, Leyte, Mindanao, Negros, Samar.

Status.— Common.

Remarks.— Like the next species, *Erionota thrax*, the well-known banana skipper, the present species lives on bananas. The absence of the species from Borneo and the restricted occurrence in the Philippines (Mindanao and the Visayas), where it apparently was only collected in recent years, suggest that the species was introduced, perhaps with plant material.

#### *Erionota thrax* (Linnaeus, 1767)

General distribution.— Oriental Region and east to the Moluccas.

Geographic variation.— Four subspecies are recognized. In the Philippines three subspecies are found: ssp. *thrax* (India to Sulawesi; type-locality: Java), ssp. *mindana* Evans, 1941 (type-locality: Mindanao) and ssp. *alexandra* Semper, 1892 (type-locality:

NW Luzon), the latter two endemic. The distinction between *ssp. thrax* and *ssp. mindana* is, however, weak. The latter is described by Evans (1949) as having the cell spot of the forewing longer, 7 mm as against 5 mm, and the entire antennal club white instead of the basal part only, but both characters are variable in the Philippines. On the average, *ssp. mindana* is found in the southern and eastern islands and *ssp. thrax* in the western and northern islands. *Ssp. alexandra* is remarkable because of the overlap of spot 3 over spot 2 of the forewing, but also in this character there is no clearcut boundary.

Distribution in the Philippines (fig. 115).— *Ssp. thrax*: Cebu, Camotes, Luzon, Marinduque, Masbate, Mindoro, Negros, Palawan, Panay, Polillo, Sibutu, Sibuyan, Tawitawi. *Ssp. mindana*: Dinagat, Homonhon, Jolo, Leyte, Mindanao, Samar. *Ssp. alexandra*: N Luzon.

Status.— *Ssp. thrax* and *ssp. mindana* common, *ssp. alexandra* uncommon.

Remarks.— For details, see de Jong & Treadaway (1992a).

*Erionota hiraca* (Moore, 1881)

General distribution.— From Sikkim and Assam to Tonkin, and through Sundaland to Sulawesi.

Geographic variation.— Four subspecies are recognized. In the Philippines only the endemic *ssp. apex* Semper, 1892 (type-locality: Luzon), occurs.

Distribution in the Philippines (fig. 115).— Leyte, Luzon, Mindanao, Mindoro, Samar, Ticao.

Status.— Very rare.

Remarks.— The species is difficult to distinguish from the next species, *Erionota surprisa*. In the latter species the underside of the hindwing is not as dark as in *E. hiraca*, with much stronger ochreous superscaling that is, moreover, concentrated in a terminal area and a discal band (dissected by the veins), whereas in *E. hiraca* the superscaling is weaker and more diffused. There are strong differences in the male genitalia. The tegumen, for instance, has a long central horn and no lateral arms in *E. surprisa*, while in *E. hiraca* the central horn is absent and there are conspicuous lateral arms. For further details and for the name change (the species has long been known as *Erionota acroleuca* Wood-Mason & de Nicéville, 1881), see de Jong & Treadaway (1992a).

*Erionota surprisa* de Jong & Treadaway, 1992 (figs. 85-86)

General distribution.— Endemic to the Philippines (type-locality: Leyte).

Distribution in the Philippines (fig. 115).— Cebu, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Panay, Polillo, Samar, Tawitawi, Ticao.

Status.— Common.

*Erionota sybiritia* (Hewitson, 1876)

General distribution.— S Burma, Thailand. Malaya, Borneo, Palawan.

Distribution in the Philippines (fig. 115).— Palawan.

Status.— The only known specimen from Palawan is the holotype of *Erionota mabillei* Staudinger, 1889 (Zoologisches Museum, Berlin), a junior synonym.



*Matapa* Moore, 1881

The genus is, with eight species, distributed throughout the Oriental Region. It was revised by de Jong (1983).

Dayflying in secondary and primary forest under 1,000 metres, very occasionally comes to ultraviolet light shortly after sunset. Quite fast flying within the forest, but can also be found in sunny clearings around and within the forest. Seems to be most often encountered between 1 to 3 metres above the ground.

*Matapa aria* (Moore, 1866)

General distribution.— Oriental Region.

Distribution in the Philippines (fig. 116).— Calamian, Camotes, Homonhon, Luzon, Mindanao, Mindoro, Negros, Palawan, Sibuyan.

Status.— Common.

*Matapa intermedia* de Jong, 1983

General distribution.— Sulawesi, Philippines.

Geographic variation.— Two subspecies are recognized, the nominotypical one in Sulawesi, and ssp. *nigrita* de Jong, 1983, in the Philippines.

Distribution in the Philippines (fig. 116).— Samar.

Status.— Rare.

*Matapa celsina* (Felder, 1867)

General distribution.— Sulawesi, Philippines.

Distribution in the Philippines.— Mindanao (not plotted as exact location on East Mindanao not known).

Status.— Very rare.

*Unkana* Distant, 1886

Three species, from Burma to Indo-China and through Sundaland to the Philippines.

Dayflying in lowland (up to 1,000 metres but more often under 150 metres) primary and secondary forest as well as semicleared partly cultivated lowland, coastal coppices and swamp areas (figs. 2, 3, 5, 7). Seems to be most often found in the range of 1 to 4 metres level above the ground. Rests with wings closed and is not easily disturbed.

*Unkana ambasa* (Moore, 1857)

General distribution.— Sundaland, Burma, Thailand, Philippines.

Geographic variation.— Five subspecies are recognized, three of which are found in the Philippines: ssp. *batara* Distant, 1886 (Malaya, Sumatra, Borneo; type-locality: Malacca), ssp. *ambasa* (Java, Palawan; type-locality: Java) and ssp. *mindanaensis* Fruhstorfer, 1911 (endemic; type-locality: Mindanao). They differ in the width of the dark tornal area on the underside of the hindwing: narrow, 3 mm, in ssp. *mindanaensis*, reaching half-way between termen and cell in ssp. *ambasa*, and still broader in ssp. *batara*.

Distribution in the Philippines (fig. 116).— *Ssp. batara*: Sibutu, Tawitawi. *Ssp. ambasa*: Palawan. *Ssp. mindanaensis*: Camiguin de Luzon, Dinagat, Homonhon, Leyte, Luzon, Mindanao, Mindoro, Negros, Panay, Samar, Sibuyan.

Status.— Common, but uncommon on Tawitawi.

Remark.— According to Evans (1949) *ssp. ambasa* (type-locality: Java) occurs in Java and Palawan. This is an unlikely distribution, since in Borneo (and Tawitawi) *ssp. batara* is found. Either the Palawan and Java populations developed the character independently, or the character is plesiomorphic.

#### *Hidari* Distant, 1886

Three species, from NE India through Burma through Sundaland, and penetrating into the Philippines.

Dayflying, but is said to come readily to light at night. Occurs in lowland (up to 1,000 metres) primary and secondary forest as well as semicleared partly cultivated areas around villages.

#### *Hidari irava* (Moore, 1858)

General distribution.— Sundaland, S Burma, Thailand.

Distribution in the Philippines.— Mindanao, Sulu Archipelago (not plotted as exact location on Mindanao and Sulu is not known).

Status.— Very rare.

#### *Acerbas* de Nicéville, 1895

Seven species in Sundaland, Sulawesi, Philippines, and northwards extending to Burma.

Dayflying in primary and well developed secondary forest up to 1,000 metres (fig. 7). Is most often seen from 1 to 4 metres above the ground resting on leaves dappled with sunlight in clearings and along trails in the forest. Fairly fast fliers.

#### *Acerbas anthea* (Hewitson, 1868)

General distribution.— Sundaland, Burma, Thailand.

Geographic variation.— Four subspecies are recognized, of which the nominotypical one (Burma to Borneo; type-locality: Singapore) and *ssp. luzona* de Jong, 1982 (type-locality: Atimonan, Quezon, Luzon) occur in the Philippines. They differ in the tornal area on the upperside and underside of the hindwing being completely white in *ssp. luzona*, while the black terminal band reaches into the tornal area in *ssp. anthea* (as well as in the remaining two subspecies).

Distribution in the Philippines (fig. 117).— *Ssp. anthea*: Leyte, Mindanao, Panaon. *Ssp. luzona*: Luzon.

Status.— *Ssp. anthea* is uncommon, *ssp. luzona* is rare.

#### *Acerbas duris* (Mabille, 1883)

General distribution.— Borneo, Philippines.

Geographic variation.— The species was described from the Philippines (type-locality: Philippines). Later Evans (1949) described the Bornean population as a separate subspecies (*dorka*).

Distribution in the Philippines (fig. 117).— Camiguin de Luzon, Camiguin de Mindanao, Leyte, Luzon, Mindanao, Mindoro, Negros.

Status.— Rare.

*Pirdana* Distant, 1886

Five species, from Sikkim and NE India to Java, Sulawesi and the Philippines. The phylogenetic relationships between the species were discussed by de Jong & Treadaway (1993d).

Dayflying within lowland (up to 1,000 metres) primary forest. Seemingly a rather secretive butterfly.

*Pirdana hyela* (Hewitson, 1867)

General distribution.— From Sikkim and Assam to the Philippines and Sulawesi.

Geographic variation.— Four subspecies are recognized. The nominotypical subspecies (type-locality: Java) flies in Sumatra, Java and Borneo as well as in the Philippines.

Distribution in the Philippines (fig. 117).— Luzon, Palawan.

Status.— Uncommon.

*Pirdana fusca* de Jong & Treadaway, 1993 (figs. 83-84)

General distribution.— Endemic to the Philippines (type-locality: Samar).

Distribution in the Philippines (fig. 117).— Only known from Samar.

Status.— Very rare.

*Taractrocera* Butler, 1870

Fifteen small species, occurring throughout the Oriental Region and the greater part of the Papuan-Australian region, reaching as far as Tasmania.

Dayflying in grassy clearings and at the edge of secondary forest, semicleared partly cultivated lowland and around small villages (figs. 4-6). Found up to 1,000 metres but more often under 350 metres, in meadows, fields, pathways and gardens, where it obviously delights in sunshine, flitting to and fro between the ground and 0.5 metre high.

*Taractrocera luzonensis* (Staudinger, 1889)

General distribution.— From S Burma and S Thailand through Sundaland to the Philippines, and to Sulawesi and its satellite islands.

Geographic variation.— Six subspecies are recognized. The nominotypical subspecies is endemic to the Philippines (type-locality: Luzon). The subspecies of Borneo, ssp. *stella* Evans, 1934 (type-locality: Borneo), just penetrates into the Philippines. They differ in the width of the yellow band on the upperside of the fore-

wing, which is at least as broad as the dark border in ssp. *luzonensis*, and generally narrower in ssp. *stella*.

Distribution in the Philippines (fig. 118).— Ssp. *luzonensis*: Balabac, Basilan, Cebu, Dinagat, Leyte, Luzon, Marinduque, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Samar, Sibuyan. Ssp. *stella*: Sibutu, Tawitawi.

Status.— Common.

Remarks.— The species has long been known under the name *Taractrocera ziclea* (Plötz, 1884). Examination of some relevant types made the change of names necessary, see de Jong (1991).

### *Oriens* Evans, 1932

Eight species with a remarkable distribution: seven are restricted to the oriental Region, while one species is found in Fiji and Samoa. The latter species is also recorded from Australia, based on two males, of which one is over a century old. Its occurrence in Australia needs confirmation (Common & Waterhouse, 1981). The three species occurring in the Philippines are keyed on p. 79.

Dayflying with *O. gola* and *O. californica* in clearings and along trails of lowland (under 1,000 metres) secondary forest, semi-cleared partly cultivated areas as well as in and around small villages and coastal coppices (figs. 4, 6). *O. fons* also inhabits meadows and grasslands as well as clearings in secondary forest but up to a much higher altitude (2,000 metres) (fig. 10). All species tend to fly and pitch under 2 metres above the ground and are sun lovers.

#### *Oriens gola* (Moore, 1877)

General distribution.— Oriental Region.

Geographic variation.— Three subspecies are recognized. The whole range of the species except the Andamans and the Lesser Sunda Islands is occupied by ssp. *pseudolus* (Mabille, 1883) (type-locality: probably Java).

Distribution in the Philippines (fig. 118).— Balabac, Calamian, Luzon, Palawan.

Status.— Uncommon.

#### *Oriens californica* (Scudder, 1872) (figs. 69-70)

General distribution.— Endemic to the Philippines (type-locality: Philippines).

Distribution in the Philippines (fig. 118).— Balabac, Homonhon, Jolo, Leyte, Luzon, Masbate, Mindanao, Mindoro, Panay, Polillo, Samar, Sibuyan, Tawitawi.

Status.— Common.

#### *Oriens fons* Evans, 1949 (figs. 77-78)

General distribution.— Endemic to the Philippines (type-locality: Los Baños, Luzon).

Distribution in the Philippines (fig. 118).— Luzon, Mindanao, Panay.

Status.— Rare.

*Potanthus* Scudder, 1872

A large genus of about 28 mostly very similarly looking species, occurring throughout the Oriental Region, extending north through China to Korea, the Amur region and Japan, and east to the Moluccas, apparently not reaching New Guinea. The male genitalia are the most secure means for identification, see next chapter. Unfortunately the female genitalia have not yet been studied systematically, and some females are practically unidentifiable. It seems likely that examination of types and additional material will necessitate taxonomic changes.

Dayflying in open areas around and in primary and secondary forest and semi-cleared areas, from sea level to 1,700 metres (figs. 5-9). Also occurs in coastal coppice areas, in grass- and wasteland around small villages and occasionally in swamp and mangrove areas (figs. 2-4). Sun loving butterfly, but can be seen on cloudy days. More often encountered flying and resting fairly close to the ground.

*Potanthus omaha* (Edwards, 1863)

General distribution.— From Burma to Indo-China, the Philippines and Sulawesi. Evans (1949) recorded it from Sumbawa, but not from Java.

Geographic variation.— Six subspecies are recognized. In the Philippines two subspecies are found. Ssp. *bione* Evans, 1949, is restricted to the Philippines (type-locality: Mindanao). In Tawitawi ssp. *maesina* (Evans, 1934) (mainly Borneo, which is also the type-locality) occurs. The two subspecies can be distinguished by their size, ssp. *bione* being larger, length of forewing 14 mm as against 12 mm for ssp. *maesina*, and the brighter and broader markings in ssp. *maesina*.

Distribution in the Philippines (fig. 119).— Ssp. *bione*: Mindanao (not plotted as exact location on Mindanao is not known). Ssp. *maesina*: Tawitawi.

Status.— Rare to very rare.

Remarks.— 1. Ssp. *bione* can only be distinguished from *Potanthus niobe* (see below) with the help of the genitalia.

2. Apart from the external differences, ssp. *bione* and ssp. *maesina* differ in the shape of the valve in the male genitalia. Interestingly the *bione* type is also found in *P. omaha nita* (Evans, 1934), from Sulawesi, while the *maesina* type is the usual *omaha* type. In view of the slight differences between many *Potanthus* species in the male genitalia, one wonders if ssp. *bione* and ssp. *maesina* are really conspecific.

*Potanthus fettingi* (Möschler, 1878)

General distribution.— Sundaland (but without Malaya), Lesser Sunda Islands, Sulawesi and surrounding islands, Moluccas, Waigeo.

Geographic variation.— Seven subspecies are recognized. In the Philippines only the endemic ssp. *alpha* (Evans, 1934) (type-locality: Philippines) occurs.

Distribution in the Philippines.— Luzon (not plotted as exact location on Luzon not known).

Status.— No experience.

Remarks.— See Maruyama (1991) for nomenclature.

*Potanthus niobe* (Evans, 1934)

General distribution.— Endemic to the Philippines.

Geographic variation.— Two subspecies are recognized: ssp. *niobe* (Evans, 1934), and ssp. *hyugai* subsp. nov. For differences, see below.

Distribution in the Philippines (fig. 119).— Ssp. *niobe*: Dinagat, Mindanao (not plotted as exact location is not known). Ssp. *hyugai*: Luzon, Mindoro.

Status.— Very rare.

Remarks.— Evans (1949) considered this species a subspecies of the more northern *P. flavus* (Murray, 1875) (China, Korea, Amur region, Japan), even though the species does not occur in Taiwan and Evans himself indicated that the shape of the valve in the male genitalia is considerably different. We consider it a separate species, of which the relationship needs further examination.

Description of *Potanthus niobe hyugai* subspecies nova (figs.75-76).— Differs from the nominotypical *niobe* in the groundcolour of the underside of the hindwing, which is warm reddish brown, with the discal spots dark orange yellow and the veins outlined in a lighter shade, also between the discal spots. In ssp. *niobe* the groundcolour of the underside of the hindwing is dark brown, strongly overshadowed by yellow scales when fresh, the discal spots are yellow and the veins are dark between the discal spots.

Material.— Holotype, ♂, N Luzon, I Fugao, nr. Kumbulo, 1300 m, 23.iv.1991, leg. Treadaway. Paratypes: 1 ♂, 1 ♀, Mindoro, Mt. Halcon, 1100 m, 27.iii.1992, leg. A. Hyuga; 1 ♂, Mindoro, Mt. Halcon, 15.vi.1992, leg. Venus; 1 ♀, same, but 11.vi.1992; 1 ♂, N Luzon, Banaue, Poitan, 3700 ft., 19.iv.1991, leg. Mona. Holotype and 1 ♂, 1 ♀ paratype in coll. Treadaway; 1 ♂, 1 ♀, paratype in coll. Hyuga; 1 ♂ paratype in National Museum of Natural History, Leiden.

#### *Potanthus confucius* (Felder, 1862)

General distribution.— From Sri Lanka to China and Japan, and east through Sumatra and Java to the Lesser Sunda Islands. Not known from Borneo, but mentioned by Evans (1949) from Palawan.

Geographic variation.— Seven subspecies are recognized. According to Evans (1949) the specimens from Palawan belong to ssp. *yojana* (Fruhstorfer, 1911) (Java, Lesser Sunda Islands, Palawan; type-locality: Java).

Distribution in the Philippines.— Palawan (not plotted as exact location on Palawan is not known).

Status.— No experience.

Remarks.— In view of the absence from Borneo and the unlikelihood of the same subspecies being found in and restricted to Java, Lesser Sunda Islands and Palawan, there is reason to doubt the reliability of the labels of the Palawan specimens in the (Natural History) Museum, London.

#### *Potanthus mingo* (Edwards, 1866)

General distribution.— Assam to Indo-China; Java; Philippines.

Geographic variation.— Three subspecies are recognized. In the Philippines only the endemic ssp. *mingo* occurs (type-locality: Philippines).

Distribution in the Philippines (fig. 119).— Basilan, Jolo, Leyte, Luzon, Mindanao, Mindoro, Negros, Panay, Samar, Tawitawi.

Status.— Uncommon.



***Potanthus pava* (Fruhstorfer, 1911)**

General distribution.— S India to C China (Sechuan), Taiwan and Malaya; Philippines; Sulawesi.

Geographic variation.— Two subspecies are recognized. In the Philippines one subspecies occurs, *ssp. lesbia* Evans, 1934 (type-locality: Sulawesi), which further occurs in Sulawesi only.

Distribution in the Philippines (fig. 120).— Dinagat, Luzon, Mindanao, Mindoro, Sibuyan.

Status.— Uncommon.

***Potanthus ganda* (Fruhstorfer, 1911)**

General distribution.— Sundaland and north through Thailand and Burma to Assam; Hainan; Lesser Sunda Islands.

Geographic variation.— Two subspecies are recognized. The Bornean subspecies, *ssp. marla* Evans, 1949, penetrates into the Philippines.

Distribution in the Philippines (fig. 120).— Calamian, Palawan.

Status.— Local.

***Potanthus hetaerus* (Mabille, 1883)**

General distribution.— Sulawesi and the Philippines.

Geographic variation.— The nominotypical subspecies is from the Philippines (type-locality: Philippines); the Sulawesi form was separated by Evans (1934) as *ssp. dina*.

Distribution in the Philippines (fig. 120).— Homonhon, Leyte, Luzon, Mindanao, Negros, Polillo, Romblon, Sibuyan, Tawitawi.

Status.— Uncommon.

Remarks.— This species was believed to be conspecific with the next species, *Potanthus serina*, but since both have been found in Tawitawi we consider them separate.

***Potanthus serina* (Plötz, 1883)**

General distribution.— Burma to Indo-China, and through Sundaland to the Philippines.

Distribution in the Philippines (fig. 120).— Calamian, Palawan, Sibutu, Tawitawi.

Status.— Uncommon.

***Telicota* Moore, 1881**

About 30 often very similar species, distributed through most of the Oriental and Australian Regions, northwards extending to Japan, eastwards to the Solomon Islands and SE Australia. The development of the genus in the Philippines is modest, five of the six species have very wide distributions, in the Oriental and Australian Regions. See next chapter (p. 79) for a key to the five Philippine species.

Dayflying up to 850 metres in primary and secondary forest as well as coastal coppices (figs. 3, 7). A sun loving butterfly seeking out sunny patches within or on the edge of the forest. Tends to fly and pitch between 1 to 4 metres.

*Telicota colon* (Fabricius, 1775)

General distribution.— Oriental and Australian Regions (but surprisingly not found in Borneo).

Geographic variation.— Nine subspecies are recognized. In the Philippines ssp. *vaja* Corbet, 1942 (type-locality: Java), is found, which further extends from Sumatra to Timor.

Distribution in the Philippines (fig. 121).— Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan.

Status.— Uncommon.

*Telicota augias* (Linnaeus, 1763)

General distribution.— From Burma to Australia, but apparently no reliable records from New Guinea.

Geographic variation.— Eight subspecies are recognized. In the Philippines two subspecies are found. One is the widespread ssp. *augias* (Burma to Java and Borneo; type-locality: "India", probably Java), the other one is the endemic ssp. *pythias* (Mabille, 1878) (type-locality: Philippines). In the former the underside of the hindwing is tawny with the band inconspicuous, in the latter the underside of the hindwing is much darker, the band is more conspicuous and divided by dark veins.

Distribution in the Philippines (fig. 121).— Ssp. *augias*: Palawan. Ssp. *pythias*: Bohol, Camiguin de Mindanao, Camotes, Cebu, Guimaras, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Panay, Samar, Sibuyan, Tawitawi.

Status.— Ssp. *augias* is uncommon, ssp. *pythias* is common.

*Telicota ancilla* (Herrich-Schäffer, 1869)

General distribution.— Oriental and Australian Regions, but not in the Pacific islands; extending north into China and to Japan.

Geographic variation.— Evans (1949) recognized eleven subspecies (but see under Remarks). In the Philippines the endemic ssp. *minda* Evans, 1934 (type-locality: Mindanao) occurs as well as the Bornean ssp. *santa* Evans, 1934. In ssp. *minda* the underside of the hindwing is much darker and the dark edging to the band is absent, while in ssp. *santa* the band is edged by conspicuous black spots. Further, the spots in spaces 4 and 5 are detached from the apical spots (spots in spaces 6-8) in ssp. *minda*, and connected to them in ssp. *santa*.

Distribution in the Philippines (fig. 121).— Ssp. *santa*: Palawan. Ssp. *minda*: Homonhon, Luzon, Mindanao, Romblon, Samar, Ticao.

Status.— Ssp. *santa* is rare, ssp. *minda* is local.

Remarks.— The subspecies not only differ in external characters, but in the male genitalia as well. Evans (1949), who depicted the differences in his well-known schematic style, did not consider the differences important enough to warrant the distinction of more than one species, but Eliot (1967) considered the differences large enough for the recognition of several species. Unfortunately he mentioned only part of the subspecies recognized by Evans, leaving the question of the species boundaries and species definitions open. The matter was further complicated by Maruyama (1991) who decided that the taxa *santa* and *bambusae*, which were considered conspecific by Eliot, were specifically distinct because of differences in the male genitalia, but again without defining the species boundaries. We think it important to draw

attention to unanswered questions, but at the same time we are of the opinion that only a complete revision of a problematic taxon can be expected to yield satisfying results. As a consequence, even though Eliot and Maruyama may be right as far as their points concern, we can only follow Evans here, since he was the only one who gave a complete overview.

*Telicota ohara* (Plötz, 1883)

General distribution.— Oriental and Australian Regions, not in Pacific islands.

Geographic variation.— Nine subspecies are recognized. In the Philippines only the endemic ssp. *janis* Evans, 1949 (type-locality: Mindanao) is known.

Distribution in the Philippines (fig. 121).— Marinduque, Mindanao, Mindoro, Negros, Palawan, Polillo, Samar.

Status.— Rare.

*Telicota hilda* Eliot, 1959

General distribution.— Burma, S Thailand, Malaya, Borneo, Palawan.

Geographic variation.— According to Maruyama (1991) the species can be divided into three subspecies, one of which (still unnamed) occurs in Palawan). Maruyama & Uehara (1992) named the Palawan form *T. hilda palawana*.

Distribution in the Philippines.— Palawan (not plotted as exact location on Palawan not known).

Status.— No experience.

*Cephrenes* Waterhouse & Lyell, 1914

A small genus of five species, of which four are restricted to the Papuan-Australian Region.

Dayflying in lowland (up to 1,000 metres but more common under 150 metres) secondary and primary forest as well as semi-cleared partly cultivated areas and around small villages (figs. 4, 5, 7). A fairly fast flier that likes sunshine and occurs up to 3 metres above the ground.

*Cephrenes acalle* (Hopffer, 1874)

General distribution.— From Sikkim and E India to Indo-China and through Sundaland to Sulawesi and the Philippines.

Geographic variation.— Seven subspecies are recognized. In the Philippines two subspecies occur: the endemic ssp. *chrysozona* (Plötz, 1883) (type-locality: Philippines), and ssp. *kliana* Evans, 1934 (type-locality: Borneo). In ssp. *chrysozona* the dark central band on the upperside of the forewing in the male is well developed, in ssp. *kliana* this band is vestigial.

Distribution in the Philippines (fig. 122).— Ssp. *chrysozona*: Bohol, Cebu, Camiguin de Mindanao, Camotes, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Polillo, Samar, Sibuyan; ssp. *kliana*: Balabac, Palawan, Sibutu.

Status.— Common.

Remarks.— The species has long been known under the name of *Cephrenes chrysozona* (Plötz, 1883). For the recent change of name, see Maruyama (1991).

*Prusiana* Evans, 1937

Only three species, with a remarkable distribution: one species is endemic to Sulawesi, the second is found in Borneo and Sulawesi, and the third occurs in the Philippines, Sulawesi and the Moluccas.

Dayflying up to 1,000 metres in primary and good secondary forest as well as coastal coppices (figs. 3, 6, 7). Seeks sunny areas and can be noticed between 1 to 5 metres above the ground.

*Prusiana prusias* (Felder, 1861)

General distribution.— Philippines, Sulawesi, Moluccas.

Geographic variation.— Two subspecies are recognized. In the Philippines ssp. *matinus* (Fruhstorfer, 1911) (type-locality: Luzon) occurs. This subspecies should also occur in Sulawesi, according to Evans (1949), where moreover the darker nominal subspecies flies. This makes one doubt the reliability of the Sulawesi record for ssp. *matinus*.

Distribution in the Philippines (fig. 122).— Basilan, Bohol, Cebu, Camiguin de Luzon, Camiguin de Mindanao, Camotes, Guimaras, Homonhon, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Palawan, Panay, Polillo, Sibuyan, Tawitawi.

Status.— Common.

*Parnara* Moore, 1881

An Afro-Oriental-Australian genus. Of the nine species recognized, six are Asian, ranging from N China, Korea and Japan to Sri Lanka and Australia.

The genus was recently revised by Chiba & Eliot (1991) and we follow their conclusions here.

Dayflying in primary and secondary forest up to 1,000 metres (most frequently encountered between 150 metres to 650 metres) (figs. 4, 6, 7). Sometimes found in coastal coppices (fig. 3) and very rarely coming to ultraviolet light during the early evening. Flies rather fast up to 3 metres above the ground. Seeks sunny patches and sun dappled areas within the forest. Can also be encountered in open areas outside the forest.

*Parnara kawazoei* Chiba & Eliot, 1991

General distribution.— Borneo, Sulawesi, Philippines.

Distribution in the Philippines (fig. 123).— Homonhon, Leyte, Luzon, Mindanao, Mindoro, Panay, Samar, Sibuyan.

Status.— Common.

Remark.— This species and the next are rather similar. They can be distinguished by the spots in spaces 2-5 of the hindwing usually all present and nearly in a straight line in *P. kawazoei*, and small and irregular *P. bada*. In the male genitalia the tegumental process is about as long as wide and narrowing to a broadly rounded tip in *P. kawazoei*, while it is half as long as wide with a hardly protruding tip in *P. bada*.

*Parnara bada* (Moore, 1878)

General distribution.— Throughout the Oriental Region, north to S Japan, eastwards extending to Australia.

Geographic variation.— Three subspecies are recognized, of which ssp. *bada* (Moore, 1878) (type-locality: Sri Lanka) covers most of the Oriental Region, including the Philippines.

Distribution in the Philippines (fig. 123).— Luzon, Masbate, Mindanao, Romblon, Palawan, Sibuyan.

Status.— Uncommon.

Remark.— For the distinction of *P. bada* and *P. kawazoei*, see under the latter species.

*Borbo* Evans, 1949

Again an Afro-Oriental-Australian genus, with 18 species in Africa (one penetrating the Mediterranean) and five in the Indo-Australian area.

In habit diurnal and crepuscular. Found in and around secondary forest and in semicleared partly cultivated areas between sea level and 1,000 metres.

*Borbo cinnara* (Wallace, 1866)

General distribution.— Oriental and Australian Regions.

Geographic variation.— In spite of the wide distribution no subspecies are recognized.

Distribution in the Philippines (fig. 123).— Balabac, Camiguin de Mindanao, Jolo, Lubang, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Samar, Sibutu, Tawitawi.

Status.— Common.

*Pelopidas* Walker, 1870

One of the most wide-spread hesperiid genera, occurring throughout Africa, the eastern Mediterranean, southern and eastern Asia north to the Amur region and Japan, and through the Papuan-Australian area to the islands in the SW Pacific. Of the ten species eight are found in the Indo-Australian area, with one species covering most of the area of the entire genus.

Dayflying, but also crepuscular. Is met with up to 1,300 metres in clearings and open areas in broken secondary forest as well as partly cleared semicultivated areas, coastal coppices and around rice fields of small villages (figs. 3-7). A rather fast flier usually encountered between 1 to 3 metres above ground.

*Pelopidas agna* (Moore, 1866)

General distribution.— Oriental Region and east to Australia and the New Hebrides.

Geographic variation.— Four subspecies are recognized. The nominotypical subspecies (type-locality: Bengal) flies throughout the Oriental Region, including the Philippines.

Distribution in the Philippines (fig. 124).— Basilan, Cebu, Camiguin de Luzon,

Homonhon, Jolo, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Panaon, Samar, Sibutu, Sibuyan, Tawitawi, Ticao.

Status.— Uncommon.

Remarks.— This species is very similar to *Pelopidas mathias*. They can be distinguished as follows. In *mathias*, spot 2 on the upperside of the forewing in the male is quadrate, the stigma reaches vein 1 before its middle, before the origin of vein 2, and before the point where a line through the cell spots crosses vein 1; in the female a line through the cell spots is directed to the spot in space 1b. In *agna*, spot 2 on the upperside of the forewing in the male is linear, the stigma reaches vein 1 in the middle, about under the origin of vein 2, and at the point where a line through the cell spots crosses vein 1; in the female a line through the cell spots crosses vein 1 well before the spot in space 1b.

The third species of the genus in the Philippines, *P. conjuncta*, is considerably larger than the other two, length of forewing 21 mm as against 16-17 mm for *P. agna* and *P. mathias*. The male of *P. conjuncta* lacks the stigma of the other two species.

***Pelopidas mathias* (Fabricius, 1798)**

General distribution.— Africa, Oriental Region, extending north to Korea and Japan, and east to New Guinea and neighbouring islands.

Geographic variation.— Three subspecies are recognized, with the nominotypical subspecies (type-locality: Tranquebar, S India) occurring in Africa and tropical Asia as far east as Tenimbar.

Distribution in the Philippines (fig. 124).— Bohol, Camiguin de Luzon, Camiguin de Mindanao, Camotes, Cebu, Guimaras, Homonhon, Jolo, Leyte, Luzon, Marinduque, Masbate, Mindoro, Negros, Palawan, Panaon, Panay, Samar, Tawitawi.

Status.— Common.

Remarks.— For the distinction from *Pelopidas agna*, see under that species.

***Pelopidas conjuncta* (Herrich-Schäffer, 1869)**

General distribution.— Oriental Region; not in Sulawesi but extending east through the Lesser Sunda Islands to Timor.

Geographic variation.— Two subspecies are recognized. *Ssp. conjuncta* (type-locality: not stated) covers the area from Assam to Timor.

Distribution in the Philippines (fig. 124).— Basilan, Bohol, Cebu, Camiguin de Luzon, Camotes, Dinagat, Homonhon, Leyte, Luzon, Marinduque, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Panaon, Samar, Sibutu, Sibuyan, Tawitawi.

Status.— Common.

***Polytremis* Mabilie, 1904**

Oriental and East Asian genus, extending north to the Amur region and Sakhalin, and east to Sulawesi and the Sula Archipelago. Eleven species are recognized, of which six are not found in the Oriental Region.

Dayflying, but also recorded in literature as crepuscular. Occurs in the Philippines at a consistently low altitude (in our experience not encountered above 50 metres). Flies in broken secondary forest, semicultivated areas and meadows (fig. 5). Is often seen on flowers and seldom flies above 2 metres.

*Polytremis lubricans* (Herrich-Schäffer, 1869)

General distribution.— Oriental Region, northward extending to China and Japan.

Geographic variation.— Two subspecies are recognized. The nominotypical subspecies (type-locality: not stated) occurs in the tropical parts of the region, from India and S China to Sulawesi and the Sula Archipelago.

Distribution in the Philippines (fig. 125).— Sibutu, Tawitawi.

Status.— Rare.

*Baoris* Moore, 1881

The genus consists of four Oriental species and one species bordering the Oriental Region in China.

Dayflying in primary and secondary forest, around small villages and coastal coppices between sea level and 1,000 metres (figs. 3-4, 6-7). Flies quite fast, visits flowers, rests with wings closed and is not easily disturbed. Can be observed up to 5 metres above ground.

*Baoris oceia* (Hewitson, 1868)

General distribution.— From S Burma through Sundaland to the Philippines.

Distribution in the Philippines (fig. 125).— Babuyan, Basilan, Biliran, Bohol, Calamian, Camiguin de Mindanao, Camotes, Homonhon, Jolo, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Negros, Palawan, Panaon, Panay, Samar, Sibutu, Sibuyan, Tawitawi, Ticao.

Status.— Common.

*Caltoris* Swinhoe, 1893

Oriental Region and east through New Guinea to the Solomon Islands; 17 species.

The four Philippine species are keyed in the next chapter (p. 80).

Frequently met with during the day from sea level to 1,700 metres in and around primary and secondary forest, grassland at higher altitude verging on forest, semi-cleared partly cultivated areas as well as coastal coppices at lower altitudes (sea level to 650 metres) (figs. 3, 5-7). Likes to bask in the sun. Often seen at flowers. Normal flight/rest elevation at which encountered is 0.5 to 2 metres.

*Caltoris brunnea* (Snellen, 1876)

General distribution.— From NE India to Indo-China and through Sundaland to the Lesser Sunda Islands.

Geographic variation.— Two subspecies are recognized. In the Philippines ssp. *caere* (de Nicéville, 1891) (type-locality: Thaungyin, Burma-Thailand border) occurs.

Distribution in the Philippines.— Calamian, Palawan.

Status.— Rare.



*Caltoris bromus* Leech, 1893

General distribution.— Assam to Indo-China, north to the Chinese provinces Sechuan and Chekiang, and to Taiwan and Okinawa, and south through Sundaland to Sulawesi and the Lesser Sunda Islands.

Geographic variation.— Two subspecies are recognized, with the nominotypical subspecies (type-locality: Chia Kou Ho) covering the whole range of the species except Taiwan and Okinawa.

Distribution in the Philippines (fig. 126).— Leyte, Mindanao, Palawan, Panay, Samar.

Status.— Rare.

*Caltoris cormasa* (Hewitson, 1876)

General distribution.— From Assam to Tonkin and south through Sundaland to Java, Borneo and the Philippines.

Distribution in the Philippines (fig. 126).— Homonhon, Leyte, Luzon, Marinduque, Mindanao, Mindoro, Palawan, Samar, Sibutu, Sibuyan, Tawitawi.

Status.— Uncommon.

*Caltoris philippina* (Herrich-Schäffer, 1869)

General distribution.— Oriental Region, but not in Sumatra, Borneo, Java and the Lesser Sunda Islands; extending east through the Moluccas and New Guinea to the Solomon Islands.

Geographic variation.— Two subspecies are recognized, with the nominotypical one (type-locality: not stated) occurring west of the Moluccas.

Distribution in the Philippines (fig. 126).— Balabac, Basilan, Cebu, Camiguin de Mindanao, Leyte, Luzon, Mindanao, Mindoro, Negros, Palawan, Panay, Sibutu, Tawitawi.

Status.— Common.

## Unreliable Philippine records

*Bibasis phul* (Mabille, 1876). The holotype, more than 100 years old, is the only known specimen supposedly coming from the "Philippines". We consider this record unreliable, until fresh material turns up.

*Choaspes benjamini formosana* (Fruhstorfer, 1911). Evans (1949) mentioned a single female from Palawan. The species is not known from Borneo, but it does occur in Sumatra and the Malay Peninsula (as ssp. *pallida* Evans, 1932) (Eliot, 1978). It would be quite surprising if the Taiwanese form would turn up in Palawan skipping the rest of the Philippines. In fact, the female recorded by Evans belongs to *C. plateni caudatus*.

*Choaspes hemixanthus* Rothschild, 1903. This species has a remarkable distribution: widely spread in China, N India, Burma, Thailand, south to Perak, in New Guinea, and further recorded from Sumatra, Palawan and Halmahera, but only one specimen from each of these islands (Evans, 1949). Until more material is available, we shall consider the Palawan record unreliable. (See also footnote on p. 19)

*Astictopterus jama jama* Felder, 1860. There are a male and female in the Natural

History Museum, London, labeled as coming from the Philippines, but not trusted by Evans (1949). The species does not occur in Borneo, Sulawesi or Taiwan.

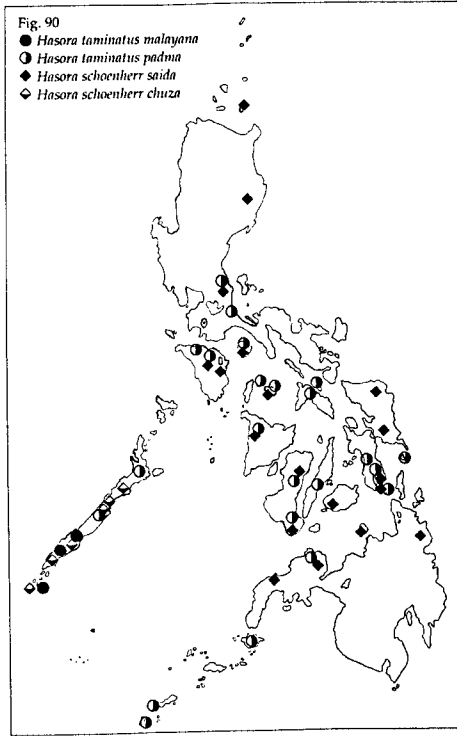
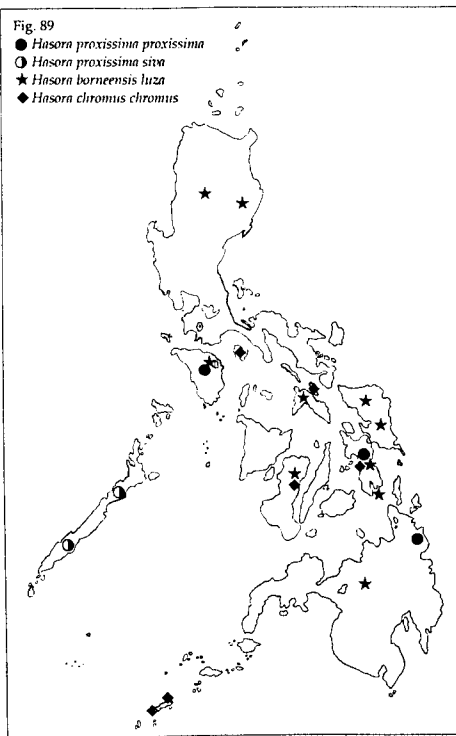
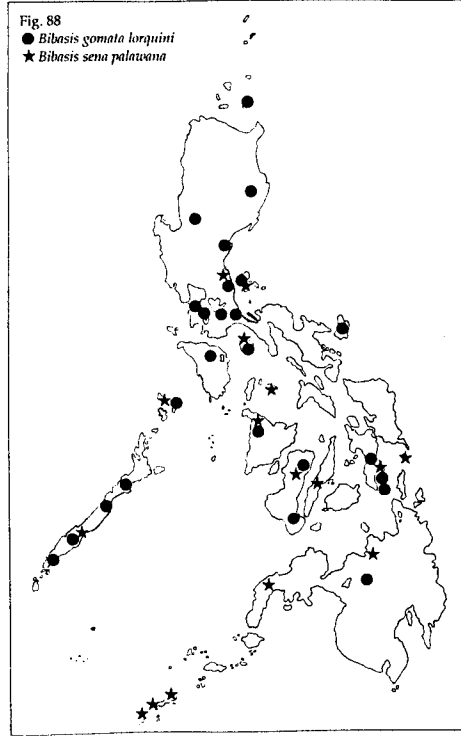
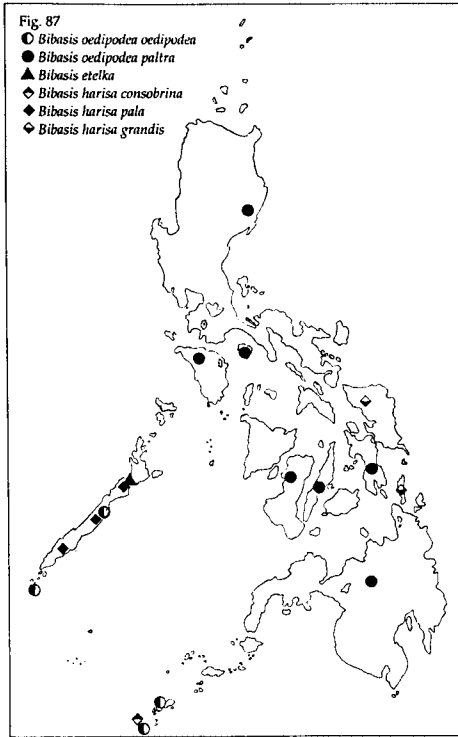
*Iambrix stellifer* (Butler, [1879]). According to Evans (1949), *Apaustus mergus* Plötz, 1884 (described from the Philippines) is a synonym of *Astictopterus stellifer* Butler. We have not seen material of *I. stellifer* from the Philippines. Either the synonymy is incorrect, or the type-locality of *A. mergus* is false, or it is an extremely rare species in the Philippines.

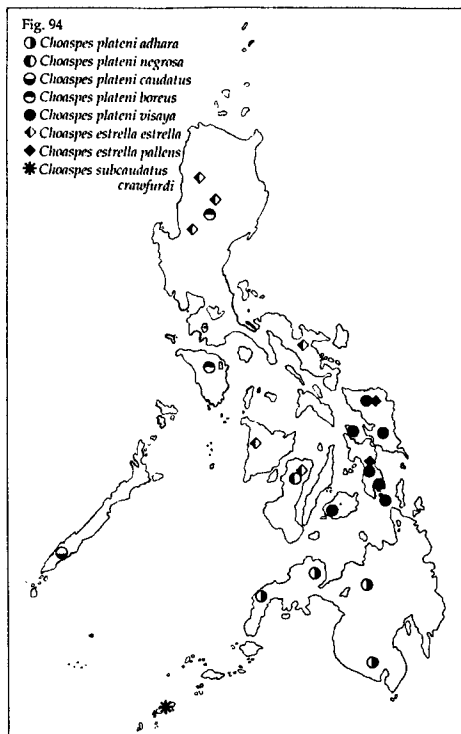
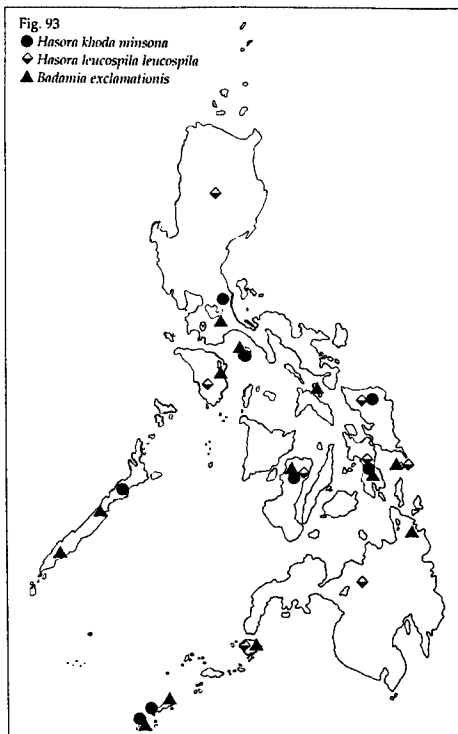
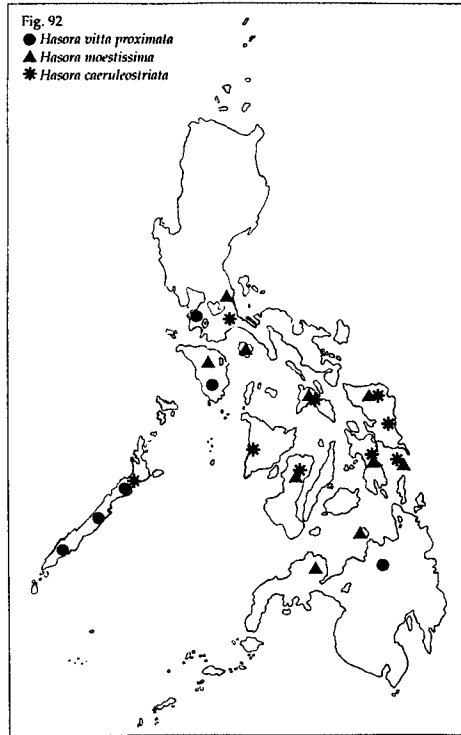
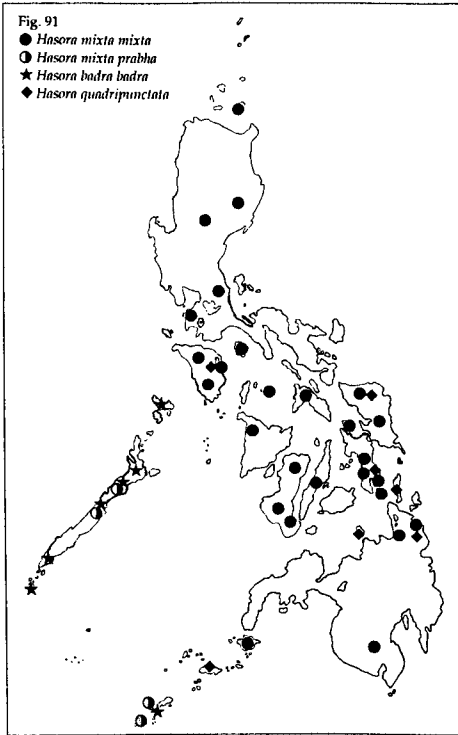
*Iambrix salsala salsala* (Moore, 1865). There is a female in the Natural History Museum, London, labeled as coming from the Philippines, but not trusted by Evans (1949). The species does not occur in Borneo, Sulawesi or Taiwan.

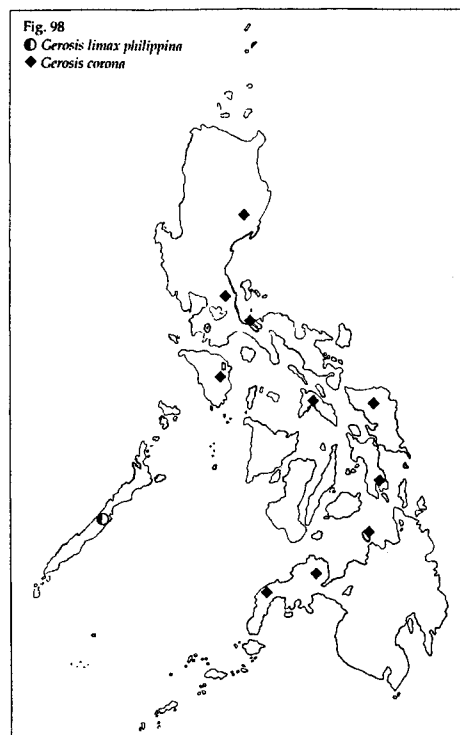
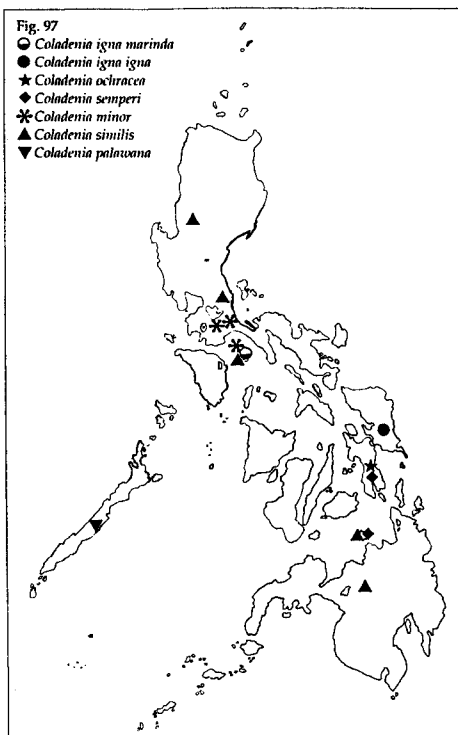
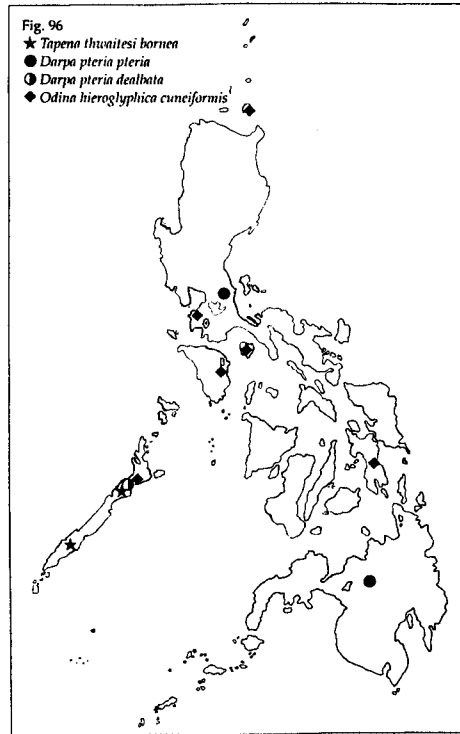
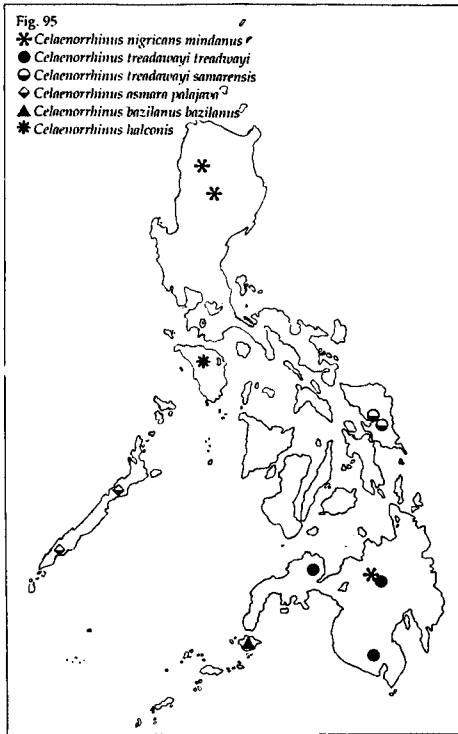
*Iambrix obliquans obliquans* (Mabille, 1893). There is a male in the Natural History Museum, London, labeled as coming from the Philippines, but not trusted by Evans (1949). The species does not occur in Sulawesi or Taiwan. It does occur in Borneo, in a different subspecies (*yamanta* Fruhstorfer, 1910). *Ssp. obliquans* is distributed from S Burma to Java.

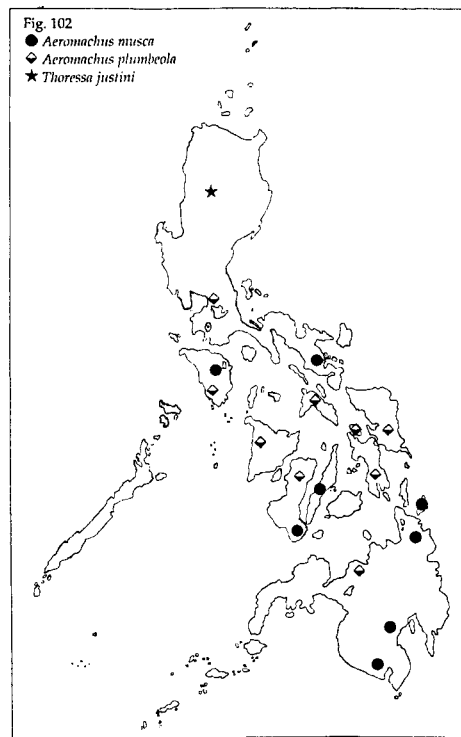
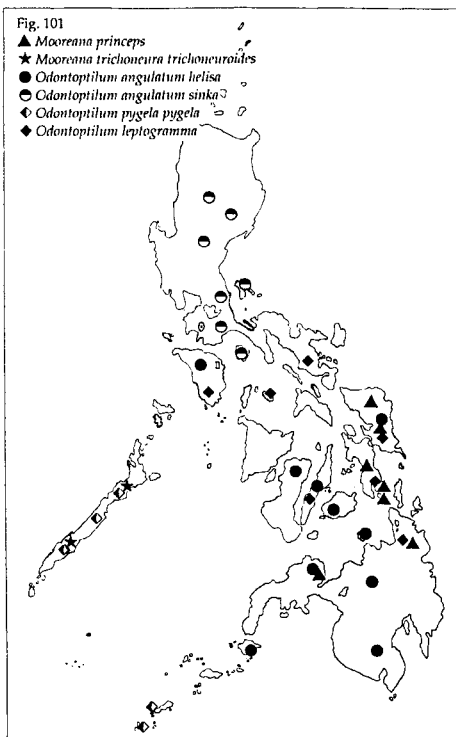
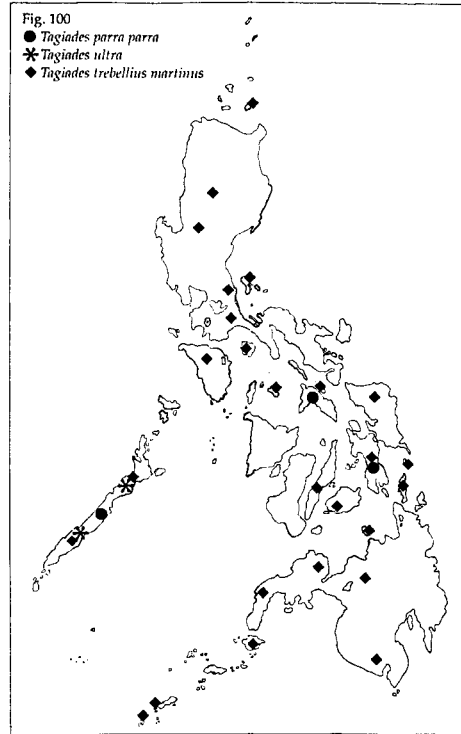
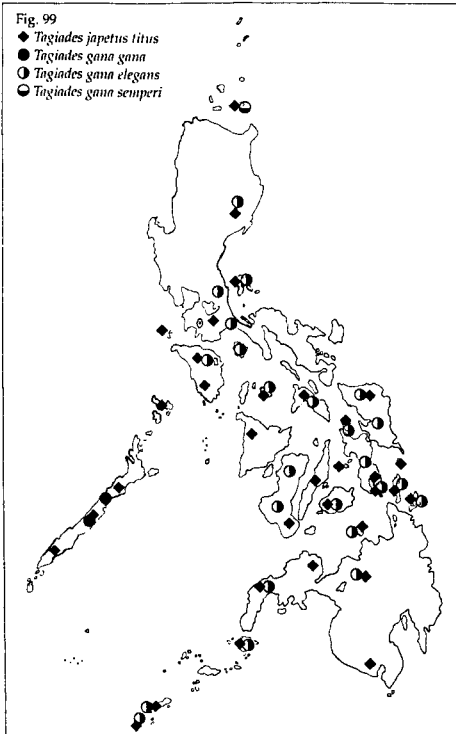
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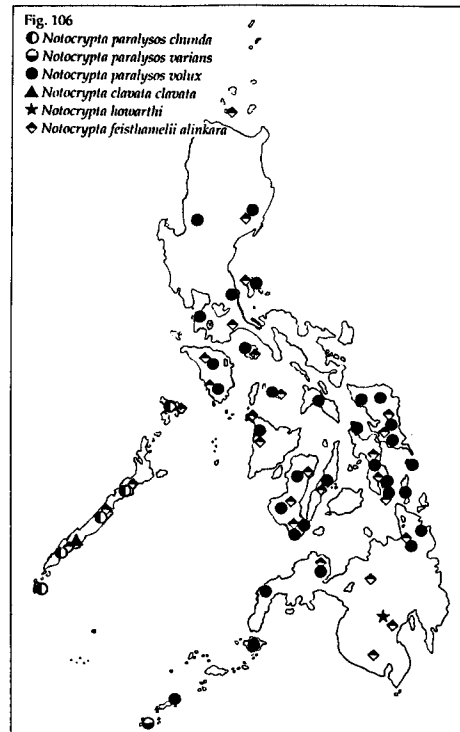
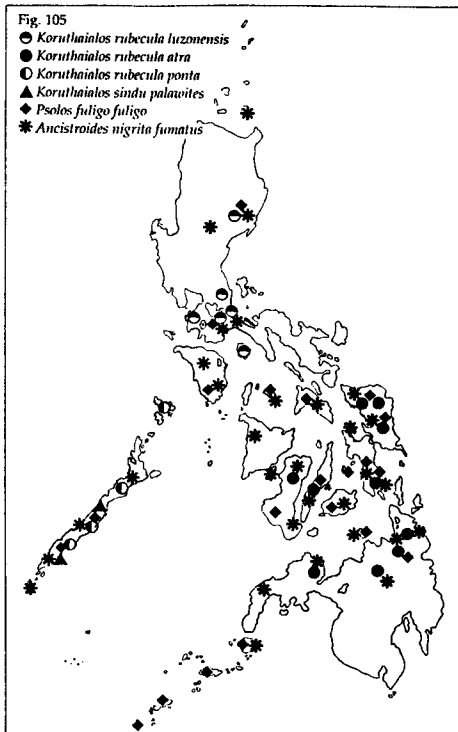
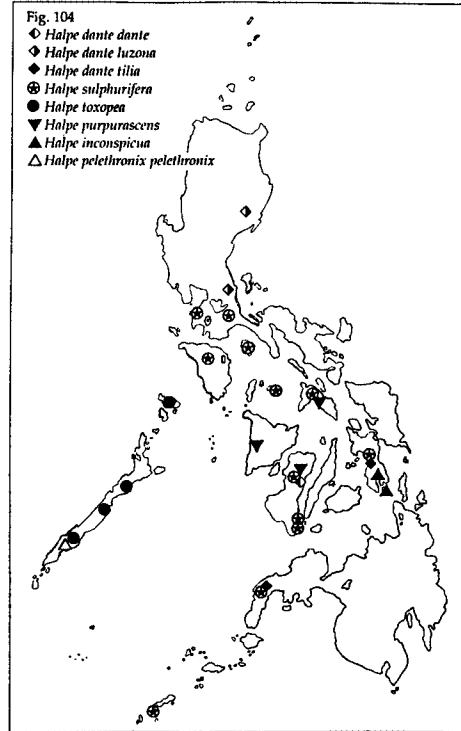
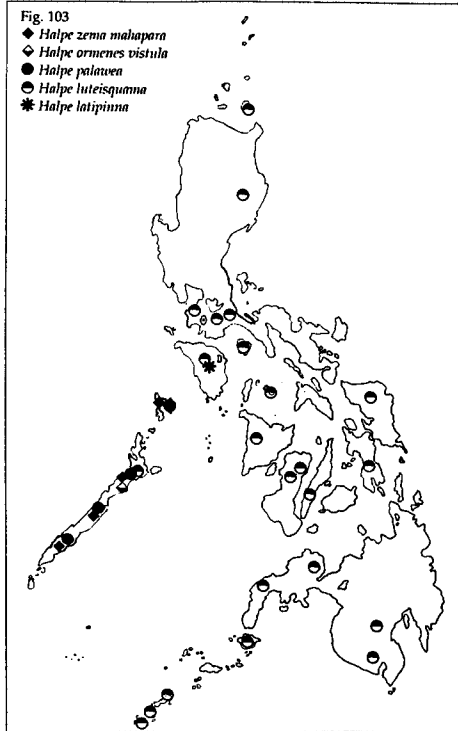
Figs. 87-126 (p. 64-73). Distribution maps. On the following pages the distributions of all species and subspecies are mapped as accurately as possible within the limits of such small maps. In cases where the exact locality is unknown, no symbol is given on the map and the situation is explained in the text. In all cases the text is authoritative.



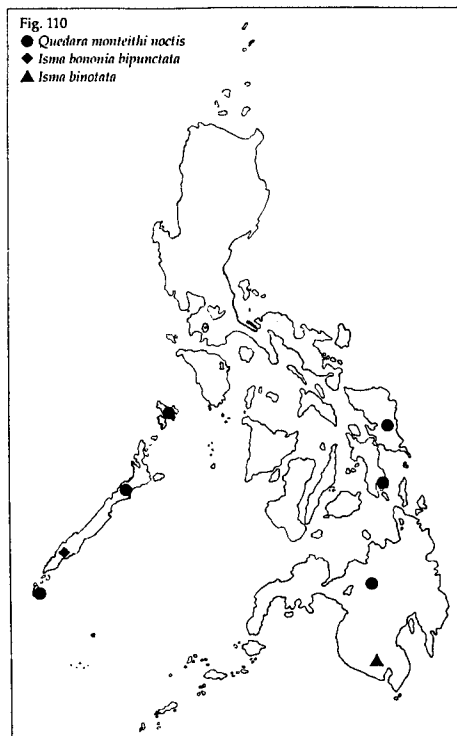
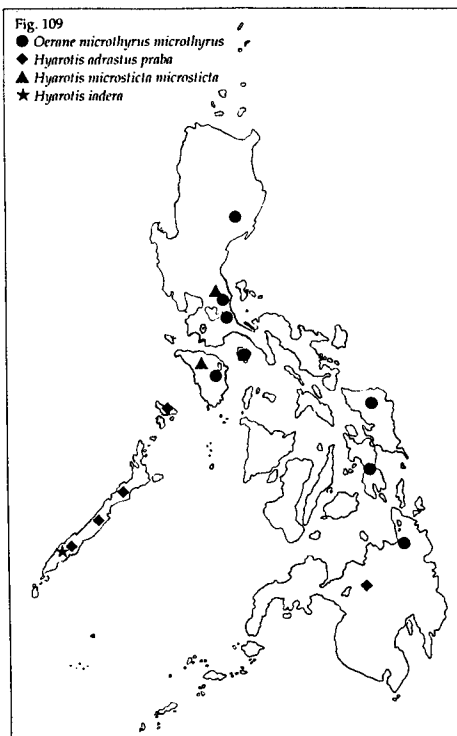
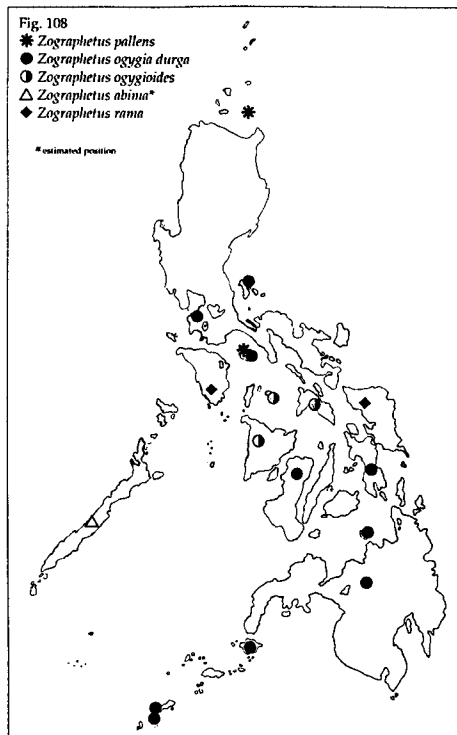
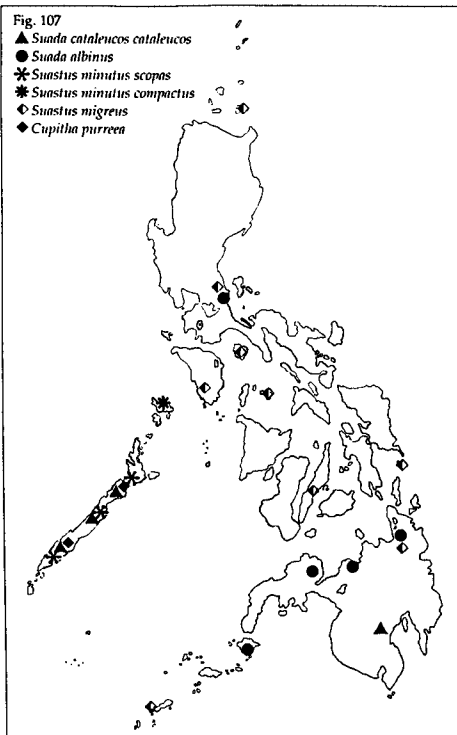


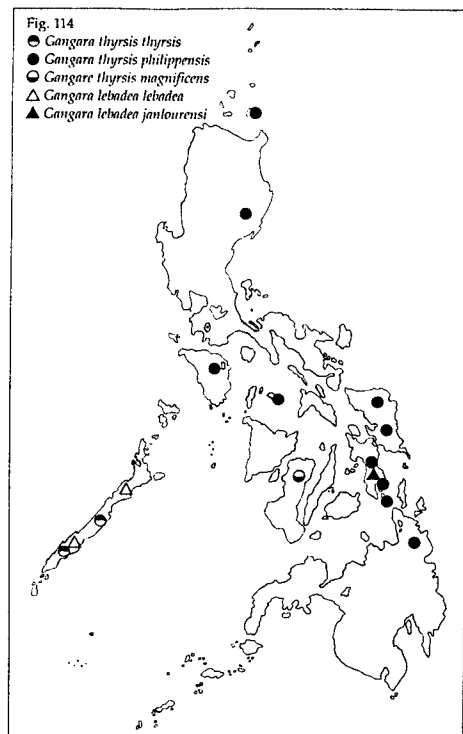
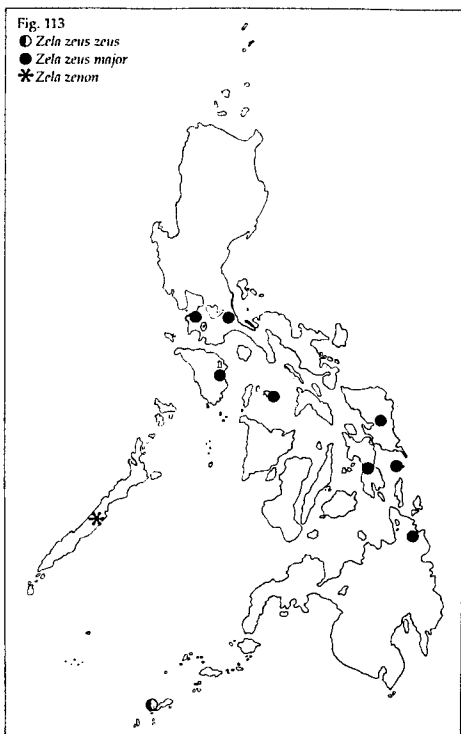
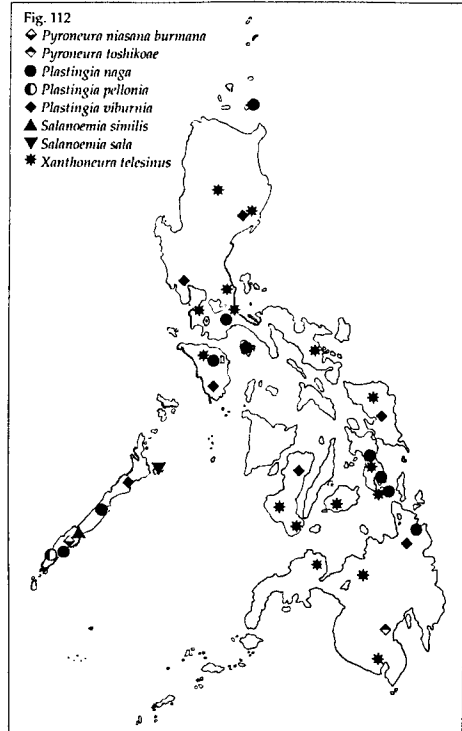
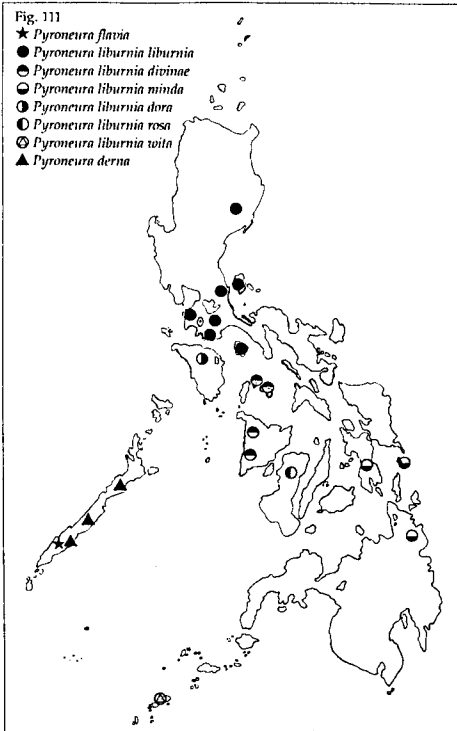


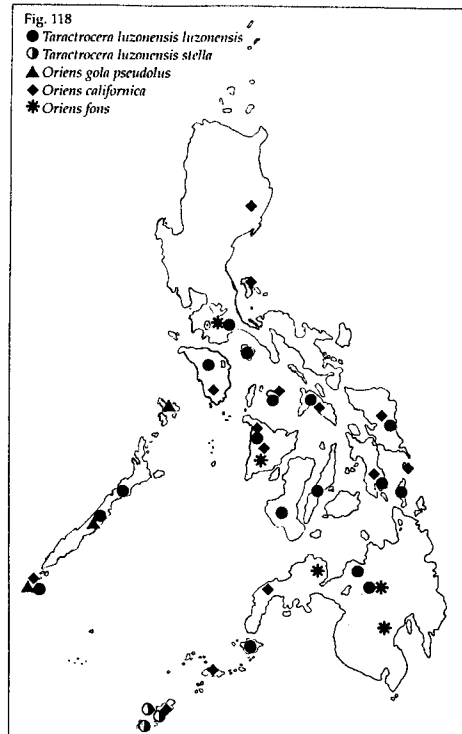
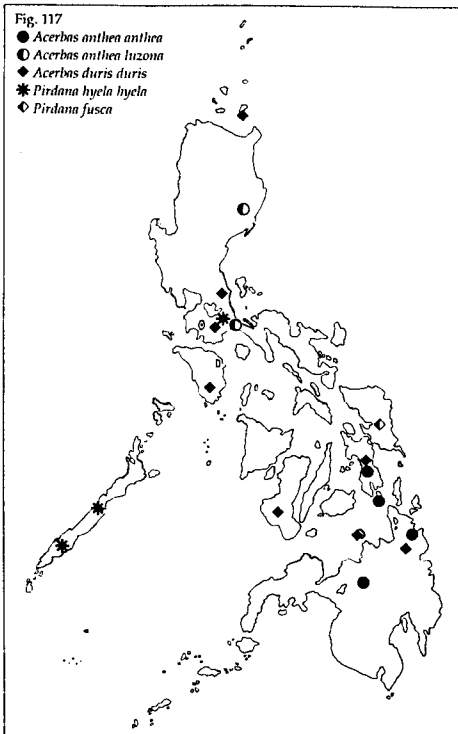
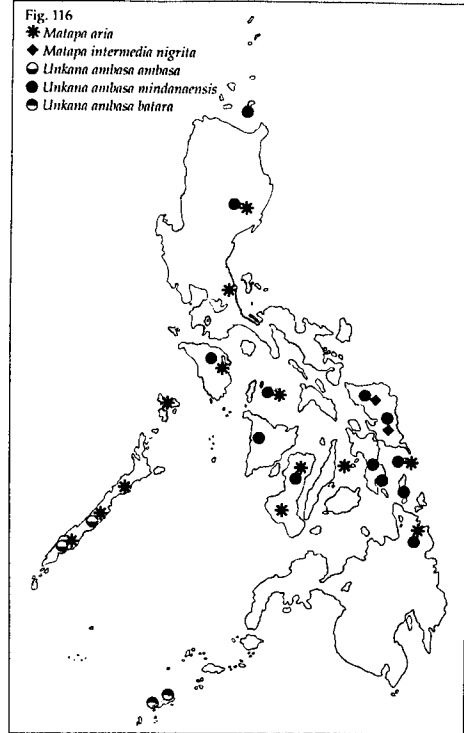
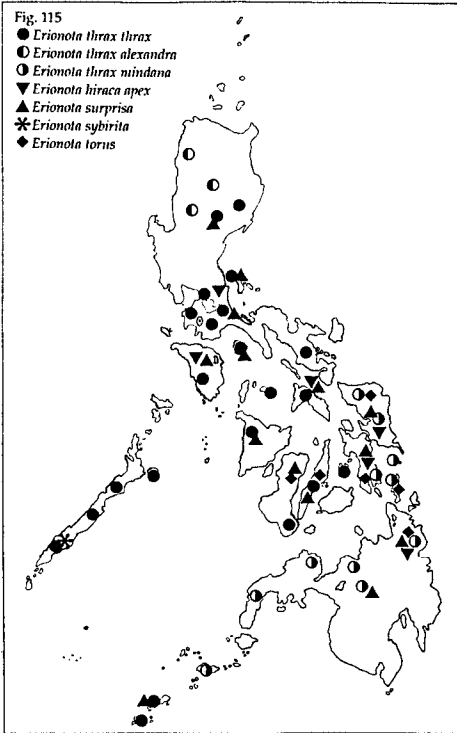


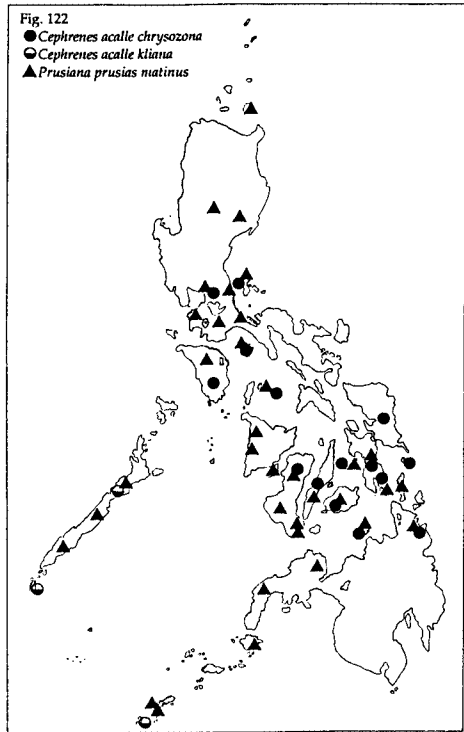
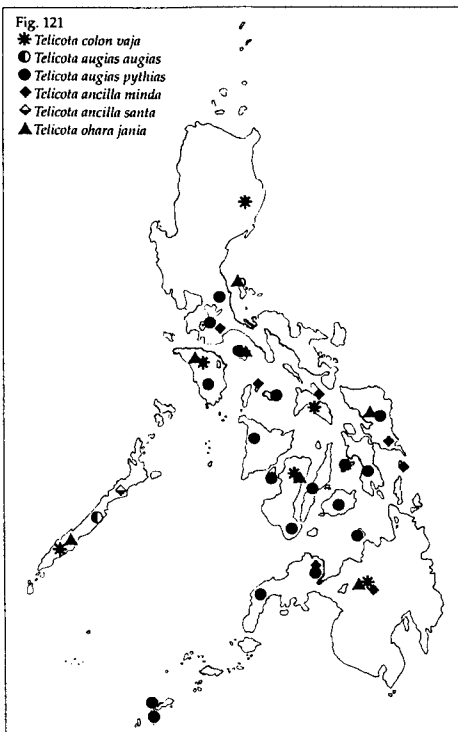
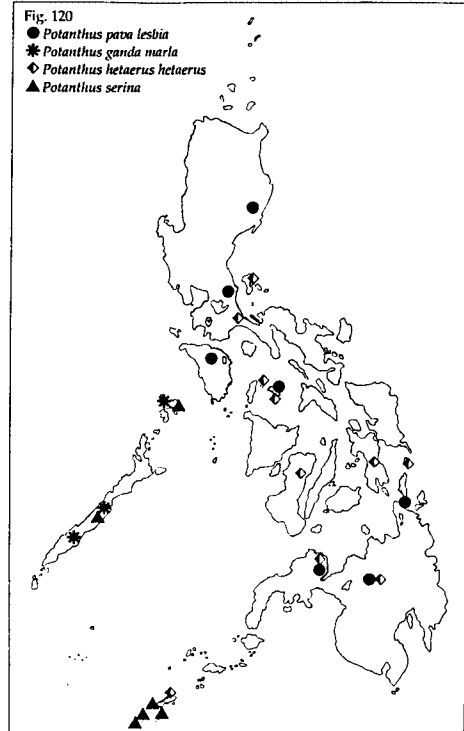
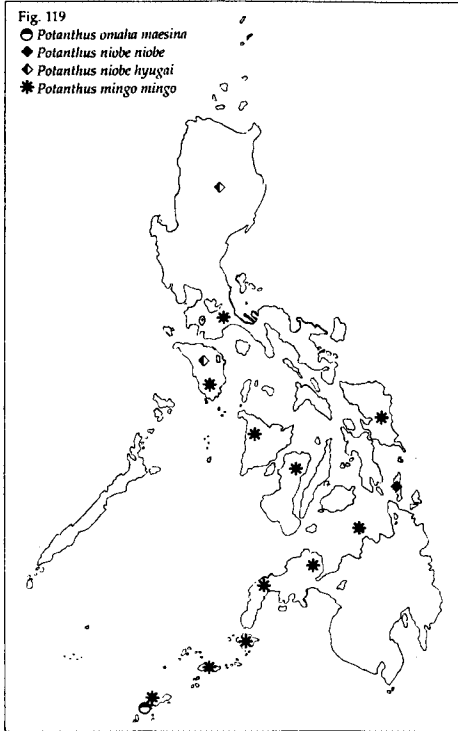


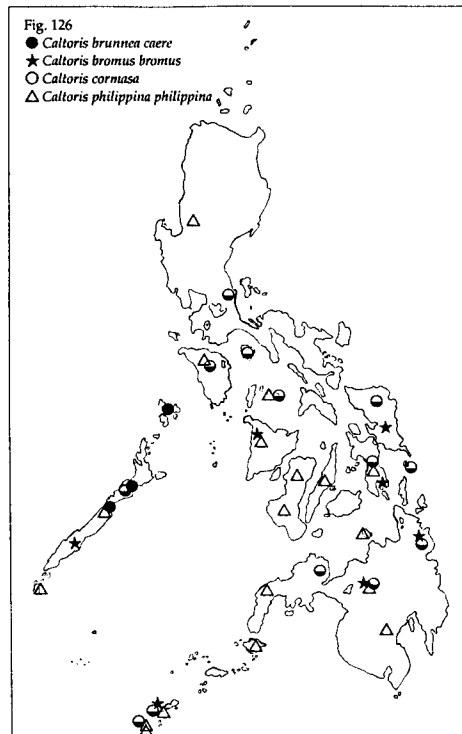
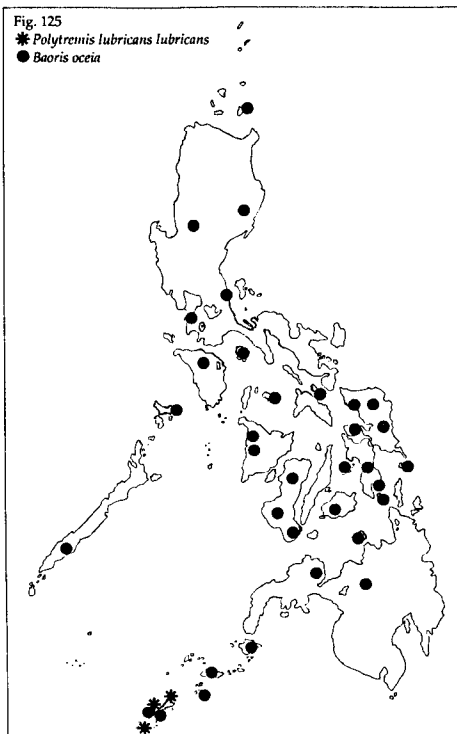
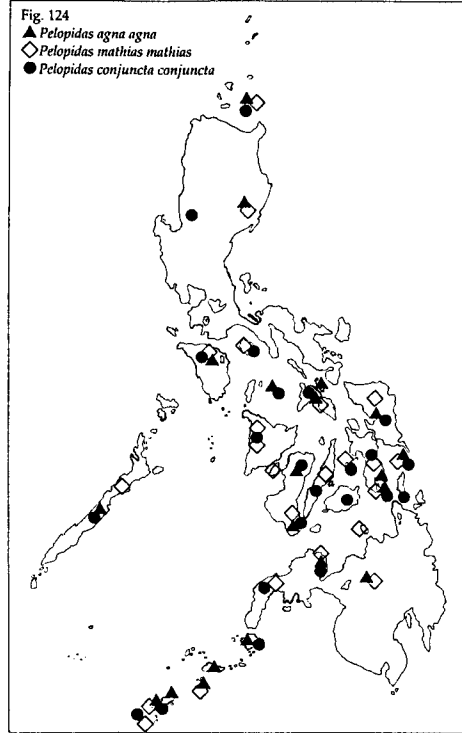
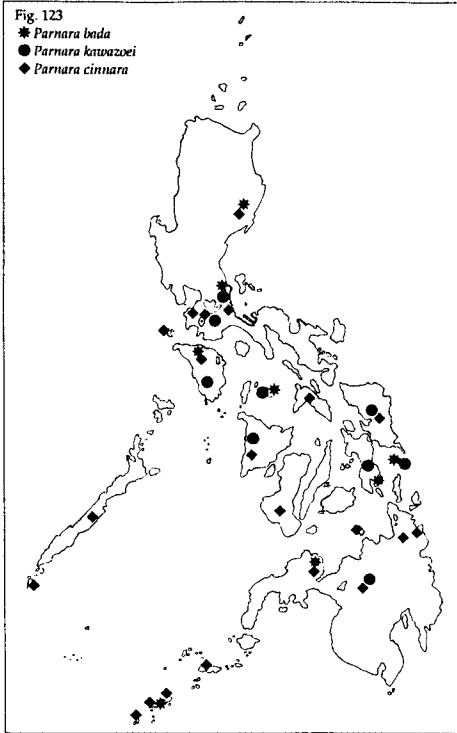












### On the identification of Philippine Hesperiidae

The famous work of Seitz (1927) is out of date now and cannot be used as a means for identification. A number of recent publications on regional butterfly faunas in Southeast Asia with colour plates can be helpful, e.g. Corbet & Pendlebury (1978; Malay Peninsula), Fleming (1983; Malay Peninsula), Maruyama (1991; Borneo), Motono et al. (1989; Laos), Pinratana (1985; Thailand). In a number of cases, however, the Philippine species are not depicted (and Philippine endemics are, of course, never figured in a publication on another region) and in some other cases the differences between species are too subtle to be appreciated from the plate. To facilitate identification of Philippine Hesperiidae we provide colour plates for most endemic species and below we give keys for genera with at least three species which may be difficult to identify. The genus *Potanthus* would certainly deserve a place here. However, Evans' (1949) arrangement of this large genus with many very similar species is in need of revision. Several changes have already been made (e.g. Maruyama, 1991; also in the present paper) and more are about to be published (Maruyama, pers. comm.). Although it may be possible to identify most fresh specimens by external characters only, the differences are usually subtle and slightly worn specimens may prove to be unidentifiable without the help of the male genitalia. Therefore we refrain from giving a key to the *Potanthus* species here.

The keys are given in the order in which the genera have been dealt with in the previous chapter. To keep the keys short we have based them on superficial characters only. It must be emphasized, however, that in some cases identification of Hesperiidae on superficial characters is very difficult. If there is any hint of uncertainty, one should check the genitalia (for which we must refer to the relevant literature). Unfortunately for many (if not for most) species the female genitalia have not yet been described and identification must rely on superficial resemblance with the male.

#### *Hasora*

In most species there is a strong sexual dimorphism, the males having the forewing unspotted, while there are hyaline spots in the females.

1. Upperside hindwing with conspicuous yellow central band or basal  $\frac{2}{3}$  yellow ..... *H. schoenherr*
- Upperside hindwing uniformly brown, at most with dense straw-coloured hairs in basal part ..... 2
2. Underside hindwing with conspicuous white spot in cell; without white discal band, only a white spot in space 1c as a remnant of it ..... 3
- Underside hindwing at most a pale spot, not a white spot in cell, with or without white discal band ..... 4
3. White cell spot on underside hindwing less than half width of cell ..... *H. badra*  
White cell spot much larger than half width of cell ..... *H. quadripunctata*
4. Underside hindwing with strong purple wash, at most faint traces of a paler band, a pale subternal spot in space 1c ..... 5
- Underside hindwing with sharply defined white or bright blue discal band or if

- band is faint, no strong purple wash ..... 6
5. Male with conspicuous brands on either side of veins 1, 2 and 3 and under vein 4 on upperside of forewing. Female with narrow spots in spaces 2 and 3, and a tiny dot in space 6 of forewing, no cell spot ..... *H. leucospila*
- Male with discal stigma on upperside of forewing. Female with spots in spaces 2 and 3 not elongate, tiny apical dots in spaces 6 and 7 may be present, conspicuous spot in cell almost as big as spot in space 2 ..... *H. mixta*
6. Underside hindwing basal area brown, no purple, blue or greenish gloss ..... 7
- Underside hindwing basal area purple, blue or greenish ..... 10
7. Wing bases on upperside broadly straw-coloured, especially in female. White band on underside hindwing strongly tapering to tornus. Male without brands or stigma ..... *H. borneensis*
- Head brown. Wing bases on upperside, if paler than rest of wing, not straw-coloured. White band on underside hindwing not strongly tapering to tornus. Male with or without brands or stigma ..... 8
8. Underside hindwing with white band, usually tapering to costa; ground colour brown, no blue or purple gloss. Male with inconspicuous brands on upperside of forewing on either side of veins 1, 2 and 3 and under vein 4 ..... *H. khoda*
- Underside hindwing with white or blue band; if white, female with blue purple gloss over hindwing, and at end of cell and distally of apical spot on forewing. Male without brands or stigma ..... 9
9. Band on underside hindwing white ..... *H. moestissima*
- Band on underside hindwing blue ..... *H. caeruleostriata*
10. Upperside forewing with tiny white apical dot in space 6. Male without brands or stigma ..... *H. vitta*
- Upperside forewing without apical spots or dots. Male without brands, with or without stigma ..... 11
11. Wing bases on upperside conspicuously paler. Male with discal stigma on upperside forewing ..... *H. chromus*
- Wing bases not conspicuously paler on upperside ..... 12
12. Underside hindwing basal area blue, purple wash over whole wing. Male without stigma ..... *H. proxissima*
- Underside hindwing basal area shining steely blue green, no purple wash. Male with discal stigma ..... *H. taminatus*

### *Tagiades*

1. Forewing without hyaline spot in space 11 over cell spot. In male, hind tibiae without hair pencil ..... 2
- Forewing with a hyaline spot in space 11 over cell spot. In male, hind tibiae with short recumbent hair pencil on inner side (difficult to see) ..... 4
2. Forewing with hyaline spots in spaces 2 and 3 ..... *T. japetus*
- Forewing without such spots ..... 3
3. Dark spot in space 6 on upperside hindwing nearer to origin of vein 7 than to termen ..... *T. gana*
- Dark spot in space 6 on upperside of hindwing nearer to termen than to origin of



- vein 7 ..... *T. parra*
4. Upperside forewing with lower hyaline cell spot but without hyaline spots in spaces 2 and 3. Underside forewing without a double subternal white spot ..... *T. ultra*
- Upperside forewing with lower hyaline cell spot and hyaline spots in spaces 2 and 3. Underside forewing with a double subternal white spot ..... *T. trebellius*

### *Halpe*

1. Underside hindwing with continuous white band from vein 1b to costa, not crossed by dark veins ..... 2
- Underside hindwing without continuous band, if there is a band then it is divided by dark veins into separate spots ..... 3
2. Underside hindwing dark brown, band white, outer edge almost regular ..... *H. ormenes*
- Underside hindwing brown, band yellowish white, outer edge irregular with brown colour penetrating along veins ..... *H. zema*
3. Antennal club with whitish spot just before apiculus. Dark species with inconspicuous greenish ochreous scales and hairs on upperside. Forewing upperside and underside only spots in spaces 2, 3 and 6, small, those in spaces 2 and 3 well separated, not overlapping. Underside hindwing with ochreous superscaling over whole wing except at tornus; no discal spots, but ochreous scales concentrated into more or less well-defined submarginal spots in a curved row parallel to termen and inwardly flanked by darker spots ..... *H. palawea*
- Antennal club without such spot. Greenish ochreous scales and hairs on upperside variable, usually more conspicuous. Spots of forewing variable, in most species larger and those in spaces 2 and 3 overlapping; on underside with or without spot in space 1bc. Underside hindwing with discal spots or, if not, submarginal spots very inconspicuous (and in that case forewing with a tiny cell spot) or the submarginal spot in space 1c larger than the other spots ..... 4
4. Underside hindwing with series of well-defined whitish or pale yellow discal spots in spaces 2 to 6 ..... 5
- Underside hindwing without well-defined discal spots ..... 10
5. Underside hindwing with submarginal spots in a straight line directed to end of vein 6 ..... 6
- Underside hindwing with submarginal spots in a curved line parallel to termen 8
6. Underside hindwing discal spots with outer edges in a straight line from vein 1c to end of vein 7, because spot in space 6 extends beyond spot in spaces 4 and 5. Male with or without grey patches in space 1bc on upperside forewing fanking the stigma ..... 7
- Underside hindwing discal spots with outer edges in a more curved line, spot in space 6 not extending beyond spot in spaces 4 and 5. Male without grey patches in space 1bc on upperside forewing ..... *H. dante*
7. Termen of forewing more strongly curved than in other *Halpe* species; termen (measured in a straight line from tornus to apex) as long as dorsum. Spots in spaces 2 and 3 of forewing small and separated by their own diameter.

- Underside hindwing spot in space 6 very wide, wider than spot in spaces 4 and 5 and the latter almost completely overlapping. Male without grey patches flanking stigma in space 1bc on upperside forewing ..... *H. latipinna*
- Termen of forewing less strongly curved, as in other *Halpe* species; termen shorter than dorsum. Spots in spaces 2 and 3 of forewing elongate, usually clearly overlapping. Underside hindwing spot in space 6 not wider than spot in spaces 4 and 5, the latter overlapping for  $\frac{1}{2}$  to  $\frac{2}{3}$ . Male with grey patches flanking stigma on upperside forewing ..... *H. luteisquama*
8. Underside hindwing discal spots yellow, spot in space 1c well-developed, more than half as large as spot in spaces 4 and 5, latter at most 1.5 times as wide as high, further from termen than its own width ..... *H. toxopea*
- Underside hindwing discal spots whitish or pale yellow, spot in space 1c absent or, if present, inconspicuous and less than  $\frac{1}{5}$  of size of spot in spaces 4 and 5; latter large, 2.5-4 times as wide as high, its distance from termen less than its own width ..... 9
9. Upperside very dark brown with dull purple gloss; spots in spaces 2 and 3 of forewing white, elongate and widely overlapping. Fringes white ..... *H. purpurascens*
- Upperside brown without any trace of purple gloss; spots in spaces 2 and 3 of forewing not clear white, rather pale yellow, not or slightly overlapping. Fringes grey ..... *H. sulphurifera*
10. Underside forewing with well-marked submarginal spots in an evenly curved line parallel to termen. Underside hindwing submarginal spots more or less developed, in space 1c large and well-developed even when other submarginal spots are weak; fine pale ochreous marginal line at tornus ..... *H. inconspicua*
- Submarginal spots on underside forewing weakly developed, parallel to termen, but near apex curving inwards. Underside hindwing submarginal spots weakly developed, in space 1c as in other spaces ..... *H. pelethronix*

### *Notocrypta*

1. Upperside or underside forewing no trace of apical spots in spaces 6 to 8 ..... 2
- Upperside or underside forewing at least traces of apical spots in spaces 6 to 8. Underside forewing white band continued above radius ..... *N. feisthamelii*
2. Underside forewing white band continued full width to costa ..... *N. clavata*
- Underside forewing white band not continued above radius, or very weakly so and never full width, nor reaching costa ..... 3
3. Larger, length of forewing 18-19 mm. Below usually with violet scaling at apex of forewing and before termen of hindwing ..... *N. paralysos*
- Smaller, length of forewing 17 mm. Below dark brown, a little paler distally ..... *N. howarthi*

### *Zographetus*

1. In male and female vein 2 of forewing mid base and vein 3. Spots white. Male

- with or without brands on upperside forewing, no swollen veins or hair pencil on underside forewing ..... 2
- In male and female vein 2 of forewing much nearer to base than to vein 3. Spots pale yellow. Male with base of vein 2 and corresponding part of cubitus swollen and partly overlaid by black hair tuft from base of dorsum ..... 3
2. Underside hindwing basal half yellowish, outer half purple brown, with or without spots. Male with inconspicuous brands on upperside forewing over basal part of vein 1, under and over basal part of vein 2, and under cubitus between veins 2 and 3 ..... *Z. ogygia*
- Underside hindwing more uniformly coloured, dark ferruginous with inconspicuous spots or without spots. Male without brands ..... *Z. ogygioides*
3. Underside hindwing overlaid with yellow scales condensed into a pale yellow broad band from vein 3 to vein 8 ..... *Z. pallens*
- Superscaling on underside hindwing not condensed into a band, uniformly scattered, only leaving dark spots ..... 4
4. Superscaling on underside hindwing dull yellow. Hyaline spot in space 2 of forewing narrow ..... *Z. rama*
- Superscaling on underside hindwing bright ochreous. Hyaline spot in space 2 of forewing as broad as high or broader ..... *Z. abima*

### *Pyroneura*

Easily distinguished from other dark brown with yellow or orange skippers, like the species of the *Taractrocera* group, by the length of the antennae (more than half of costa of forewing) and by the presence of hyaline or subhyaline spots on the forewing.

1. Underside hindwing dark brown with a large milky white central patch (actually the widened discal band) ..... *P. toshikoe*
- Underside hindwing with yellow streaks in addition to the discal band ..... 2
2. Upperside forewing apical spots in spaces 6 and 7 directed to dorsum ..... 3
- Upperside forewing apical spots in spaces 6 and 7 directed to termen ..... 4
3. Antennal club entirely yellow. Underside hindwing yellow streak in space 1b reaching  $\frac{2}{3}$  to termen, yellow streak in space 1c reaching termen ..... *P. flavia*
- Antennal club plain brown above, whitish under club. Underside hindwing yellow streaks in spaces 1b and 1c not reaching beyond halfway to termen..... *P. liburnia*
4. Male, antennal shaft black, club yellow; female unknown ..... *P. agnesia*
- Male, antennal shaft and club white or yellow; female, club only ..... 5
5. Underside hindwing vein 8 edged with yellow along lower side only .... *P. derna*
- Underside hindwing vein 8 ochreous or red edged on both sides ..... *P. niasana*

### *Taractrocera* group

The species of the genera *Taractrocera*, *Oriens*, *Potanthus* and *Telicota* (with a number of other genera united into the *Taractrocera* group by Evans, 1949) are more or less similar, all being dark brown with orange or yellow spots or bands. The genera can be differentiated with the following key (which

applies to the Philippine representatives only). Maruyama (1991) transferred the genus *Prusiana*, placed in the *Taractrocera* group by Evans, to the *Gegenes* group (called *Pelopidas* group by him); in this group it is the only genus with orange markings.

1. Forewing with lower cell spot confluent with spot in space 2 or these spots separated by a dark vein only ..... *Oriens*
- Forewing with lower cell spot and spot in space 2 well separated ..... 2
2. Antennal club flattened to a hollow disk without apiculus ..... *Taractrocera*
- Antennal club not flattened, with well-marked apiculus ..... 3
3. Palpi 3rd segment short and stout ..... 4
- Palpi 3rd segment thin as antennal shaft, long and protruding. Male without stigma, with more or less visible brand along vein 1 on upperside forewing ..... *Potanthus*
4. Length of forewing up to 16 mm. Male with discal stigma ..... *Telicota*
- Length of forewing 18 mm. Male without stigma or brand ..... *Cephrenes*

#### *Oriens*

1. Upperside forewing cell spot conjoined to spot in space 2. Inner edge of discal band on upperside hindwing even ..... *O. gola*
- Upperside forewing cell spot conjoined to spot in space 2 or separated by dark vein. Inner edge of discal band on upperside hindwing conspicuously indented in space 3 ..... 2
2. Upperside forewing cell spot completely conjoined to the spot in space 2, as in *gola*; underside hindwing ground colour orange yellow more or less darkened by dark brown scales, but darkening not predominant ..... *O. californica*
- Upperside forewing veins narrowly dark, separating the discal spots inter se and from the cell spot; underside hindwing orange yellow ground colour largely replaced by dark brown ..... *O. fons*

#### *Telicota*

1. Male, base of space 2 on upperside of forewing yellow; stigma nearer to inner edge of black discal band than to outer edge. Origin of vein 3 much nearer to origin of vein 2 than to origin of vein 4. Female, underside hindwing greenish ochreous ..... *T. colon*
- Male, base of space 2 on upperside of forewing yellow or blackened; stigma central on black discal band. Origin of vein 3 not nearer to origin of vein 2 than to origin of vein 4. Female, underside hindwing ochreous without greenish tinge ..... 2
2. Male, upperside forewing base of space 2 yellow or orange. Upperside hindwing yellow band continued into space 6. Underside hindwing orange ochreous, veins not darkened where they cross the band in the male, only lightly darkened in the female ..... *T. augias*
- Male, upperside forewing base of space 2 darkened. Upperside hindwing band rarely continued into space 6. Underside hindwing veins with or without darker scales where they cross the band ..... 3

3. Male, stigma narrow, about half as wide as the black band. Female, underside hindwing sparsely overlaid by fuscous scaling, darker than in other species ..... *T. ohara*
- Male, stigma wide, almost as wide as the black band. Female, underside hindwing without or with very light fuscous superscaling ..... 4
4. Underside hindwing veins darkened where they cross the band ..... *T. hilda*
- Underside hindwing veins not darkened ..... *T. ancilla*

### *Gegenes* group

The genera *Parnara*, *Borbo*, *Pelopidas*, *Polytremis*, *Baoris* and *Caltoris* were, with two other genera, placed in the *Gegenes* group by Evans, 1949 (called the *Pelopidas* group by Eliot, 1978, and Maruyama, 1991). They contain the bulk of the brown species. Maruyama (1991) transferred *Prusiana*, a genus with orange marked species and originally placed in the *Taractrocera* group by Evans (1949), to the present group. The brown genera differ from other genera with brown species, like *Halpe*, in the antennal club, which is constricted before the apiculus, and in vein 5 of the hindwing, which is completely lost (or almost so). The six brown genera can be separated as follows.

1. Mid tibiae spines ..... 2
- Mid tibiae unspined ..... 3
2. Underside hindwing with spots (sometimes very small). With with stigma on upperside forewing in two of the three species ..... *Pelopidas*
- Underside hindwing unmarked. Male with black brush on upperside hindwing correlated to a speculum with brand on underside forewing ..... *Baoris*
3. Underside hindwing with spots (sometimes very small) ..... 4
- Underside hindwing unmarked ..... *Caltoris*
4. No spot in space 1bc of forewing ..... *Parnara*
- With spot in space 1bc of forewing, at least on underside ..... 5
5. Upperside forewing cell spots absent or two tiny dots ..... *Borbo*
- Upperside forewing cell spots conjoined to form an hourglass figure ..... *Polytremis*

### *Caltoris*

1. Forewing with one or two cell spots ..... 2
- Forewing without cell spots ..... *C. philippina*
2. Forewing with cell spots usually well-developed. Male with discal stigma on upperside forewing ..... *C. brunnea*
- Forewing upper cell spot, if present, smaller than lower cell spot. Male without discal stigma ..... 3
3. Forewing spot in space 2 midway between lower cell spot and spot in space 3; usually only a lower cell spot. Underside hindwing with dense ochreous brown scaling, often tinged purple ..... *C. cormasa*
- Forewing spot in space 2 closer to spot in space 3 than to lower cell spot; upper and lower cell spot present. Underside hindwing brown ..... *C. bromus*

## Biogeography

### Introduction

The first and, so far, only comprehensive treatment of the biogeography of the Philippines is found in Dickerson (1928). Although much of it is out of date now, the work is still interesting reading. Starting from a steady state of the earth and, more precisely, of the position of the islands, Dickerson explained the distribution of life across the islands as a consequence of fluctuations in sea level, uniting and separating islands several times. With the acceptance of continental drift and plate tectonics in the last 25 years the complexity of the geological history of the Philippines became obvious. It is still uncertain how far this has shaped the distribution of the present fauna across the Philippines. Although each possibility must be examined, it should be realized that there is no general agreement among geologists, and even if there is agreement about the drifting history of a particular sliver of continental crust or of an island arc terrane, it is often uncertain, obscure, or unknown if such parts have always been subaerial and thus can have carried a terrestrial fauna over long distances. Consequently, explaining a distributional pattern by reference to the history of a sliver of continental crust may be as speculative as the postulation of land-bridges in pre-continental drift times. On the other hand, a recurrent distribution pattern found in unrelated groups may be better explained by reference to a common historical cause (Sober, 1988: vertical transmission; Page, 1993: vertical transfer) than by coincidence of a number of unrelated dispersal events (horizontal transmission or transfer). It is an unanswered question, how many congruent distributions are needed to decide upon a common historical cause (Page, 1993: 83: "[...] raises the question of how much incongruence would force us to abandon the hypothesis of multiple lineages [i.c. vertical transfer] in favor of horizontal transfer [i.c. dispersal]."; Wiley, 1988: 288: "Where will vicariance analyses begin to breakdown when dispersal is common?"). Moreover, dispersal is not a random process. In view of ecological constraints and variation in dispersibility among species also dispersal can be expected to lead to patterns. Such patterns are ecologically rather than historically determined. Viewed in this light it seems that leaving ecology out of distributional considerations can only lead to incomplete conclusions. Unfortunately, the ecological information is not always sufficient and it may be difficult to discriminate between ecological and historical constraints.

As explained by Sober (1988) phylogenetic inference and biogeographic inference differ essentially in that the former is only concerned with vertical transmission (characters are only transmitted in a lineage, not between lineages), while in the latter both vertical and horizontal transmission are involved. As a consequence comparing phylogenetic hypotheses involves "counting how many instances of a single kind of event each requires" (and choosing the most parsimonious one), while competing biogeographic hypotheses "disagree about the *kinds* of process involved." (emphasis in original); (Sober, 1988: 250).

Bearing this in mind we try to unravel the distributional history of the Hesperiidae in the Philippines in this chapter. Unfortunately, the phylogeny of the Hesperiidae is still poorly known. It is therefore not feasible to examine possible links between speciation events which have led to the origin of endemic species, and geo-

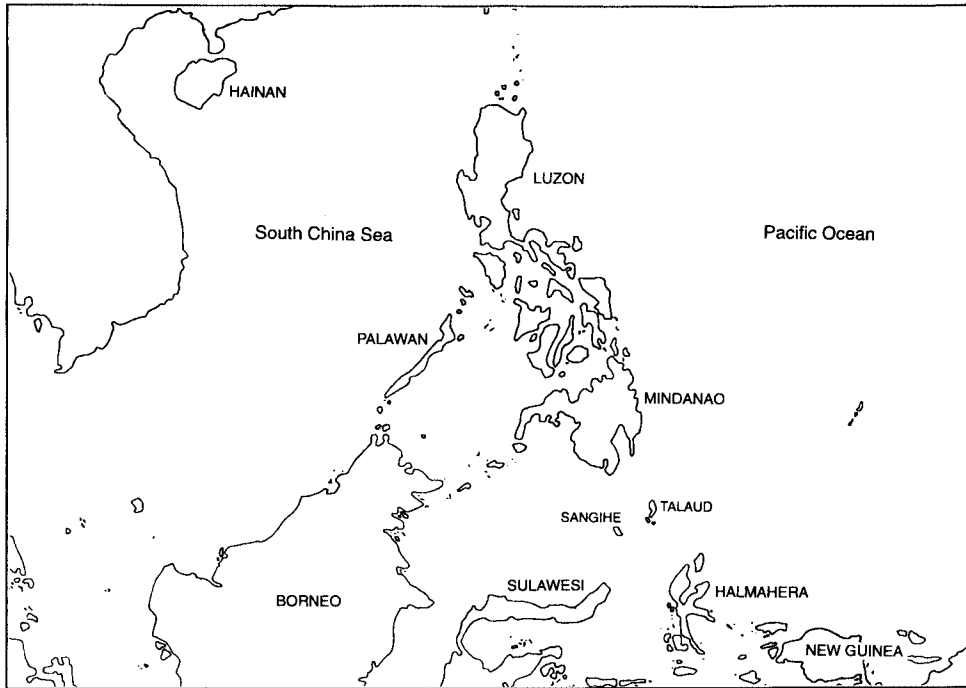


Fig. 127. Present position of the Philippines in relation to other islands.

logical events by the methods of cladistic biogeography, since the latter only recognizes distribution patterns based on the phylogenetic trees of a number of groups of organisms (as summarized in area cladograms). This leads to the recognition of a hierarchical pattern of area relationships, enabling comparison with historical (particularly geological) events from widely diverging periods. Recognizing the strength of the method, we feel it as a hindrance that the phylogeny of the Hesperiidæ is so poorly known. On the other hand, we are convinced that area cladograms are not the only meaningful distribution patterns in a historical-biogeographic context. Without further dwelling on relative merits of methods, we take a different approach from cladistic biogeography here. Instead of inferring common causes from congruent patterns (leading to a paleogeographic, and not to a biogeographic hypothesis, eventually to be compared with geological or other evidence), we start from (supposed) geological events, which must have had a bearing on the distribution of all terrestrial life, and examine if these events are retraceable in the distribution of the Hesperiidæ. We do this by comparing hypothesized distribution patterns derived from (known or supposed) geological events, with patterns actually found. Congruence is taken as evidence in favour of a causal connection. If a predicted pattern is not found in reality, it is concluded that the Hesperiidæ do not bear evidence of the process on which the predicted pattern was based, and dispersal rather than a geological event is taken as the plausible cause. Crucial to this approach is that the predicted patterns cannot plausibly have arisen in more than one way. This approach is not new. Eldredge (1981: 36), for instance, was very outspoken about it: "There is no other way, as I see it, to improve our theories of process, be they evolutionary or biogeographical." And is it

not process we are ultimately interested in?

Since among the patterns to be expected there are also patterns of relative relationship between species (as expressed in a cladogram), such information is also important here. All information available will be used and as long as we have no reasons for doubt, we shall start from the monophyly of the genera recognized (which, like a phylogenetic tree, is in fact a hypothesis to be tested in future).

Most of the terrestrial vertebrates of the Philippines have received more or less recent attention with regard to their distributional history (e.g. Brown & Alcala, 1970; Diamond & Gilpin, 1983; Dickinson, 1991; Heaney, 1986; Inger, 1954). Vertebrates are less well dealt with. Although already Semper (1892) divided the Philippines into six faunal regions ("Bezirke") based on the distribution of the butterflies, this butterfly distribution was only discussed almost a century later in relation to surrounding areas by Vane-Wright (1990).

### Paleogeography of the Philippines

The following account of the geological history of the Philippines is a compilation and summary of recently published reports: Audley-Charles & Harris (1991), Daly et al. (1991), Fuller et al. (1983), Metcalfe (1988, 1991), Mitchell et al. (1986), Moore & Silver (1983), Rangin et al. (1990a, 1990b), Taylor & Hayes (1980, 1983), and Wolfe (1983). Summaries can also be found in Dickinson (1991) and Heaney (1986). Some of the information is conflicting, but we shall try to give a coherent and consistent picture.

The Philippines in their present form (fig. 127) are the result of interactions of continental and oceanic plates, rifting of continental margins, and collisions of island arcs inter se and with continental fragments. Details are often a matter of conjecture, and there may be even widely diverging views with regard to the age and former position of the islands as a whole. For instance, Audley-Charles (1981, fig. 4.12) depicts the Philippines at 200 Ma (million years ago) in a more northern position than at present, and about in the present position at 60 Ma with a widening South China Sea, whereas in other reconstructions spreading in the South China Sea occurred from 32 Ma to 17 Ma, and whatever existed of the proto-Philippines before that time was located far to the southeast. Similarly, Halmahera is seen either as part of an island arc related to Talaud and E Mindanao (e.g. Moore & Silver, 1983) or as an island arc terrane originating from much further east and only much later getting involved in the Talaud-E Mindanao Arc by collisions (Daly et al., 1991). In spite of such divergences of opinion a general picture emerges that can be described as follows.

*Paleocene to late Eocene (Pre-42 Ma).* The margin of proto-China started to rift in the latest Cretaceous or Paleocene (about 65 Ma) (Taylor & Hayes, 1983). By interaction of the Pacific plate, the north-moving Australian plate and the Eurasian plate two intra-oceanic arc systems, the E Mindanao Arc (with extension to the southeast) and the W Mindanao Arc (with southward continuation in the Sangihe Arc), active since the Cretaceous, started to move towards each other, at least in their northern



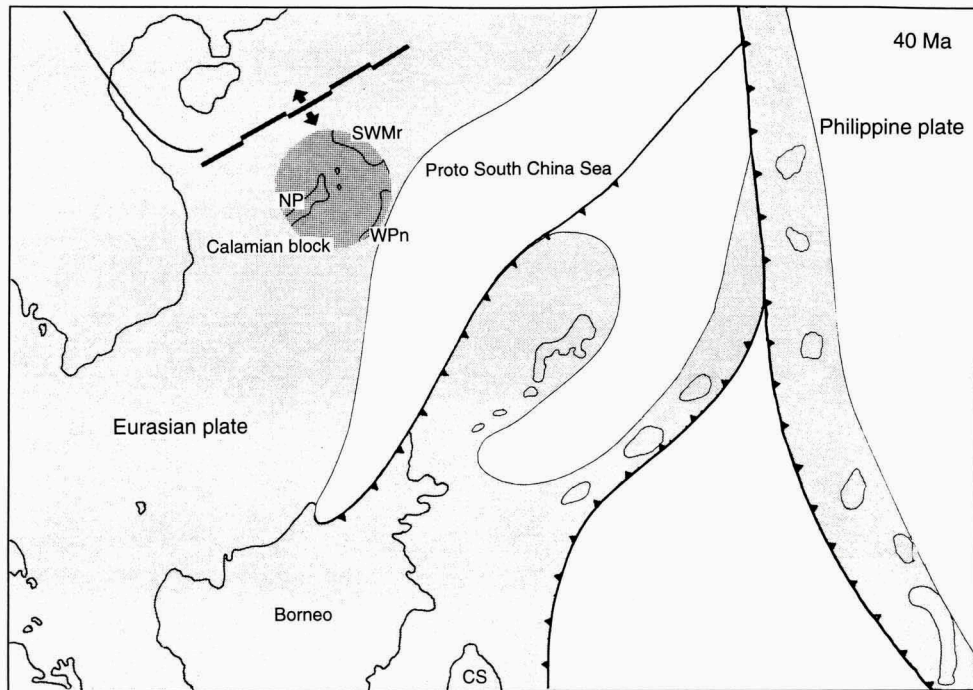


Fig. 128. Evolution of the Philippines, 40 million years ago. CS = Central Sulawesi, NP = North Palawan, SWMr = Southwest Mindoro, WPn = West Panay. Coast lines are only given to facilitate location. Mainly after Daly e.a. (1991), Mitchell e.a. (1986), and Rangin e.a. (1990a, 1990b).

part. There is some uncertainty in the literature about the eastern arc. It was an east-facing arc system associated with a westward subduction zone. Apparently later it was replaced or topped by a west-facing arc system (Halmahera Arc, see below), while the subduction zone flipped to an eastward direction. An east-facing island arc has also been inferred in eastern Luzon from Cretaceous and Paleogene volcanics and pyroclastics (Hamburger et al., 1983). It is obscure if this arc belonged to the same system, but it seems plausible that they were both associated with the moving edge of the Philippine plate.

*Late Eocene (42 Ma)* (fig. 128). The Philippine plate, entirely consisting of oceanic crust, broke off the Pacific plate and started a life of its own. It rotated clockwise and moved northwest over a distance of more than 2000 km at a rate of 4-10 cm/yr, subducting under the Eurasian plate along the Philippine trench. The latter is still recognizable as the Philippine fault, a line running roughly from Central Luzon through the Visayas and East Mindanao southward (there are other trenches to the east and to the west of the Philippines now). As a result island arc systems arose along its southern and western edge (probably incorporating existing arcs), and it does not seem unlikely (though there is no geological evidence) that a more or less continuous arc of islands (perhaps of varying composition) existed over a long period from the Asian mainland to proto-New Guinea. Some authors (Daly et al., 1991) suggest that

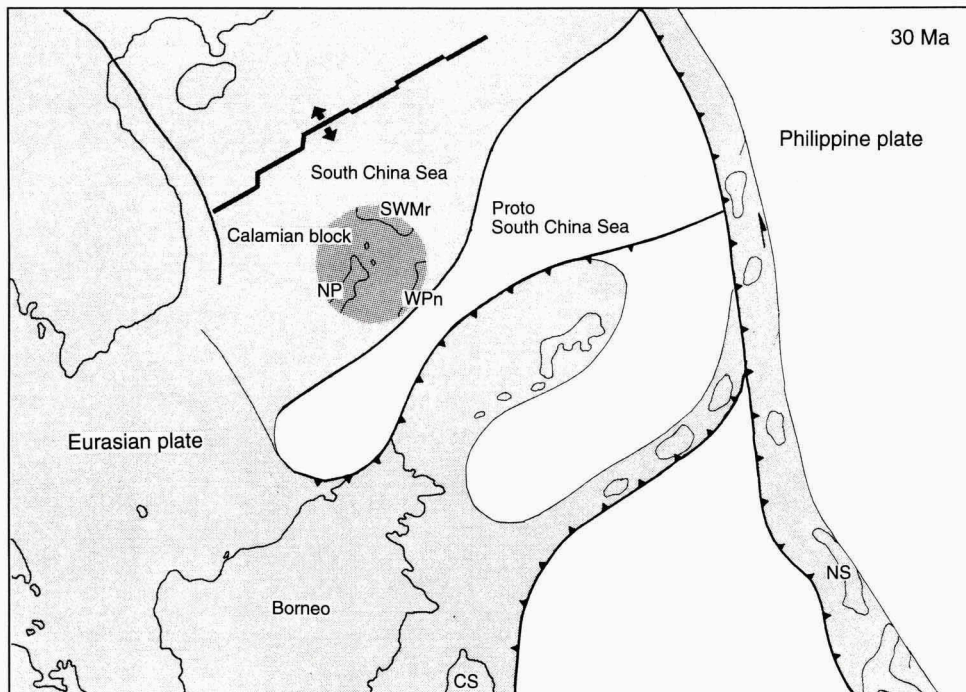


Fig. 129. Evolution of the Philippines, 30 million years ago. NS = North Sulawesi. See further legend of fig. 128.

N Sulawesi was part of the same system, others (Rangin, 1990b) postulate a relation with the Zambales of W Luzon. Apparently the origin and early life of N Sulawesi is very obscure.

*Oligocene (25-35 Ma)* (fig. 129). Following the rifting of the proto-China margin sea floor spreading started at 32 Ma in the South China Sea pushing continental fragments southward. One of these fragments, possibly forming a single block, the Calamian block (Fuller e.a., 1983), comprised N Palawan, the Calamian islands and southwestern Mindoro (and possibly pieces of other islands as well, for instance Panay). It broke off from the margin southwest of the present position of Taiwan. East of this south drifting block the northwest moving Philippine plate disappeared under the Eurasian plate. The fate of the island arc associated with the subduction zone is not clear. Perhaps it partly slipped along the Eurasian edge, and partly disappeared under it. The drift of the Calamian block towards the subduction zone to the south of the South China Sea caused uplift in the northern extension of the Borneo block (C and S Palawan). Meanwhile the collision of the E Mindanao Arc with the W Mindanao Arc went on, but the former lost momentum and finally became inactive. The W Mindanao/Sangihe Arc remained active through the Quaternary.

*Miocene (5-25 Ma)* (figs. 130, 131). N Palawan collided with the subduction zone to the south of the South China Sea at 17 Ma and stopped subduction in this area. N Palawan joined C and S Palawan (along the Ulugan fault). Uplift still went on until

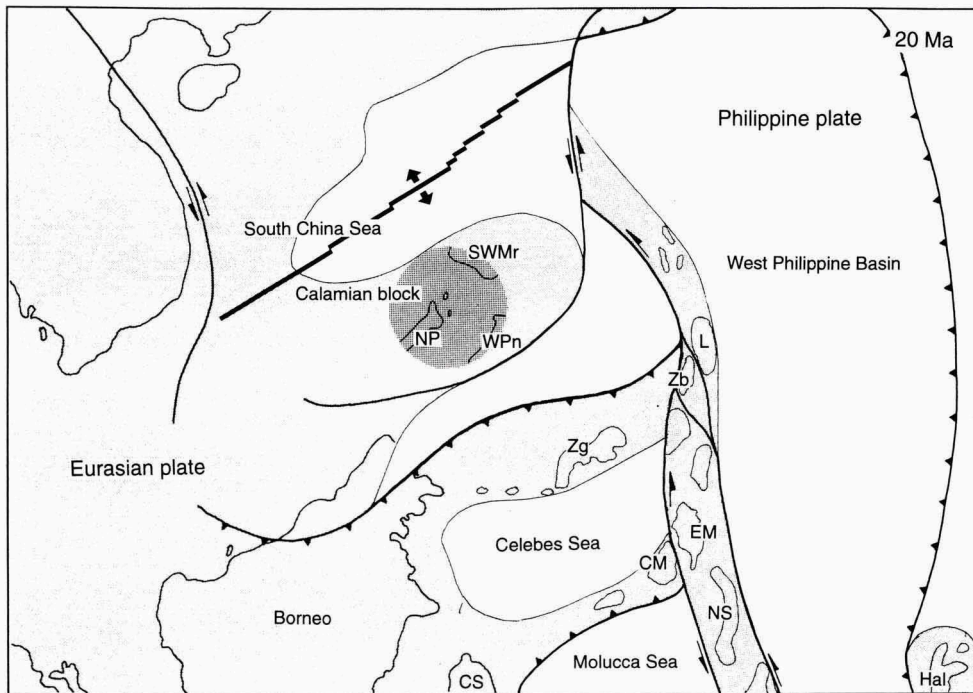


Fig. 130. Evolution of the Philippines, 20 million years ago. CM = Central Mindanao, EM = East Mindanao, Hal = Halmahera, L = Luzon, Zb = Zambales, Zg = Zamboanga. See further legends of figs. 128 and 129.

12 Ma. Apparently a new arc system moved in from the east, but details are very uncertain. It may have been an arc terrane originated north of proto-New Guinea, that carried among others proto-Halmahera (Daly et al., 1991: 17: "possibly an oceanic plateau or other shallow marine feature"), and drifted west with the clockwise rotation of the Philippine plate (see e.g. Rangin et al., 1990b). It collided with the westward subduction zone with which the E Mindanao Arc was associated. The subduction zone flipped to an eastward direction and the Halmahera Arc, which now replaced or included the E Mindanao Arc, became a west-facing arc system. The sea between the western Sangihe Arc and the eastern Halmahera Arc is called the Molucca Sea. The collision of what we shall now call the Halmahera Arc with the Mindanao/Sangihe Arc in the north was completed by the end of the Miocene, but further south the Halmahera Arc kept moving in (until the present).

In the late Miocene (10 Ma) the northern part of the Philippine arc, the Luzon arc terrane, began to collide with N Palawan and, continuing its motion to the north, finally collided with Taiwan. As a consequence of the collision of the Philippine arc with N Palawan the Cagayan ridge was formed by uplift in the Sulu Sea, and subduction took place to the south below the Sulu arc. The origin and history of the latter arc is not clear in the literature, but apparently it existed in the late Miocene. It was mainly built on a metamorphic basement. The Zamboanga peninsula of Mindanao belongs to this arc.

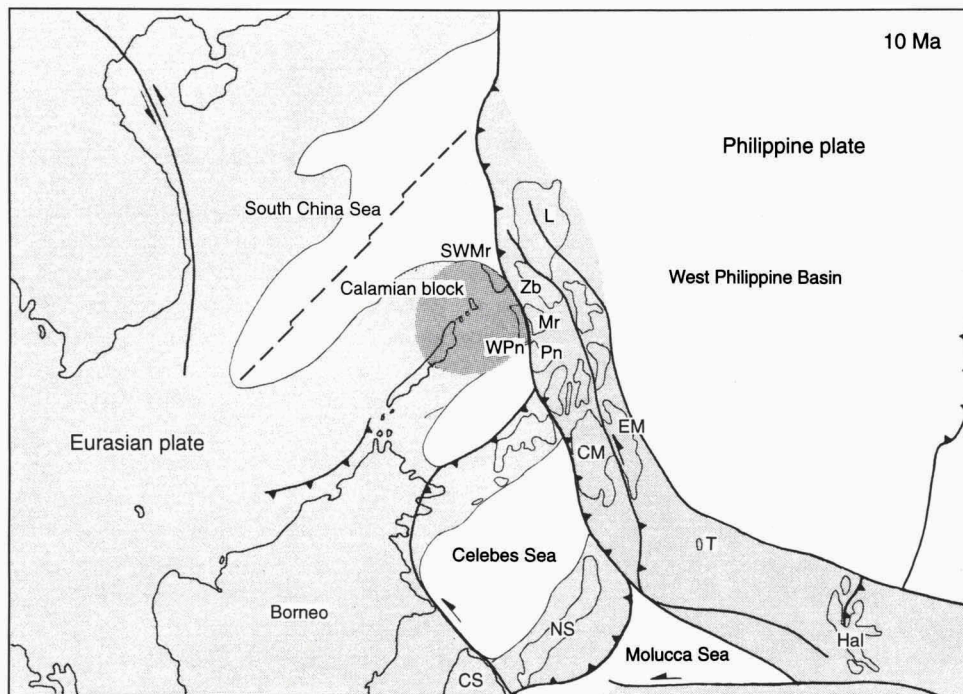


Fig. 131. Evolution of the Philippines, 10 million years ago. Mr = Mindoro, Pn = Panay, T = Talaud. See further legends of figs. 128-130.

*Pliocene (2-5 Ma).* Morris et al. (1983) suggest that the width of the Molucca Sea, now about 250 km, was still 1000-1500 km in the mid-Pliocene (3 Ma). This is practically impossible, since it would imply a rate of at least 25 cm/yr. Daley et al. (1991, fig. 15) depict Halmahera in the Pliocene north of the Vogelkop peninsula (west New Guinea), some 500 km east of its present position. Supposing this was at 5 Ma, it means a rate of 10 cm/yr. This seems a more realistic figure. The westward progression of Halmahera was the result of the west-facing Philippine trench flipping to be east-facing at 5 Ma.

*Quaternary (2 Ma - present time).* The Philippine archipelago had reached its present position by this time. During their whole history the shape of the islands changed, not only by drift but also by uplift, volcanism and sedimentation. Luzon, e.g., although having parts which are at least some 30 million years old, only became a single large island by the late Pliocene. Volcanism is still active in various parts of the Philippines, indicating that the area is not at rest.

The lowering of the sea level during the Pleistocene Ice Ages changed considerably the configuration of land and sea in the area. In the late Pleistocene, some 18,000 years ago, this lowering was about 120 m. As a result many islands were united into larger islands. Although the water gaps between Borneo and the Philippines became narrower, they still existed. The channel between Palawan and Borneo is 145 m deep. Many of the islands of the Sulu Archipelago were united, but at least in the western

part there remained a water gap between Sibutu and Sanga Sanga/Bongao (Sibutu Passage) where the sea is more than 200 m deep. Sibutu itself, however, separated from Borneo by the relatively shallow Alice Channel (not more than 100 m deep), must have been joined to Borneo several times. There also remained water gaps between the Palawan chain and the rest of the Philippines, and between Jolo (central Sulu Archipelago) and Mindanao/Basilan. In the late middle Pleistocene, about 160,000 years ago, the sea level was 160-180 m below present. If the sea depths were the same as at present (this is uncertain since the area has been in motion all the time) it would have united Palawan with Borneo, but still not Mindanao with Borneo through the Sulu Archipelago. There would also still have existed a wide gap between larger-Palawan and the rest of the Philippines (see also the discussion below, on faunal regions).

*Summary of paleogeography.* The Philippine archipelago is a geologically complex and composite area that originated by accretion of oceanic material to drifted fragments of the Eurasian landmass over most of the Tertiary. The continental fragments are restricted to the western part of the archipelago. By far the greater part of the islands emerged from the sea and never formed part of a landmass.

#### Distribution patterns to be expected

Crucial to the evaluation of the geological history outlined above as the underlying factor for the distribution of life across the Philippines, is the question whether and to which degree there was dry land in the area. The presence of Eocene rocks in Luzon, for instance, does not imply that there was any land above sea level in the Luzon area during the Eocene. Since this kind of information is not always evident from the literature, we take a conservative stand in the sense that, if it is not clear from the literature, we suppose that in an island arc or a drifting continental block there was enough dry land to support a terrestrial biota, unless there is evidence to the contrary. From this position we deduce the following expected distribution patterns.

*Philippines—continental Asia.* This pattern is deduced from the continental origin of the N Palawan/SW Mindoro region. If these areas were emerged throughout their life, they could have carried a terrestrial fauna. During the long isolation of more than 30 million years taxonomic divergence can be expected to have taken place, leading to a sister group relationship between taxa of the Philippines and continental Asia. If such a relationship is found and one of the two sister taxa also occurs in Borneo or Taiwan, we cannot be sure that the pattern did not arise by dispersal through Borneo or Taiwan. Therefore only patterns involving sister taxa exclusively occurring in the Philippines and continental Asia will be considered support for origin by rifting of blocks from the margin of the Eurasian continent.

It may be questionable if such a pattern, if it ever existed, would not have been completely obscured by later dispersal and extinction. Support from other animal groups is so scarce that we can hardly call it a pattern. There is one mammal, the tamaraw (*Bubalus mindorensis* Heude, 1888), a small buffalo endemic to Mindoro.



According to Nowak (1991) this species forms the subgenus *Bubalus*, together with the Asian water buffalo, *B. bubalis* (Linnaeus, 1758), which originally occurred at least from Nepal to Vietnam and Malaysia. If subgenus *Bubalus* Frisch, 1775, is monophyletic, this case could, indeed, be indicative for a Philippines-Continent pattern. However, the genus, as conceived by Nowak (1991), has one other subgenus, *Anoa* Smith, 1827, with two (or maybe only one) endemic species in Sulawesi. Without further information about the phylogenetic relationships between these taxa even this very simple case remains uninformative. Further, there is one amphibian, *Barbourula busuangensis* Taylor & Noble, 1924, endemic to Busuanga Island (Calamian group), which belongs to the small family Discoglossidae (eight species in all), that is distributed in the West Palaearctic with three genera, of which one, *Bombina* Okem, 1816, also occurs in the East Palaearctic from Manchuria to SW China and Tonkin (Inger, 1954; Darlington, 1957). It seems unlikely that, if these continental blocks carried a terrestrial fauna, only one mammal and one amphibian survived. Either these blocks did not transport a terrestrial fauna, or the traces have been lost by extinction and dispersal. The fossils are not much of a help here: no pre-Pleistocene vertebrate fossils seem to be known from the Philippines (de Vos, pers. comm.).

Finally, in the butterflies there is the case of *Athyma perius* (Linnaeus, 1758). This species is widespread in the Oriental Region, but absent from Borneo and the Philippines, except for Busuanga Island, where it occurs in the mainland form. Its absence from Borneo is not suggestive of a southern origin in the Philippines. Similarly, its absence from Luzon makes a northern origin (from Taiwan, where it also occurs in the mainland form) improbable. On the other hand, it seems equally unlikely that a small island population, isolated for over 30 million years, remained undifferentiated, while the species differentiated into a number of subspecies in Sumatra, Java and the Lesser Sunda Islands. Long distance dispersal or extinction over large areas seems a more plausible explanation.

Nevertheless we shall check this pattern among the HesperIIDae. If not found we shall hypothesize that all similarity between the hesperiid faunas of continental Asia and the Philippines is due to dispersal, either through Borneo or through Taiwan, until new evidence turns up.

*Philippines—N Moluccas/Papuasia.* Although island arcs moved through the area south and east of the present Philippines, details are so vague that it is difficult to deduce expectations about pattern(s) from them. Fossil evidence has shown that, since the Miocene, some reptiles and mammals of Asian origin reached Australia (Heatwole, 1987; Rage, 1988). Probably a large part of the Australian fauna and the greater part of the Papuasian fauna is of (ultimately) Oriental origin, but fossil or phylogenetic evidence is scarce. De Jong (1990) showed that for some genera of HesperIIDae there is phylogenetic evidence of migration to Australia with secondary radiation there. The question arises how this migration was possible in the absence of a continuous land connection. One possible route could have been by island hopping through the island arcs, which in the Tertiary stretched from the Asian mainland through the (present) Philippines, N Moluccas to N New Guinea and further east (Luzon arc, Halmahera arc, Outer Melanesian arc). Clearly, if such a route existed, it could, in principle, have been used in both directions. Evidence of the existence of this route in the form of taxa restricted to (parts of) this area (maybe also occurring

in Australia) is found, for instance, in mammals (Musser, 1981; Groves, 1984), birds (Dickinson, 1991), amphibia (Inger, 1954), and cicadas (Duffels, 1986). Only in the latter case the evidence is supported by a phylogenetic analysis.

It can be argued that, in case N Sulawesi originated from the same arc systems, Sulawesi could also be included in this pattern. This is, however, very uncertain and would complicate the pattern considerably. We shall not further expatiate on this pattern, since it is of minor importance in the Hesperiidæ (it may become more important if phylogenetic information is more extensive).

If and insofar the islands of the Philippines did not carry a fauna from some other place, they must have received it by jump dispersal across water barriers. Possible source areas are all lands and islands around the Philippines, with the following gateways:

- through Taiwan, the Batan Islands and the Babuyan Islands;
- from Borneo through Balabac, Palawan and the Calamian group to Mindoro;
- from Borneo through the Sulu archipelago to W Mindanao;
- from NE Sulawesi through the Sangihe archipelago to S Mindanao;
- from Halmahera through the Talaud archipelago to S Mindanao.

The exclusive occurrence of a taxon in the Philippines and one of the possible "source" area is taken as evidence of the use of this particular gateway, irrespective of the direction in which it was traversed.

*Taiwan connection.* Taiwan lies on the continental shelf. The shortest distance to mainland China is about 140 km. Although this is a wide gap, the sea is not deeper than 100 m here and even less than 50 m over much of the distance. As a consequence the lowering of the sea level during the Pleistocene Ice Ages connected Taiwan to the mainland. The distance from Taiwan to Luzon is about 350 km. The sea is much deeper here and even a lowering of the sea level of 200 m would leave water gaps of up to 80 km. Two groups of islands, the Batan Islands and the Babuyan Islands, lie as stepping stones between Taiwan and Luzon.

There is no geological evidence for Luzon ever having been closer to Taiwan than at present, to the contrary it is supposed to have come from far away. If a taxon occurs in Taiwan and the Philippines, it either crossed the water barrier between Taiwan and Luzon, or it came to Taiwan from the mainland and to the Philippines from Borneo (see below for the Borneo connection).

*Palawan connection.* The northern part of Palawan originated from continental Asia, the central and southern part is an uplifted part of the northern edge of Borneo. The island can have received its fauna in several ways: by rafting from the continental edge, from Borneo by jump dispersal over the Balabac Strait, from Borneo through a dried up Balabac Strait, or by jump dispersal from other Philippine islands. The continental connection was described above. Here we are only interested in the connection between the Philippines and Borneo through Palawan. Only taxa occurring in Borneo and Palawan and possibly other Philippine islands, but not in Mindanao, will be considered support to the hypothesis that use was made of this gateway. The question arises if and how we can distinguish between jump dispersal and dispersal over land. Even when the connection was dry land, it was narrow relative to the size of Borneo, and certainly to the size of the Sunda shelf that had com-

pletely fallen dry. Moreover, it was flat, low-lying country. Consequently, it was not freely accessible to all of Borneo's fauna: it must have acted as a filter, just as the sea channel acted as a filter, albeit a stronger one. It seems, therefore, unlikely that we shall ever be able to differentiate between species that jumped and those that made use of the land connection, except for "very early jumpers". Palawan has been sub-aerial and in the same position relative to Borneo for at least 17 million years. It would be highly unlikely that the island remained devoid of butterflies until a dry land connection with Borneo was established about 160,000 years ago. Thus we can expect to find species in Palawan that show different degrees of divergence from the original Bornean stock, from taxonomically indistinguishable populations to highly distinctive species. It is conceivable that (part of) the endemic Philippine species originate from the earliest immigrants in Palawan. Given the long time elapsed, immigrants may have spread all over the Philippines, including Mindanao, obscuring their geographic origin. In that case we shall underestimate the importance of the Palawan connection.

In summary, support for the existence of a connection through Palawan will be found if species or higher taxa are found in Borneo and Palawan, and possibly other Philippine islands except Mindanao, and the supposed age of the connection will be supported if alleged Bornean immigrants show a wide range of divergence from the Bornean roots.

*Sulu connection.* If the present sea depths between the islands also existed in the Pleistocene, then there have always been water gaps between Borneo (or at least Sibu) and the Philippines. These gaps and the narrowness of the Sulu connection must have acted as a pretty strong filter. Since the island chain is much younger than Palawan, maybe not older than some 5 million years, a less wide range of divergence from the parental Bornean stock is expected here than in Palawan. We shall consider the occurrence of a taxon in Borneo and Mindanao, and possibly other Philippine islands, but not in Palawan, as support for the hypothesis that this gateway was used.

*Sangihe connection.* The northeastern tip of Sulawesi and the southernmost tip of Mindanao are about 430 km apart. In between are a number of islands, the Sangihe Archipelago and the Kawio Archipelago. Even a lowering of the sea level of 200 m would, under the present conditions of positions of islands and sea depths, leave a number of water gaps ranging from 40 to 70 km. Not an easy passage for terrestrial organisms.

We shall only take those distributions as evidence for the use of this connection, in which a taxon occurs in Mindanao (and maybe other islands of the Philippines) and Sulawesi (and possibly other islands further east), but not in Borneo.

*Talau connection.* This pattern is not essentially different from the one described under Philippines—N Moluccas/Papuasia, but is more restrictive in time and direction. By this pattern we only try to examine if the Philippines can have received species from Halmahera. Supposing that Halmahera reached its present position only recently and that it was still some 500 km to the east at the beginning of the Pliocene (5 Ma), it has never been closer to the Philippines than at present, although there may have been a more extensive island chain. Being oceanic, Halmahera must,



in its turn, have received its fauna from elsewhere. The only plausible source seems to be New Guinea (how it came there, is not our concern here). We shall only take those distributions as evidence for the use of this connection, in which a taxon occurs in Mindanao (and maybe other islands of the Philippines) and Halmahera with a root (as evidenced by the phylogeny) in New Guinea.

The distance between Mindanao and Halmahera is even larger than between the former island and Sulawesi, viz. about 480 km. Almost midway lies the Talaud archipelago. The seas around the archipelago are deep. Even a drop in sea level of 200 m would leave water gaps of 150 km wide between Mindanao and Halmahera.

*Intra-Philippine patterns.* The pattern to be expected within the Philippines is related to the repeated changes of sea level during the Pleistocene, uniting and separating islands. Following present-day isobaths we can visualize various combinations of islands into larger blocks according to the supposed drop of sea level. Since the terrestrial fauna could move around dry-shod through these blocks, the faunas of the islands making up a block can be expected to be more similar inter se than to islands from other blocks. At the same time, the forming of more extensive land areas and the narrowing of sea channels must have contributed to an increased uniformity of the fauna also between the islands blocks. Regional differences, on the other hand, caused by speciation and local extinction, most probably originated at a time of maximum isolation, when the sea level was high. Best indicators for the former existence of larger island blocks are taxa that originated on an island of a block (at a time of maximum isolation) and could not (yet) spread beyond the confines of that block. It is hardly useful to put all taxa together, calculate a faunal similarity index and apply a cluster method, since the "power of resolution" is blurred by the widespread taxa. If the method gives any results, it is because of a high proportion of endemics. Thus it is better to focus on the endemics from the start.

The first students who subdivided the Philippines into a number of fauna regions were Steere (1890) and Semper (1892). They based their divisions on the distribution of birds and butterflies, respectively. The divisions were not only surprisingly congruent, but they even survived the tooth of time. Heaney (1986; mammals) and Vane-Wright (1990; butterflies) introduced a few refinements, but essentially the divisions remained the same. In fig. 132 we have reproduced Vane-Wright's biogeographic map which differs from Heaney's map in dividing the Mindanao region into the East Visayan subregion and the Mindanao subregion. Heaney (1986) found that the regions coincided with the extent of land during a fall of the sea level of 120 m in the late Pleistocene (about 18.000 years ago).

It is only a single step from characterizing a region by the distribution of endemic taxa to calling it an area of endemism (Vane-Wright, 1990). However, this could be misleading, since vicariant events leading to new taxa probably did not occur between regions (defined by late Pleistocene islands), but between islands like the present ones which belonged to the same region (if they did not, speciation did not follow a vicariant event but rather jump dispersal). As a consequence it is not to be expected that a hierarchical relationship will be found between the regions when they are used as areas of endemism in a cladistic-biogeographic study. This hypothesis can be tested if there are enough cladistic data available. Since such data are largely absent, at least for butterflies, it must be left to a future study.

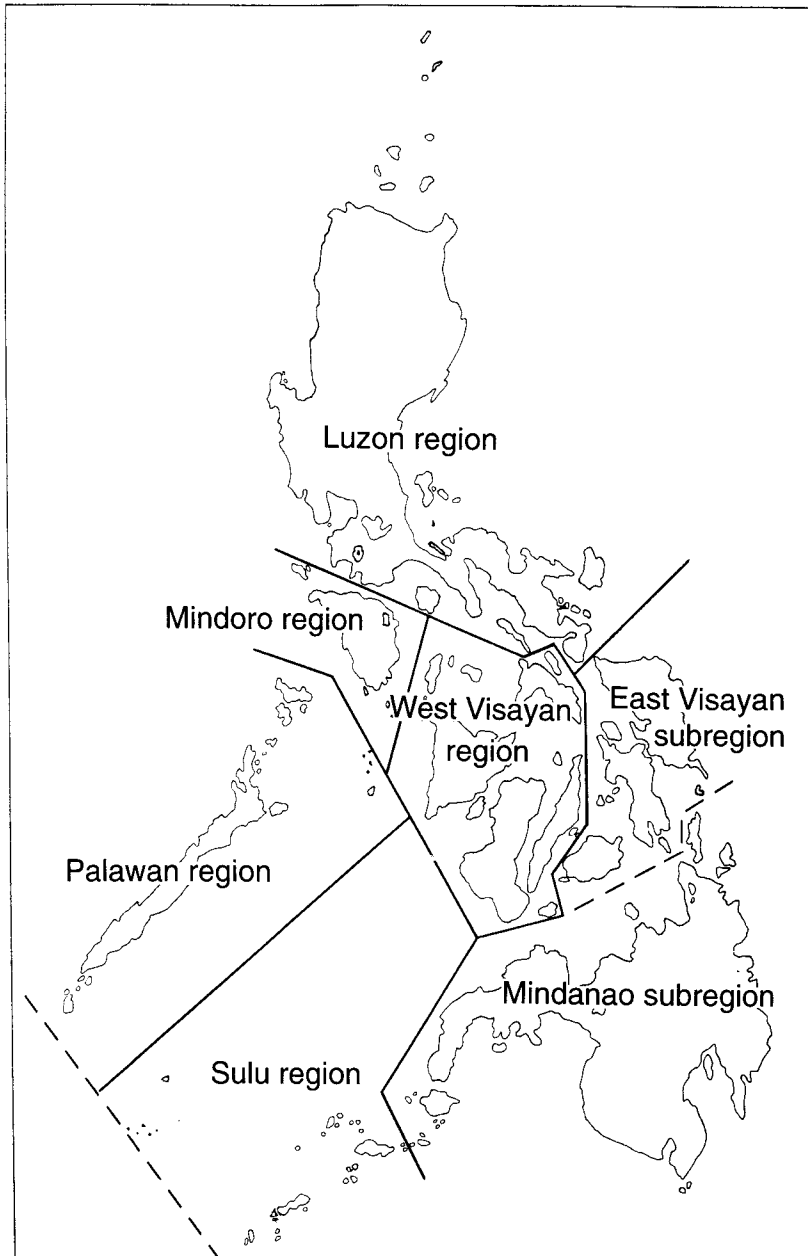


Fig. 132. Faunal regions as distinguished by Vane-Wright (1990), based on a consensus of faunal regionalization by several authors. The East Visayan and Mindanao subregions together constitute the Mindanao region. The Palawan region is considered part of the Greater Sundas. The Sulu region is an anomalous region or a subregion of Borneo or the Greater Sundas. Homonhon may be better included in the Mindanao subregion, and the position of the line through the Sulu Archipelago is debatable.

## Distribution patterns found in the Hesperidae

As basic data we use the distribution of species and subspecies. There are no endemic genera of Hesperidae in the Philippines. In only one other family of the Rhopalocera, viz., Lycaenidae Leach, 1815, endemic genera are recognized (*Poriskina* Druce, 1895, and *Matsutaroa* Hayashi, Schröder & Treadaway, 1984). For most of the Hesperidae the phylogeny is still unknown, but wherever phylogenetic data are available and relevant they are used.

Comparative distributional data for Borneo have been taken from Maruyama (1991), for Taiwan from Chiba et al. (1992) and Shirôzu (1960), and for Sulawesi from Vane-Wright et al. (in prep.). General data mainly originate from Evans (1949).

*Philippines-continental Asia*

In view of the long time of isolation of the continental "rafts" it can be safely supposed that, if species came to the Philippines in this way, they are now specifically distinct from their Asian ancestors. Thus we should look for species among the Philippine endemics that have a sister species on the continent. Since the phylogeny of the Philippine Hesperidae (and of any other animal group, for that matter) is badly known, the first step we take is to examine if there are genera occurring in the Philippines and the continent, but not in Borneo, Sulawesi or the Moluccas. Two such genera exist (table 2), viz. *Thoessa* and *Aeromachus*.

*Thoessa* has a single species in the Philippines: *T. justini*, endemic to N Luzon. The genus counts 17 further species on the Asian mainland, one in Japan and the Kurile islands and one in Taiwan. Without knowing the relationship between *T. justini* and the Taiwanese *T. horishama* (Matsumura, 1910), it still seems more likely that *T. justini* originated from a colonization from the north, than that its ancestor was brought to the Philippines on a sliver of continental crust, finally reached N Luzon and became extinct elsewhere. See further under the Taiwan connection.

The situation in *Aeromachus* is different. The genus is distributed from India to Japan and through Sundaland to Java, but surprisingly absent from Borneo. There is no evidence for a closer relationship of the two endemic Philippine species with a strictly continental-Asian species than with one of the three species found in Sundaland, and a clue to the geographic relationship of the Philippine endemics is missing so far.

Checking the 19 other genera with endemic species in the Philippines (table 2), it turns out that all have representatives in Borneo. Most have one or two species restricted to the continent. Only a phylogenetic analysis can elucidate the relationships, but prospects of evidence of a distribution pattern due to rifting of the continental rim seem poor.

*Philippines-Moluccas-New Guinea*

There is no genus of the Hesperidae restricted to this area. The only genus suggestive of an eastern origin because of its absence from the Asian continent, is

Table 2. Distribution of genera of Philippine HesperIIDae over selected areas (distribution may be more extensive). A = Asia mainland, B = Borneo, C = Sulawesi, M = Moluccas, N = New Guinea. Genera with an asterisk contain one or more endemic species in the Philippines.

<i>Bibasis</i>	ABC	<i>Isma</i>	AB
* <i>Hasora</i>	ABCMN	* <i>Pyronaura</i>	ABC
<i>Badamia</i>	ABCMN	* <i>Plastingia</i>	ABC
* <i>Choaspes</i>	ABCMN	<i>Salanoemia</i>	ABC
* <i>Celaenorrhinus</i>	ABCM	* <i>Xanthoneura</i>	ABC
<i>Tapena</i>	AB	<i>Lotongus</i>	ABC
<i>Darpa</i>	AB	<i>Zela</i>	AB
<i>Odina</i>	ABC	<i>Gangara</i>	ABC
* <i>Coladenia</i>	ABC	* <i>Erionota</i>	ABCM
* <i>Gerosis</i>	ABC	<i>Matapa</i>	ABC
<i>Tagiades</i>	ABCMN	<i>Unkana</i>	ABC
* <i>Mooreana</i>	AB	<i>Hidari</i>	AB
* <i>Odontoptilum</i>	ABC	<i>Acerbas</i>	ABC
* <i>Aeromachus</i>	A	* <i>Pirdana</i>	ABC
* <i>Thoressa</i>	A	<i>Taractrocera</i>	ABCN
* <i>Halpe</i>	ABC	* <i>Oriens</i>	ABC
<i>Koruthaialos</i>	AB	* <i>Potanthus</i>	ABCM
<i>Psolos</i>	ABC	<i>Telicota</i>	ABCMN
<i>Ancistroides</i>	ABC	<i>Cephrenes</i>	ABCMN
* <i>Notocrypta</i>	ABCMN	<i>Prusiana</i>	BCM
* <i>Suada</i>	AB	<i>Parnara</i>	ABCMN
* <i>Suastus</i>	AB	<i>Borbo</i>	ABCMN
<i>Cupitha</i>	ABC	<i>Pelopidas</i>	ABCMN
* <i>Zographetus</i>	ABC	<i>Polytremis</i>	ABC
<i>Oerane</i>	AB	<i>Baoris</i>	AB
<i>Hyarotis</i>	AB	<i>Caltoris</i>	AB
<i>Quedara</i>	AB		

*Prusiana*, but this genus has no endemic species in the Philippines. It is also found in Sulawesi and Borneo, and it does not occur east of the Moluccas. The 14 other genera with representatives in the Moluccas and New Guinea (table 2) have very wide distributions, including the Asian mainland and often Australia as well. Although this does not exclude the possibility of an Australian origin (de Jong, 1990), such wide distributions point to active dispersal and not to rafting.

Only in the genera *Hasora*, *Choaspes*, and *Notocrypta* there are endemic species both in the Philippines and in the Moluccas and/or New Guinea, and these are thus the only cases in which a sister group relationship between the two areas can be hoped for. A very poor prospect indeed. On the basis of phylogenetic considerations, the genera *Taractrocera* and *Cephrenes* are supposed to have radiated in New Guinea / Australia with a secondary migration to the west. The Philippine representatives of these genera have wide distributions, also covering at least Sulawesi and the greater part of Sundaland, and although their distribution does not contradict it, there is no reason to suppose that the distribution of these genera originated from the use of a Tertiary island arc from the Philippines to New Guinea.

#### *The Taiwan connection*

As can be seen from table 3, 28.1% of the species of HesperIIDae in Taiwan (18 of

Table 3. Number of species per area and of species shared between A and B (left), and percentages of species of A occurring in B (right).

A \ B	Philippines	Taiwan	Borneo	Sulawesi	A \ B	Philippines	Taiwan	Borneo	Sulawesi
Philippines	152	18	105	47	Philippines	100	11.8	69.1	30.9
Taiwan	18	64	19	17	Taiwan	28.1	100	29.7	26.6
Borneo	105	19	214	41	Borneo	49.1	8.9	100	19.2
Sulawesi	47	17	41	85	Sulawesi	55.3	20	48.2	100

the 64) also occur in the Philippines. This is a very high proportion in view of the large barrier between the two areas. However, 14 of the shared species also occur in Borneo and they could quite well have reached the Philippines from Borneo, and Taiwan from the mainland. Before studying these 14 species in more detail we shall check the four remaining species for which the crossing of the water barrier seems probable in view of their absence from Borneo.

Of the four species, two occur in Sulawesi as well. They are *Potanthus pava* and *Telicota colon*. The first is a widespread species in mainland Asia, occurring from India to southern China and then re-appearing in a different geographic form (ssp. *lesbia*) in the Philippines and Sulawesi. It is absent from the whole of Sundaland. Thus it is likely that it crossed the water gap between Taiwan and Luzon. The genus *Potanthus* is with about 28 species widely distributed in the Oriental Region. Some species go as far east as Sulawesi, and one species reaches the Moluccas, but there are no endemics in Sulawesi or the Moluccas. Without knowing the sister species of *P. pava* the distribution of the genus makes it probable that the species crossed the water gap from Taiwan to Luzon and not vice versa. *T. colon* has a much wider distribution, throughout the Oriental Region, except Borneo, and eastwards to Australia and the Solomon Islands. Many subspecies are recognized. The subspecies occurring in Taiwan (*stinga*) is the same as in southeast mainland Asia, the one in the Philippines (*vaja*) is found from Sumatra to Sulawesi and Timor. It is, therefore, more likely that the Philippine population originated from the south, and the Taiwan population from the west than that there was a more direct connection between the two.

Two Philippine species are not found in Borneo or Sulawesi but do occur in Taiwan. They are *Erionota torus* and *Potanthus confucius*. Outside the Philippines and Taiwan the first species is restricted to the mainland. As discussed under this species, it could well be a recent introduction. For the widespread *P. confucius* the occurrence in the Philippines is rather doubtful. It is better to omit this species from biogeographic considerations as long as its occurrence has not been confirmed.

Of the 14 species occurring in the Philippines, Taiwan and Borneo (12 of these occur in Sulawesi as well) most are so widespread that it is quite possible that they reached Taiwan and the Philippines from different sources. For six species this is indicated by the occurrence of the same subspecies or very similar subspecies in the Philippines and Borneo, and of a different form in Taiwan (the latter form either being

the same as on the mainland, or endemic to Taiwan). They are: *Hasora taminatus*, *Notocrypta feisthamelii*, *Telicota ohara*, *Pelopidas mathias*, *Polytremis lubricans*, and *Caltores bromus*. For these species it is most likely that they reached the Philippines from Borneo, and Taiwan from the mainland. Strictly speaking this is contestable, since the similarity between populations in Borneo and in the Philippines could be based on symplesiomorphy, but in the absence of further arguments we keep to our hypothesis that these species reached the Philippines from Borneo. (Following the same line of reasoning three species could also have reached the Philippines from Sulawesi, but see below, the Sangihe connection.)

Seven species occur over a very wide range without geographical variation. They are: *Hasora chromus*, *H. badra*, *Badamia exclamatoris*, *Parnara bada*, *Borbo cinnara*, *Pelopidas agna*, and *P. conjuncta*. In these cases it seems likely that they reached Taiwan and the Philippines from different sources, but there are no other arguments than the difference in accessibility to the Philippines in the north and south.

Finally, one species shows a different pattern: *Tagiades trebellius* has a very wide distribution from Borneo, Taiwan and the Philippines to the Solomon Islands. Since the species is completely absent from the Asiatic mainland, it must have reached Taiwan from Luzon. Evans (1949) doubted the reliability of the locality labels of two specimens from Taiwan in the Natural History Museum, London, but there is also a male in the Nationaal Natuurhistorisch Museum, Leiden, labeled as coming from that island and there is no reason for doubt here.

So far we have dealt with shared species only. We could, however, follow the same line of reasoning for higher taxa as well, i.e. the Philippine endemics and their sister species. The only problem is that virtually nothing is known of the phylogenetic relationships of the Philippine endemics. As discussed above (Origin by rafting from Asian mainland), all genera with endemic species in the Philippines also occur in Borneo (and thus it is possible that the sister species will be found in Borneo), except two. It was made plausible that *Thoressa justini* originated from a colonization from Taiwan. A similar situation is found in the Papilionidae: the endemic *Papilio benguetanus* Joicey & Talbot, 1923, of Luzon is either a subspecies of *P. xuthus* Linnaeus, 1760, or its sister species (Tsukada & Nishiyama, 1980; Collins & Morris, 1985). *P. xuthus* is found from N Burma through S China to Taiwan, Japan, Ogasawara-shoto (Bonin islands), Guam and Hawaii. *Papilio chikae* Igarashi, 1965, could be another example. It is only found high in the mountains of N Luzon (and possibly N Mindoro, since the recently described *Papilio hermeli* Nyuda, 1992, could as well be a subspecies of *P. chikae*). It belongs to the *paris* group of species, an assemblage of 12 species which are mainly distributed in eastern continental Asia. According to Tsukada & Nishiyama (1980) *P. chikae* forms a monophyletic group with *P. paris* Linnaeus, 1758, and *P. karna* Felder & Felder, 1864, the only other species of the group reaching the Southeast Asian islands, but a phylogenetic analysis of the group has not yet been given. Another papilionid butterfly species, *Papilio polytes* Linnaeus, 1758, exemplifies the difficult passage of the Taiwan connection. It is widely distributed in the Oriental Region and occurs in Taiwan and Borneo, but is absent from the Philippines except for the Batan Island, which is relatively close to Taiwan. In the Nymphalidae-Satyrinae *Zophoessa dataensis* Semper, 1887, is a striking example. The species is endemic to N Luzon and N Mindoro. The 27 other species of the genus are found in continental Asia, with three species occurring in Taiwan and one species reaching

Japan. The genus is not represented in Sundaland.

*Summary of the Taiwan connection.* There is evidence of two successful crossings of the water gap from Taiwan to Luzon, in one case leading to the evolution of an endemic Philippine species. If at the time of the crossing the Taiwan fauna had as many species as today, then 3.1% of the Taiwanese fauna of Hesperidae made a successful crossing. This is a more realistic figure than the 28.1% the shared species suggest at first glance. Only a single species succeeded in the reverse crossing. This is only 0.66% of the Philippine fauna, a neglectable quantity. Thus we come to the conclusion that the similarity between Taiwan and the Philippines at the species level is not due to frequent crossings of the water gap between Taiwan and Luzon but to immigration of the same species from different sources. Successful crossings do occur (or have occurred) but very rarely and twice as many times from Taiwan to Luzon as in the reverse direction (but numbers are not significant here, respectively being 2 and 1). Apart from chance a possible reason for this one-way traffic may be the course of the typhoons, which in this area come from the north. Ecological differences between Taiwan and Luzon may play an important, if not crucial role, but without knowing more of the ecology of the species concerned, it is pure speculation and, in view of the low numbers involved, irrelevant.

#### *The Palawan and Sulu connections*

The importance of the Borneo connection(s) for the fauna of the Philippines is clear from table 3: almost 70% of the species in the Philippines also occur in Borneo, and of the rich Borneo fauna almost half of the species occur in the Philippines. On the other hand, the latter figure also makes clear that over half of the Bornean species did not succeed in reaching the Philippines, in other words the connection had the character of a bottle-neck. (The number of successful colonizations from Borneo to the Philippines is undoubtedly underestimated, since part of the endemic species in the Philippines must be of Bornean origin.) Diamond & Gilpin (1983), studying the bird fauna of the Philippines, described the connection as an umbilicus (or rather as two umbilici, through Palawan and through the Sulu Archipelago).

Of the 104 species shared by the Philippines and Borneo, 62 do not occur in either Taiwan or Sulawesi, 10 are found in Taiwan and Sulawesi, 29 do not occur in Taiwan but are represented in Sulawesi, and 3 do not occur in Sulawesi, but are found in Taiwan. The Taiwanese species have been dealt with under the Taiwan connection. It was concluded there, that none of the species that were also found in Borneo came to the Philippines from Taiwan. Thus the three of them not occurring in Sulawesi (*Hasora chromus*, *Telicota ancilla*, *Pelopidas conjuncta*) must have come from Borneo. In 12 of the 39 species found in Borneo and Sulawesi the geographic variation shows a greater resemblance of the Philippine populations to those of Borneo (usually considered the same subspecies) than to those of Sulawesi, and for that reason it seems likely that the species reached the Philippines from Borneo, and not from Sulawesi. (The alternative would be that the species reached the Philippines from Sulawesi, differentiated there and subsequently invaded Borneo.) For the remaining 27 species no such clue is available. In four of these species the distribution in the Philippines is limited to Balabac-Palawan-Calamian (*Hasora badra*, *Celaenorrhinus asmara*, *Cupitha*

*purreea*) or to the Sulu archipelago (*Polythremis lubricans*). This is taken as evidence of Bornean origin.

Summing up, at least 81 and possibly all 104 species common to Borneo and the Philippines (respectively 54 and 69.3% of the Philippine hesperiid fauna) reached the Philippines from Borneo. In principle the species could also have migrated in the reverse direction. That would imply origin in the Philippines and subsequent spread to far corners (in many cases) of the Oriental and even Australian regions. It would, of course, shift the problem to the origin of the ancestors, but apart from that it is improbable for two reasons. Firstly, the time span available seems rather short. Secondly, and perhaps more important, the Philippine fauna was (and probably still is, at least in comparison with Borneo) unsaturated. It seems unlikely that species from an unsaturated fauna would be able to successfully colonize an area with a saturated fauna to any important degree. Four species are not widespread, but occur outside the Philippines only in Borneo, and for these the available time could have been sufficient, if they originated in the Philippines. They are *Celaenorrhinus bazilanus*, *Suada cataleucos*, *Isma binotatus*, and *Acerbas duris*. Their restricted range may also have an ecological background. Without further data on phylogeny and ecology we have no other argument for choosing either Borneo or the Philippines as area of origin than the saturation of the Bornean fauna and the unsaturated Philippine fauna. For purists: the species can also have originated in Borneo+Philippines, but apart from the fact that there is no geological evidence for such a single area of endemism, it would not solve any problem, only shift it to the ancestors.

The figure of 54% or even 69.3% for species with Bornean roots is certainly an underestimate as (the ancestors of) a number of endemic species in the Philippines may also have come from Borneo. With the present uncertainty about the phylogenetic relationships of the species concerned we can not say much about it. Inspection of table 2, however, shows that of the 21 genera with endemic species in the Philippines, 5 (*Mooreana*, *Aeromachus*, *Thoressa*, *Suada*, *Suastus*) do not occur in Sulawesi. The genera *Aeromachus* and *Thoressa* (together with three Philippine endemics), without representation in Borneo, were discussed under Philippines-continental Asia. A Bornean ancestry for these could not be established. For the three other genera (each with one Philippine endemic), a Bornean ancestry is most likely. The genus *Mooreana*, for instance, has two species only: *princeps* is a Philippine endemic, while *trichoneura* occurs from N India to Borneo and Palawan. Supposing that the genus *Mooreana* is monophyletic, *princeps* must be an offshoot of an Oriental species that extended from Borneo northwards. For the remaining 16 genera (those which are also represented in Sulawesi) a Bornean ancestry for the Philippine endemics is also possible, but we do not yet have decisive arguments.

This brings the number of Philippine HesperIIDae with a probable Bornean ancestry to 84 (56%), and with a possible Bornean ancestry to 135 (90%) (the latter figure is biased, since each Philippine endemic is counted as having a Bornean ancestry, also in those cases where more than one endemic occurs in a genus, some of which apparently have a Philippine ancestry).

In the above discussion we have not made a distinction between the Palawan chain of islands and the Sulu Archipelago as a gateway to the Philippines. In most cases the species have become so widespread in the Philippines, occurring in both



Palawan and the Sulu-Mindanao area as well as in other islands, that it is impossible now to trace back the entry route. However, if we take the presence of a species in the Sulu Archipelago and/or Mindanao and absence from Palawan (including Balabac and the Calamian group) as evidence for the use of the Sulu gate and the reverse situation as evidence for the use of the Palawan gate, then we find that of the 51 Bornean species (almost 50% of all species common to Borneo and the Philippines) that are either absent in Palawan or in Sulu/Mindanao, 31 have used the Palawan gate and 20 the Sulu gate. Even though these figures may be biased by local extinctions or by undercollecting the difference possibly reflect the easier entrance to Palawan during periods of low sea level and the older age of this gate. Ecological differences may also be involved, since the taxonomic distribution of the 51 species over the two areas is not at random. For instance, Sulu/Mindanao has four *Hasora* species which are not found in Palawan, while the latter has only one *Hasora* species lacking from Sulu/Mindanao. Similarly, Palawan has four Bornean species of *Pyrroneura*, while Sulu/Mindanao has none.

Still, it does not necessarily mean that the Palawan gate is more important for the fauna of the Philippines than the Sulu gate. Of the 31 species that apparently used the Palawan gate only 4 are found on other Philippine islands as well, whereas of the 20 species of the Sulu gate, 14 are also found elsewhere in the Philippines. An explanation could be that the proportion of weak dispersers among the Palawan gate users was much larger than among the Sulu gate users. This would be in agreement with the more easily accessible Palawan gate, while the barrier between Palawan and the rest of the Philippines was so big that it could only be taken by the strong dispersers which were at the same time so strong that they dispersed all over the Philippines obscuring their origin. The possible entry route of the ancestors of the Philippine endemics is left out of consideration here. Also possible double invasions (as indicated by geographic variation) are not taken into account.

From the figures just given we can see that 27 of the Bornean species are, in the Philippines, only found in Palawan, i.e. 30.7% of all species in Palawan (88) or, more illustrative, 34.2% of the 79 Bornean species in Palawan. There are six Bornean species, which in the Philippines are only found in Palawan and the Sulu/Mindanao area. This brings the number of possible users of the Palawan gate that did not disperse beyond to 33, or 41.8% of the Bornean species in Palawan. Faced with this number we could almost call the Palawan gateway a cul-de-sac. Nevertheless, of the 33 endemic hesperiid species in the Philippines four occur in Palawan (one of these being an endemic of Palawan), and for these (or at least for three of them) the barrier on the way to Borneo must have been greater than between Palawan and the rest of the Philippines.

Conditions are quite different in the Sulu/Mindanao area. Of the 69 Bornean species in the area (out of a total of 95), 12 do not occur elsewhere in the Philippines (with the possible exception of Palawan), meaning that 17.4% of the invaders from Borneo were "trapped" here (or they simply have not yet had time enough to disperse further). Apparently the barrier (in time and/or space) between Mindanao and the rest of the Philippines was much weaker than between Palawan (or the Calamian islands) and the rest of the Philippines. With the present configuration of land and sea this is conceivable. The Sulu Archipelago itself does not seem to have acted as a strong filter. Although it has been incompletely explored and more Bornean species

may be expected to turn up there, it is remarkable that only three of the 30 Bornean species in Tawitawi (10%) do not occur further east. Apparently once they reached this far, the way to Mindanao was relatively open. Illustrative in this respect is also, that 5 of the 33 endemic Philippine hesperiid species occur in Tawitawi. Apparently they could more easily cover the long distance from Mindanao than the relatively short distance to Borneo. This is even more remarkable if one realizes that the faunistic boundary (if one may call it as such) is not between Tawitawi and Borneo, but between Tawitawi and Sibutu, only about 30 km to the west across the Sibutu Passage, which is not deeper than 290 m. The latter island, politically belonging to the Philippines, has a purely Bornean hesperiid fauna.

*Summary of Bornean connections.* The figures given above should not be taken too absolutely because of the following reasons: (a) the ancestry of the Philippine endemics could not be taken into account because of lack of phylogenetic data; (b) incomplete exploration; and (c) some species probably invaded the Philippines more than once. Nevertheless, an obvious pattern arises. The majority, maybe as much as 90%, of the 150 Philippine Hesperidae species also occur in Borneo, or the closest relatives live there. In view of the much larger Bornean fauna (214 species) and the known geological history of the area, the similarity between the Bornean and Philippine faunas is explained as the result of a large-scale invasion from Borneo into the Philippines. This may have started as far back as 17 million years ago, and probably got an extra impetus when the sea level dropped during the Pleistocene Ice Ages and water gaps became narrower or disappeared altogether.

Of the two gateways the Palawan connection is the older and more easily accessible one, but more than 40% of the Bornean invaders never got further. The younger Sulu connection was used by fewer Bornean species, but once they got there, they could much more easily reach other islands of the Philippines, and more than 80% dispersed beyond Mindanao.

#### *The Sangihe connection*

In terms of number of shared species the Philippine hesperiid fauna is much more similar to the Bornean fauna (almost 70% also in Borneo) than to the Sulawesi fauna (47 species, 31.1%, also in Sulawesi, see table 3). Nevertheless, and in spite of the large stretch of water between Mindanao and Sulawesi, there are four species of Hesperidae restricted to Sulawesi and the Philippines (*Hasora moestissima*, *Zographetus abima*, *Matapa intermedia*, *M. celsina*), as many as the number of species restricted to Borneo and the Philippines. The difference must be due to the isolation of Sulawesi and the fact that Borneo, lying on the Sunda shelf, was broadly connected to Java and Sumatra as well as to the Asian mainland during the Pleistocene Ice Ages. The Sangihe connection is further illustrated by one species found in the Philippines, Sulawesi and the Moluccas (*Prusiana prusias*) and one species occurring in the Philippines, Sulawesi and continental Asia (*Zographetus rama*). To these cases may be added the presumably monophyletic taxon consisting of the sister species *Oriens californica* (the Philippines) and *O. alfurus* (Sulawesi) (de Jong, 1990), and *Potanthus pava* discussed above (under the Taiwan connection). In all nine cases we have no choice but

to postulate that the species crossed over from Mindanao to Sulawesi or in the reverse direction, unless the species were once widespread and became extinct over most of their areas. For such a large-scale extinction there is no evidence whatsoever.

There are 40 species in the Philippines and Sulawesi which occur also in Borneo as well as outside these islands. For these species we concluded above that they most probably reached the Philippines from Borneo, but this leaves open the possibility that they reached Sulawesi from the Philippines rather than from Borneo. A closer link between the Philippines and Sulawesi than between Borneo and Sulawesi has been suggested before for Lepidoptera by Holloway (1987) and Vane-Wright (1990). As explained by de Jong (1990) for HesperIIDae, 17 (recte 19) of the HesperIIDae involved are not (yet) known from Mindanao and unless they became extinct in Mindanao, they must have reached Sulawesi directly from Borneo. The remaining 21 species could either have dispersed directly from Borneo to the Philippines and from Borneo to Sulawesi or from Borneo through the Philippines to Sulawesi. At the moment there is no way to distinguish between the two possibilities. It is a case in point here that among the species occurring in the Philippines, Borneo and Sulawesi there are no species with a subspecies occurring exclusively in Sulawesi and the Philippines suggesting a closer (more recent) link between these islands than between any of these and Borneo. The only evidence for such a closer contact is the higher number of species restricted to the two areas (but see above for the reason) and the slightly greater similarity of the hesperiid fauna of Sulawesi to that of the Philippines (shared species 55.3% of the Sulawesi fauna) than to that of Borneo (shared species 48.2% of the Sulawesi fauna). Even in the case of species restricted to Sulawesi and the Philippines it is still uncertain how they got there. For instance, the sister species *Matapa celsina* and *M. intermedia* are both restricted to Sulawesi and the Philippines, while the sister species of the two, *M. sasivarna*, is distributed from E India to Borneo (de Jong, 1983). Although indicating a recent contact between Sulawesi and the Philippines it does not explain anything about the distributional history of *M. celsina* and *M. intermedia* or of their ancestor, i. e. whether it dispersed from Borneo to Sulawesi or to the Philippines, or from Sulawesi to Mindanao or the other way around. In other words, the HesperIIDae do not provide evidence for the assumption that there was an important dispersal route from Borneo through the Philippines to Sulawesi. The possibility that the similarity between Sulawesi and the Philippines with regard to the HesperIIDae is at least partly due to independent dispersal of the same species from Borneo to the Philippines and from Borneo to Sulawesi (comparable with the cause for the similarity between Taiwan and the Philippines) must be taken seriously.

#### *The Talaud connection*

We can be short about this connection: there are no hesperiid taxa exclusively occurring in the Philippines and N Moluccas and/or further east. The 15 shared genera (table 2) all have a wide to very wide distribution, in three cases even including Africa (*Parnara*, *Borbo*, *Pelopidas*). Also the 21 shared species are more widely distributed than only in the Philippines and Moluccas or further east. The possibility of sister species with a vicariant distribution, in the Philippines on one side and in the

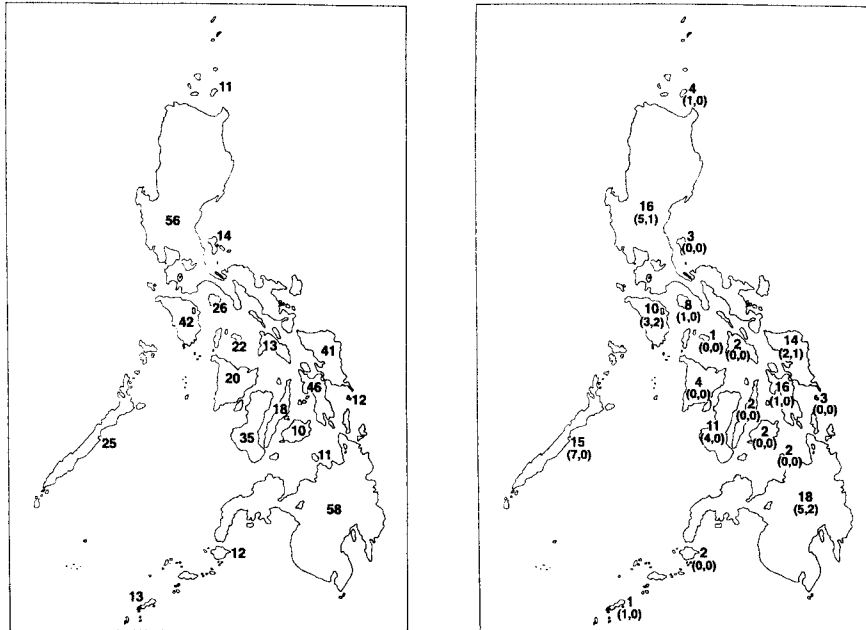


Fig. 133. Numbers of endemic taxa (species and subspecies) of Hesperiidae on various islands.

Fig. 134. Numbers of non-widespread (not occurring in both Luzon and Mindanao) endemic taxa (species and subspecies) of Hesperiidae on various islands. In brackets: numbers of taxa (subspecies and species) and of species endemic to the island only.

Moluccas/New Guinea on the other, cannot be ruled out, but can only be expected in the genus *Hasora*, this being the only genus with endemics in both areas. Not a hopeful prospect.

#### *Intra-Philippine patterns*

There are 107 endemic species and subspecies of Hesperiidae in the Philippines (table 4). They are not distributed at random over the islands, as can be seen in fig. 133 where the number of Philippine endemics is given for a selection of islands. Undoubtedly the differences are biased by the different degree to which the islands have been explored: a better exploration can be expected to expand the known ranges of taxa, thus increasing uniformity. Widespread taxa tend to blur the distinction between islands, particularly when they are numerous. Since they are uninformative with regard to the recognition of patterns we omit them for this purpose. We consider a taxon widespread, if it occurs on both Luzon and Mindanao, irrespective of whether it is known to occur on the islands in between or not. There are 38 such taxa (35.5%). The resulting figures per island are given in fig. 134. Another category of uninformative taxa with respect to the recognition of connections between islands are the island endemics, i.e. taxa occurring in one island only (they could be informative if their sister taxa were known to live in another island). These number 32, leaving us only 37 taxa for the recognition of distribution patterns.

Table 4. Distribution of endemic species and subspecies of Hesperidae in the Philippines. Endemic species are marked with an asterisk. The distribution is given for 35 islands (0 = absent, 1 = present); for the position of the islands, see fig. 1.

<i>Bibasis oedipodea paltra</i>	00000	00000	10000	10110	11100	00000	00000
<i>Bibasis harisa pala</i>	00000	00000	00000	00000	00010	00000	00000
<i>Bibasis harisa grandis</i>	00000	00000	01000	00000	00000	00010	00000
<i>Bibasis gomata lorquini</i>	00000	01100	00000	10110	11110	11000	00000
<i>Bibasis sena palawana</i>	00000	01000	10010	10110	10110	11000	11010
<i>Hasora proxissima proxissima</i>	00000	00000	00000	10000	11000	00000	00000
<i>Hasora borneensis luza</i>	00000	00000	00000	10101	11101	00010	00000
<i>Hasora schoenherr saida</i>	00000	10110	00000	10110	11101	10010	01000
<i>Hasora mixta mixta</i>	00011	00100	10000	10111	11101	10010	01000
<i>Hasora vitta proximata</i>	00000	00000	00000	00100	11010	00000	00000
* <i>Hasora caeruleostriata</i>	00000	00000	00010	10101	00110	10010	00000
<i>Choaspes plateni adhara</i>	00000	00000	00000	00000	10000	00000	00000
<i>Choaspes plateni negrosa</i>	00000	00000	00000	00000	00100	00000	00000
<i>Choaspes plateni boreus</i>	00000	00000	00000	00100	01000	00000	00000
<i>Choaspes plateni visaya</i>	00001	10000	00000	10000	00001	00010	00000
* <i>Choaspes estrella estrella</i>	00000	00000	00000	00100	00100	10000	00000
* <i>Choaspes estrella pallens</i>	00000	00000	00000	10000	00000	00010	00000
* <i>Celaenorrhinus nigricans mindanus</i>	00000	00000	00000	00100	10000	00000	00000
* <i>Celaenorrhinus treadawayi treadawayi</i>	00000	00000	00000	00000	10000	00000	00000
* <i>Celaenorrhinus treadawayi samarensis</i>	00000	00000	00000	00000	00000	00010	00000
<i>Celaenorrhinus bazilanus bazilanus</i>	00010	00000	00000	00000	10000	00000	00000
* <i>Celaenorrhinus halconis</i>	00000	00000	00000	00000	01000	00000	00000
<i>Darpa pteria pteria</i>	00000	00000	00000	00100	10000	00000	00000
<i>Odina hieroglyphica cuneiformis</i>	00000	00100	00000	10110	01010	00000	00000
* <i>Coladenia igna igna</i>	00000	00000	00000	00100	00000	00010	00000
* <i>Coladenia igna marinda</i>	00000	00000	00000	00010	00000	00000	00000
* <i>Coladenia ochracea</i>	00000	00000	00000	10000	10000	00000	00000
* <i>Coladenia semperi</i>	00000	00010	00000	10000	00000	00000	00000
* <i>Coladenia minor</i>	00000	00000	00000	00110	00000	00000	00000
* <i>Coladenia similis</i>	00000	00010	00000	00110	10000	00000	00000
<i>Gerosis limax philippina</i>	00000	00000	00000	00000	00010	00000	00000
* <i>Gerosis corona</i>	10000	00010	00000	10101	11000	00010	00000
<i>Tagiades japedus titus</i>	10011	11111	10100	11101	11110	11011	11010
<i>Tagiades gana elegans</i>	00011	10011	01000	10111	11101	01011	01000
<i>Tagiades gana semperi</i>	00000	00100	00000	00000	00000	00000	00000
<i>Tagiades trebellius martinus</i>	01010	10010	11010	10110	11010	01010	01011
* <i>Mooreana princeps</i>	00000	00000	00000	10000	10001	00010	00000
<i>Odontoptilum angulatum helisa</i>	00010	10000	10000	00000	11100	00010	00000
<i>Odontoptilum angulatum sinka</i>	00000	00000	00000	00110	00000	01000	00000
* <i>Odontoptilum leptogramma</i>	00000	00000	10000	10100	11000	00010	01000
* <i>Aeromachus musca</i>	00000	00000	10000	00100	11100	00001	00000
* <i>Aeromachus plumbeola</i>	00001	00000	00000	10101	11100	10010	00000
* <i>Thoressa justini</i>	00000	00000	00000	00100	00000	00000	00000
* <i>Halpe palawea</i>	00000	01000	00000	00000	00010	00000	00000
* <i>Halpe luteisquama</i>	00010	00100	10000	10110	11110	10010	11010
* <i>Halpe latipinna</i>	00000	00000	00000	00000	01000	00000	00000
* <i>Halpe dante dante</i>	00000	00000	00000	00000	00100	00000	00000
* <i>Halpe dante luzona</i>	00000	00000	00000	00100	00000	00000	00000
* <i>Halpe dante tilia</i>	00000	00000	00000	10000	10000	00000	00000
* <i>Halpe sulphurifera</i>	00000	00000	00001	10111	11100	00000	01010
* <i>Halpe purpurascens</i>	00000	00000	00000	00001	00100	10000	00000
* <i>Halpe inconspicua</i>	00000	00000	00000	10000	00001	00000	00000
<i>Koruthaialos rubecula atra</i>	00000	00000	10000	10000	10100	00010	00000
<i>Koruthaialos rubecula luzonensis</i>	00000	00000	00000	00110	00000	00000	00000
<i>Koruthaialos rubecula ponta</i>	00000	01000	00000	00000	00010	00000	00000
<i>Koruthaialos sindu palawites</i>	00000	00000	00000	00000	00010	00000	00000
<i>Ancistroides nigrita fumatus</i>	01111	10010	10100	10101	11110	10010	01000
<i>Notocrypta paralyos chunda</i>	00100	01000	00000	00000	00010	00000	00000
<i>Notocrypta paralyos volux</i>	00011	00000	11010	10111	11100	11010	01010
* <i>Notocrypta howarthi</i>	00000	00000	00000	00000	10000	00000	00000
<i>Notocrypta feisthamelii alinkara</i>	01000	01000	10000	10110	11111	10100	01000
* <i>Suada albina</i>	00010	00000	00000	00100	10000	00000	00000
<i>Suastus minutus scopas</i>	00000	00000	00000	00000	00010	00000	00000

<i>Suastus minutus compactus</i>	0000 01000 00000 00000 00000 00000 00000
* <i>Suastus migreus</i>	01000 00000 10010 00110 11000 00000 01010
* <i>Zographetus pallens</i>	00000 00100 00000 00010 00000 00000 00000
<i>Oerane microthyrsus microthyrsus</i>	00000 00000 00000 10110 11000 00010 00000
<i>Quedara monteithi noctis</i>	00100 01000 00000 10000 10010 00010 00000
<i>Isma bononia bipunctata</i>	00000 00000 00000 00000 10010 00000 00000
<i>Pyroneura flavia flavia</i>	00000 00000 00000 00000 00010 00000 00000
<i>Pyroneura agnesia limbanga</i>	00000 00000 00000 00000 00000 00010 00000 00000
* <i>Pyroneura liburnia liburnia</i>	00000 00000 00000 00110 00000 01000 00000
* <i>Pyroneura liburnia divinae</i>	00000 00000 00000 00000 00000 10100 01000
* <i>Pyroneura liburnia minda</i>	00000 00000 00010 10000 10000 00000 00000
* <i>Pyroneura liburnia rosa</i>	00000 00000 00000 00000 00100 00000 00000
* <i>Pyroneura liburnia dora</i>	00000 00000 00000 00000 01000 00000 00000
* <i>Pyroneura liburnia wita</i>	00000 00000 00000 00000 00000 00000 00010
* <i>Pyroneura toshikoeae</i>	00000 00000 00000 00000 10000 00000 00000
* <i>Plastingia viburnia</i>	00000 00000 00000 00100 11110 00010 00000
* <i>Xanthoneura telesinus</i>	00000 10000 00000 10100 11100 00010 00000
<i>Zela zeus major</i>	00000 00000 00010 10100 11000 00010 01000
<i>Gangara thyrasis philippensis</i>	00000 00100 00000 10100 11001 00010 01000
<i>Gangara thyrasis magnificens</i>	00000 00000 00000 00000 00100 00000 00000
<i>Gangara lebadea janlouremsi</i>	00000 00000 00000 10000 00000 00000 00000
<i>Erionota thrax alexandra</i>	00000 00000 00000 00100 00000 00000 00000
<i>Erionota thrax mindana</i>	00000 00000 01011 10000 10000 00010 00000
<i>Erionota hiraca apex</i>	00000 00000 00000 10100 11000 00010 00001
* <i>Erionota surprisa</i>	00000 00000 10000 10110 11100 11010 00011
<i>Matapa intermedia nigrita</i>	00000 00000 00000 00000 00000 00000 00010 00000
<i>Unkana ambasa mindanaensis</i>	00000 00100 01010 10100 11100 10010 01000
<i>Acerbas anthea luzona</i>	00000 00000 00000 00100 00000 00000 00000
<i>Acerbas duris duris</i>	00000 00110 00000 10100 11100 00000 00000
* <i>Pirdana fusca</i>	00000 00000 00000 00000 00000 00010 00000
<i>Taractrocera luzonensis luzonensis</i>	00110 00000 11000 10111 11110 10010 01000
* <i>Oriens californica</i>	00100 00000 00011 10101 11000 11010 01010
* <i>Oriens fons</i>	00000 00000 00000 00100 10000 10000 00000
<i>Potanthus omaha bione</i>	00000 00000 00000 00000 10000 00000 00000
<i>Potanthus fettingi alpha</i>	00000 00000 00000 00100 00000 00000 00000
* <i>Potanthus niobe niobe</i>	00000 00000 01000 00000 10000 00000 00000
* <i>Potanthus niobe hyugai</i>	00000 00000 00000 00100 01000 00000 00000
<i>Potanthus mingo mingo</i>	00010 00000 00001 10100 11100 10010 00010
<i>Potanthus hetaerus hetaerus</i>	00000 00000 00010 10100 10100 01100 01010
<i>Telicota augias pythias</i>	00000 10011 10100 10110 11100 10010 01010
<i>Telicota ancilla minda</i>	00000 00000 00010 00100 10000 00110 00001
<i>Telicota ohara jania</i>	00000 00000 00000 00010 11110 01010 00000
<i>Telicota hilda subsp.</i>	00000 00000 00000 00000 00010 00000 00000
<i>Cephrenes acalle chrysozona</i>	00000 10011 10000 10110 11100 01010 01000

1 Alabat	8 Camiguin de L.	15 Jolo	22 Mindoro	29 Samar
2 Babuyan	9 Camiguin de M.	16 Leyte	23 Negros	30 Siargao
3 Balabac	10 Camotes	17 Lubang	24 Palawan	31 Sibutu
4 Basilan	11 Cebu	18 Luzon	25 Panaon	32 Sibuyan
5 Biliran	12 Dinagat	19 Marinduque	26 Panay	33 Sulu
6 Bohol	13 Guimaras	20 Masbate	27 Polillo	34 Tawitawi
7 Calamian	14 Homonhon	21 Mindanao	28 Romblon	35 Ticao

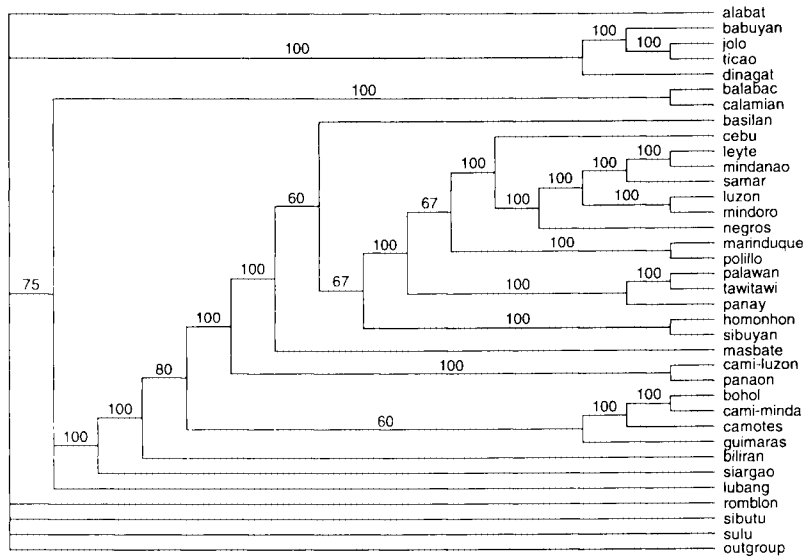


Fig. 135. Cluster dendrogram (not a cladogram) of all taxa (species and subspecies) over all islands, computed by PAUP. The dendrogram is a majority consensus tree based on 100 equally parsimonious trees, the figures refer to the percentage of the 100 trees in which the particular grouping is found. See text for further explanation.

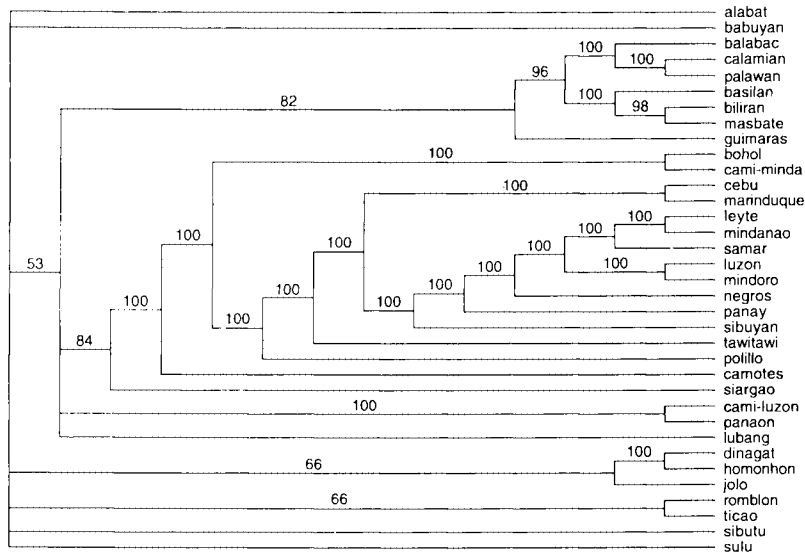


Fig. 136. As fig. 135, but for endemic species and subspecies only.

For further analysis of the 37 taxa we used a selection of 13 islands. From the list of endemics occurring in these islands again the single-island occurrences were omitted, but we added the distribution of endemic species in those instances in which the endemic species was represented by two or more subspecies in the islands to increase the number of taxa potentially indicating previous closeness or junction of islands. On the basis of these taxa we applied a cluster analysis (for which we used the heuristic options of PAUP 3.0s) to the islands with regard to their content of species and subspecies, and to the subspecies and species with regard to their distribution over the islands. There was a certain clustering of the islands Mindanao, Leyte and Samar, and of these three islands with Cebu, Negros and Mindoro. It does not support former divisions very strongly, but it does not strongly contradict them either (compare fig. 132). Figs. 135-138 (N.B. dendrograms; they can only become cladograms, if the bifurcation points are interpreted as historical events) give the results of the analyses with endemics only or with all taxa, and with all islands or with a selection of islands.

The endemics, on the other hand, clearly fall apart into two groups, one group centred on Luzon, the other on Mindanao. There are only three endemics that occur in more than one island and are not found in either Luzon or Mindanao. This is not an artifact of the omission of the endemics occurring in both Luzon and Mindanao, as there is no obvious reason why the remaining taxa would not be distributed more equally over the islands, except for some historical factor. Most "multi-island" endemics in Leyte and Samar fall within the Mindanao group, but a few are also found in the Luzon group. For Negros these numbers are equal. This suggests that the faunas of Luzon and Mindanao are kept apart to some degree by the islands in between (Visayas) which act as a buffer, receiving influx from north and, particularly, south (perhaps in different periods), while the large islands to the north and south of the Visayas are not subject to such diverse influences. Notice that Palawan does not play a part in this pattern.

Addition of the island endemics reinforces the pattern of Luzon and Mindanao as concentration areas of endemics, but it also shows that Mindoro and several islands of the Visayas have endemics of their own indicating the biogeographic complexity of the area (table 5). This is in accordance with the supposition that the islands have been interconnected more than once. There is not much sense in trying

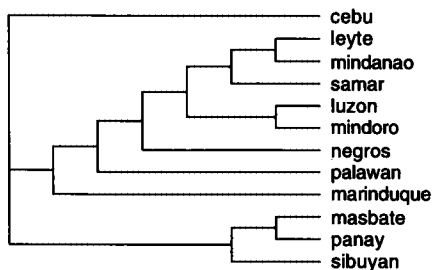


Fig. 137. As fig. 135, but for a selection of islands.

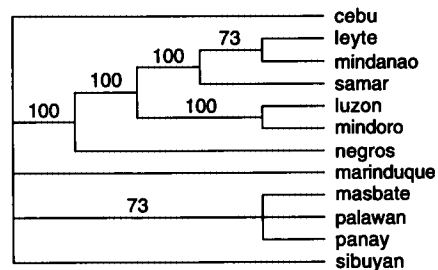


Fig. 138. As fig. 136, but for a selection of islands.



Table 5. Distribution of non-widespread endemics over selected islands (see text).

1 Bohol	5 Marinduque	8 Mindoro	11 Panay
2 Cebu	6 Masbate	9 Negros	12 Samar
3 Leyte	7 Mindanao	10 Palawan	13 Tawitawi
4 Luzon			
centred on Luzon		centred on Mindanao	
<i>H. caeruleostriata</i>	00110 10011 110	<i>H. proxissima proxissima</i>	00100 01100 000
<i>C. plateni boreus</i>	00010 00100 000	<i>C. plateni adhara</i>	00000 01000 000
<i>C. estrella</i>	00110 00010 110	<i>C. treadawayi</i>	00000 01000 010
<i>C. estrella estrella</i>	00010 00010 100	<i>C. treadawayi treadawayi</i>	00000 01000 000
<i>O. hieroglyphica cuneiformis</i>	00111 00101 000	<i>C. bazilanus bazilanus</i>	00000 01000 000
<i>C. igna</i>	00011 00000 010	<i>C. ochracea</i>	00100 01000 000
<i>C. igna igna</i>	00010 00000 010	<i>M. princeps</i>	00100 01000 010
<i>C. minor</i>	00011 00000 000	<i>O. angulatum helisa</i>	11000 01110 010
<i>O. angulatum sinka</i>	00011 00000 000	<i>H. dante tilia</i>	00100 01000 000
<i>T. justini</i>	00010 00000 000	<i>K. rubecula atra</i>	01100 01010 010
<i>H. dante luzona</i>	00010 00000 000	<i>N. howarthi</i>	00000 01000 000
<i>K. rubecula luzonensis</i>	00011 00000 000	<i>Q. monteithi noctis</i>	00100 01001 010
<i>P. liburnia liburnia</i>	00011 00000 000	<i>I. bononia bipunctata</i>	00000 01001 000
<i>E. thrax alexandra</i>	00010 00000 000	<i>P. liburnia minda</i>	00100 01000 000
<i>A. anthea luzona</i>	00010 00000 000	<i>P. toshikoe</i>	00000 01000 000
<i>P. fettingi alpha</i>	00010 00000 000	<i>E. thrax mindana</i>	00100 01000 010
<i>P. niobe hyugai</i>	00010 00100 000	<i>P. omaha bione</i>	00000 01000 000
		<i>P. niobe niobe</i>	00000 01000 000
		<i>T. ohara jania</i>	00001 01111 010
various endemics			
<i>B. harisa grandis</i>	00000 00000 010		
<i>C. plateni negrosa</i>	00000 00010 000		
<i>C. plateni visaya</i>	10100 00000 010		
<i>C. estrella pallens</i>	00100 00000 010		
<i>C. treadawayi samarensis</i>	00000 00000 010		
<i>C. halconis</i>	00000 00100 000		
<i>C. igna marinda</i>	00001 00000 000		
<i>C. semperi</i>	00100 00000 000		
<i>H. purpurascens</i>	00000 10010 100		
<i>H. dante dante</i>	00000 00010 000		
<i>H. inconspicua</i>	00100 00000 000		
<i>H. latipinna</i>	00000 00100 000		
<i>Z. pallens</i>	00001 00000 000		
<i>P. liburnia divinae</i>	00000 00000 100		
<i>P. liburnia rosa</i>	00000 00010 000		
<i>P. liburnia dora</i>	00000 00100 000		
<i>P. liburnia wita</i>	00000 00000 001		
<i>G. thyraxis magnificens</i>	00000 00010 000		
<i>G. lebadea janloureasi</i>	00100 00000 000		
<i>M. intermedia nigrita</i>	00000 00000 010		
<i>P. fusca</i>	00000 00000 010		
		endemics of Palawan	
		<i>B. harisa pala</i>	00000 00001 000
		<i>G. limax philippina</i>	00000 00001 000
		<i>H. palawea*</i>	00000 00001 000
		<i>K. rubecula ponta*</i>	00000 00001 000
		<i>K. sindu palawites</i>	00000 00001 000
		<i>N. paralysos chunda**</i>	00000 00001 000
		<i>S. minutus scopas</i>	00000 00001 000
		<i>P. flavia flavia</i>	00000 00001 000
		<i>P. agnesia limbanga</i>	00000 00001 000
		<i>T. hilda subsp.</i>	00000 00001 000
		*also on Calamian islands	
		** also on Calamian islands and Balabac	

to define boundaries here. It may be better to speak of the islands between Luzon and Mindanao as an area of ever changing opportunities for dispersal. This leaves open the question of actual land connections.

When also taking island endemics into account, Palawan shows up as another concentration area of endemics. Interestingly there is no endemic species in Palawan, and the endemic subspecies belong to Sundaland species (they may even be the sole representation of such species in the Philippines), except for *Halpe palawea* which is an endemic of Palawan and Calamian islands (by taking only the selection of islands listed in table 5 into consideration it shows up as an endemic of Palawan only). This underlines the concept of Palawan being a part of Sundaland rather than being something special or closer to the rest of the Philippines.

In summary, we must conclude that with the applied technique the division of the Philippines into faunal regions as proposed by previous authors does not clearly emerge from the distribution of the HesperIIDae. Instead, the HesperIIDae show a pattern of relatively high concentrations of endemics in Luzon and Mindanao with a complex intermediate area. The islands of this area show relationships with Luzon and Mindanao and inter se, but they cannot be clustered into well-defined groups characterized by a good number of endemics of their own, i.e. the endemics found there are either restricted to only one island, are found on some of the islands of a faunal region only, or if found on all islands, are very few. This pattern does not contradict the supposed junction of islands during periods of low sea level, but it does not support it either, since the same pattern can be expected to arise by dispersal under the present conditions. To define boundaries here seems to be rather arbitrary and futile.

Evidently PAUP has not been designed to recognize faunal regions, but to find the most parsimonious phylogenetic trees. As such it clusters objects (i.c. taxa) in such a way that changes in properties (i.c. characters) are minimal over the whole tree. As the properties are only vertically transmitted (see also the introduction of this chapter), the resulting trees are hypotheses of hierarchical relationships. Since in biogeography also horizontal transmission is possible, the application of PAUP to distributional data will not lead to a hypothesis of hierarchical relationship of areas, but it should bring together objects (islands) which share characters (species) in such a way that the number of horizontal transmissions is minimal. Actually it is incorrect to apply parsimony here, since different kinds of processes are involved (dispersal and vicariance) (Sober, 1988). However, since we are not interested in finding a hierarchical pattern in this case, but only possible clusters, and it does not matter for the moment how the similarity or dissimilarity originated, we think the application of PAUP justified here.

As a check we subjected the same data to a cluster analyses using Squared Euclidean Distance and the Unweighted Pair Group-Average Strategy. Fig. 139 gives the dendrogram based on the same set of islands and taxa als used for fig. 138. Although the islands cluster slightly differently, the faunal regions are still not evident. It makes one wonder about the meaning or even the reality of the regions. The difference in outcome from, for instance, Heany (1986) cannot be simply attributed to the strong dispersive powers of the HesperIIDae. True enough the endemism among non-volant mammals in the Philippines, on which Heany (1986) based his regions, is,

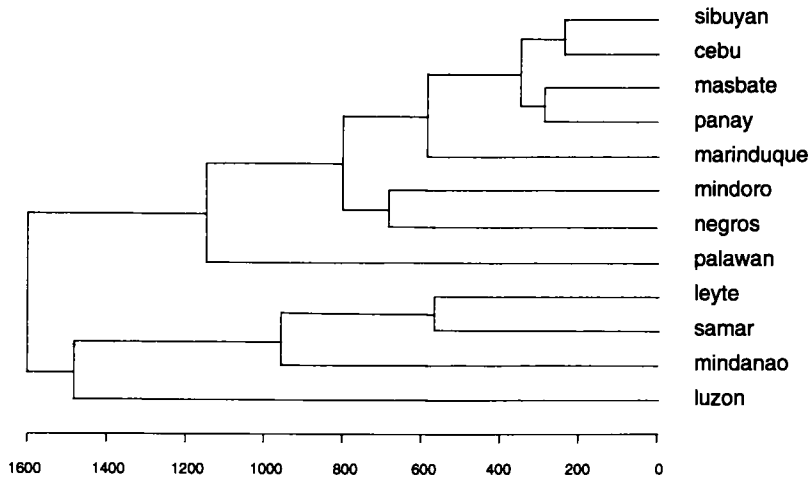


Fig. 139. Cluster analysis using Squared Euclidean Distance and Unweighted Pair-Group Method for same data set as fig. 138.

with 85%, much higher than among the Hesperidae suggesting weaker dispersive powers, but for the examination of the intra-Philippine relationships among the Hesperidae we only took the endemic taxa into account. Interestingly, while dealing with the endemic birds of the Philippines Parkes (1991) found a similar pattern to ours: a north-south division with a complex intermediate area. The recognition of regions (and consequently of boundaries) seems to be the outcome of the chosen approach. If one is interested in subdividing an area emphasis is laid on local or regional differences and boundaries are drawn even if only a small part of the fauna comply with them. Once regions have been defined they tend to become self-confirming: each taxon confined to a region or to a part of a region is taken as evidence of the reality of the region.

If one, on the other hand, is interested in the coherence and relationships of faunas, the connections are found to be much more diverse than suggested by the recognition of regional boundaries. If there are clear-cut boundaries, they will appear in the course of the analysis. If the local or regional differences are diverse and strongly dependent on the taxa chosen, however, the local or regional fauna can be expected to have a hybrid origin.

#### *Vicariance and areas of endemism in the Philippines*

The bipartition of the Philippine fauna into a northern and a southern component is not only quantitative, but is also reflected in the relationships of taxa in the two components: northern endemic subspecies are often conspecific with southern endemic subspecies (see table 5). Thus there is a pattern of vicariance in the Philippines with a northern and a southern area of endemism. The number of endemic species in the two components is too low to show the same pattern: only in the genus

*Coladenia* a sister group relationship between north and south can be expected. A further intra-Philippine pattern of vicariance is not evident among the HesperIIDae.

For an assessment of the biogeographic relationship (in a cladistic sense) of the Philippines with areas outside the archipelago, the Philippines as a whole or at least the Philippines proper (i.e. without Palawan; Vane-Wright, 1990, also excluded the Sulu Archipelago, but the HesperIIDae do not give a reason for that except for the westernmost island, Sibutu), to which about 76% of the endemic Philippine taxa is restricted, could be taken as a single area of endemism, since in a sistergroup relationship with, for instance, Sulawesi or Borneo, it is irrelevant whether an endemic occurs throughout the Philippines proper or is confined to one or a few islands.

### Conclusions

1. The distribution of the HesperIIDae in the Philippines agrees with the relatively young age of the islands or at least of the fauna (there are no endemic genera).

2. There are no traces of an old Asian continental fauna in the Philippines.

3. The rate of endemism at the species level (23.2%) is almost the same as for Sulawesi (23.8%), but much higher than that of Borneo (5.6%). This agrees with a largely oceanic character of the islands. Diamond & Gilpin (1983) found the same for birds.

4. By far the greater part of the fauna was derived from Borneo. Two routes were used, namely through Palawan (but for many species this was a cul-de-sac) and through the Sulu Archipelago. There is a remarkable change in species composition in the extreme western end of the latter archipelago: Sibutu has a purely Bornean fauna, while on the other side of the narrow (about 30 km) Sibutu Passage, which is not deeper than 290 m, the Philippine endemics appear in Tawitawi.

5. Faunistically (and geologically as far as its southern half is concerned) Palawan is a northward extension of Sundaland.

6. The isolation from Sulawesi was more severe than from Borneo and it is questionable if there was any influx into the Philippines, the contact could as well have been in the reverse direction.

7. Taiwan did not play a part in the colonization of the Philippines, except for a few individual cases. The similarity between the hesperiid faunas of Taiwan and the Philippines is based on the same species colonizing the two areas from different sources.

8. There are no exclusive links with the fauna of the northern Moluccas or New Guinea.

9. No strong support is found for a division of the Philippines into faunal regions. Instead two areas with high endemism are found, Luzon and Mindanao, while the intermediate islands are populated by taxa with northern or southern links and by endemic taxa without forming a definite pattern.

10. The situation described under 9 is explained as follows: the faunas of Luzon and Mindanao are kept separate by distance and by the buffering effect of the intermediate islands. The latter are an area of changing opportunities for dispersal leading to local, and locally different, mixtures of island faunas. Pleistocene fluctuations in sea level probably enhanced the change in opportunities.

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## An evaluation of the diversity of subspecies, species and genera of HesperIIDae within The Philippines, using the WORLDMAP computer program

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Williams' WORLDMAP computer program is designed to identify maximally efficient configurations of areas, or reserve networks (Margules et al., 1988), for the conservation of biodiversity, and priorities for action within those configurations (Williams, 1992, and in press; Williams & Humphries, in press; Pressey et al., 1993; Vane-Wright, in press; Vane-Wright et al., in press). To achieve this goal the program integrates three factors to make biotic comparisons between areas: taxon richness (number of subspecies, species or higher taxa), taxon disparity (taxonomic difference, based on a given taxonomic hierarchy) and complementarity (taxon turnover, or labelled gamma diversity). The program also incorporates an aggregate inverse range-size measure, endemism weight (Williams et al., 1993).

The data on Philippine HesperIIDae analysed here comprise known distribution records amongst 34 Philippine islands for 53 genera, 152\* species and 198 subspecies (de Jong and Treadaway, this paper), and hierarchical "clade codes" (Vane-Wright et al., in press) expressing their mutual taxonomic relationships (table A1; based largely on Evans, 1949). The taxon disparity measure employed is the latest formulation of dispersion (Williams & Humphries, in press).

Applying the taxon richness (without disparity), endemism weight and dispersion measures to the generic data results in a four-area configuration comprising Palawan, Mindanao, Luzon and Tawitawi (table A2). Using the Pressey & Nicholls (1989) measure, this gives an efficiency score for single representation of genera of 0.882 ( $1 - 1/34$ ). Taxon richness gives a first-step tie between Palawan and Mindanao. Either choice is followed by the other in the optimised step-wise sequence, then Luzon and Tawitawi, in that order. The P>M>L>T sequence is not repeated by endemism weight (P>L>M>T) or by dispersion, but the latter does repeat the alternative taxon richness sequence (M>P>L>T). As demonstrated by Williams &

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\* Based on the inclusion of *Isma feralia* (Hewitson, 1868). The exact identity of the specimens concerned is still under study and for that reason the species was not listed and counted in the preceding pages.

Humphries (in press), for the purpose of biodiversity evaluation, endemism generally performs poorly compared with dispersion, or even just against unweighted species richness, and so the preferred sequence can be taken as Mindanao>Palawan>Luzon>Tawitawi.

On moving from genera to the 152 species, all three measures select the same critical configuration, now increased to 10 areas (efficiency = 0.796). Variations in the sequence are minor, with species richness and dispersion identical except for reversal of the last two areas (table A3). Moreover, as the first four places in both these lists are identical to the preferred sequence for genera, dispersion is again preferred over endemism weight, which produces a substantially different sequence for the first four places. (In all cases, step-wise incremental ties have been broken by absolute species richness.)

For the subspecies, 14 areas are required (efficiency = 0.588), all three measures again giving the same critical configuration, but with some differences in sequence (table A4). Taxon (subspecies) richness, as with generic richness, gives the first two steps as either Palawan>Mindanao or the reverse, with the subsequent 12 steps all the same. The top-four sequence of Mindanao>Palawan>Luzon>Tawitawi is found by one of the two taxon richness results, and by dispersion (but not by endemism weight). The configurations for the first 10 areas, derived by dispersion and by taxon richness, differ from the species 10-area configuration by substituting Sibutu for Dumarán, and give identical sequences for the first 7 or 8 islands.

The optimised 4 step priority set Mindanao>Palawan>Luzon> Tawitawi thus covers 100% of genera, 93.4% of species, and 86.4% of subspecies. In biogeographical terms, these four areas represent the four most disparate of the seven widely-recognised Philippine realms discussed by Vane-Wright (1990); two of the other realms, represented by Samar and Negros, are identified at steps 5 and 6 in the species and subspecies sequences, while the seventh and final realm, Mindoro, is included at step 8. Thus, despite undoubted inequality of sampling effort on the smaller islands, these analyses are highly consistent, endorsing both the higher-taxon approach advocated by Gaston & Williams (in press), and traditional biogeography. However, the analyses using species (up to six additional areas) and subspecies (up to 10 additional areas) offer the possibility of going beyond the short list of four top-priority areas recognised by using genera, as well as beyond the seven unordered areas identified by descriptive biogeography.

Kremen (1992) has suggested that, in searching for good indicator groups for conservation evaluation, it is likely that highly endemic taxa will prove to give the best, or most sensitive results. Amongst butterflies, HesperIIDae show relatively very low levels of endemism, which de Jong (1990) has suggested is a reflection of their strong capacity for dispersal. It remains to be seen, therefore, if the clear and consistent patterns for the diversity of Philippine HesperIIDae found here will be repeated, or contradicted, by similar analyses of the more endemic Papilionoidea - and how any patterns found compare with other groups for which comparable data are available (such as birds, mammals and palms).

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Table A1. Hierarchical codes (see Vane-Wright et al., in press) expressing inter-relationships of Philippine hesperiid genera and species, mainly based on Evans (1949). The Pyrginae (21...) + Hesperinae (22...) are treated as sister group to the Coeliadinae (1...). To include subspecies (not shown here), where particular species include more than one subspecies within the Philippines, these are simply coded as terminal polychotomies (...1, ...2, ...3), etc. Letters are used instead of arabic numerals where unresolved parts of the classification exceed nine components (as with species of the genus *Halpe*).

<i>Bibasis oedipodea</i>	(111)	<i>Halpe zema</i>	(22122A)	<i>zeus</i>	(223212)
<i>etelka</i>	(112)	<i>ormenes</i>	(22122B)	<i>zenon</i>	(223213)
<i>harisa</i>	(113)	<i>palawea</i>	(22122C)	<i>Gangara thyrasis</i>	(223221)
<i>gomata</i>	(114)	<i>luteisquama</i>	(22122D)	<i>lebadea</i>	(223222)
<i>senia</i>	(115)	<i>latipinna</i>	(22122E)	<i>Erionota thrax</i>	(223231)
<i>Hasora proxissima</i>	(121)	<i>dante</i>	(22122F)	<i>hiraca</i>	(223232)
<i>borneensis</i>	(122)	<i>beturia</i>	(22122G)	<i>surpresa</i>	(223233)
<i>chromus</i>	(1231)	<i>toxopea</i>	(22122H)	<i>sybirita</i>	(223234)
<i>taminatus</i>	(1232)	<i>pelethronix</i>	(22122I)	<i>torus</i>	(223235)
<i>choenherr</i>	(1233)	<i>inconspicua</i>	(22122J)	<i>Matapa aria</i>	(223241)
<i>mixta</i>	(1241)	<i>purpurascens</i>	(22122K)	<i>intermedia</i>	(223242)
<i>badra</i>	(1242)	<i>Koruthaialos rubecula</i>	(22211)	<i>celsina</i>	(223243)
<i>quadripunctata</i>	(1243)	<i>sindu</i>	(22212)	<i>Unkana ambasa</i>	(22331)
<i>vitta</i>	(1244)	<i>Psolos fuligo</i>	(2222)	<i>Hidari irava</i>	(22332)
<i>moestissima</i>	(12451)	<i>Ancistroides nigrita</i>	(2223)	<i>Acerbas anthea</i>	(223331)
<i>caeruleostriata</i>	(12452)	<i>Notocrypta paralysos</i>	(22241)	<i>duris</i>	(223332)
<i>khoda</i>	(1251)	<i>clavata</i>	(22242)	<i>Pirdana hyela</i>	(223341)
<i>leucospila</i>	(1252)	<i>howartha</i>	(22243)	<i>fusca</i>	(223342)
<i>Badamia exclamationis</i>	(13)	<i>feisthamelii</i>	(22244)	<i>Taractrocera luzonensis</i>	(2241)
<i>Choaspes plateni</i>	(141)	<i>Suada cataleucos</i>	(2231A1)	<i>Oriens gola</i>	(22421)
<i>estrella</i>	(142)	<i>albinus</i>	(2231A2)	<i>californica</i>	(22422)
<i>subcaudatus</i>	(143)	<i>Suastus minutus</i>	(2231B1)	<i>ons</i>	(22423)
<i>Celaenorrhinus nigricans</i>	(2111)	<i>migreus</i>	(2231B2)	<i>Potanthus omaha</i>	(22431)
<i>treadawayi</i>	(2112)	<i>Cupitha purreea</i>	(2231C)	<i>fettingi</i>	(22432)
<i>asmara</i>	(2113)	<i>Zographetus pallens</i>	(2231D1)	<i>niobe</i>	(22433)
<i>bazilanus</i>	(2114)	<i>ogygia</i>	(2231D2)	<i>confucius</i>	(22434)
<i>halconis</i>	(2115)	<i>ogygioides</i>	(2231D3)	<i>mingo</i>	(22435)
<i>Tapena thwaitesi</i>	(21211)	<i>abima</i>	(2231D4)	<i>pava</i>	(22436)
<i>Darpa pteria</i>	(21212)	<i>rama</i>	(2231D5)	<i>ganda</i>	(22437)
<i>Odina hieroglyphica</i>	(21213)	<i>Oerane microthyrus</i>	(2231E)	<i>hetaerus</i>	(22438)
<i>Coladenia igna</i>	(212141)	<i>Hyarotis adrastus</i>	(2231F1)	<i>serina</i>	(22439)
<i>ochracea</i>	(212142)	<i>microsticta</i>	(2231F2)	<i>Telicota colon</i>	(22441)
<i>semperi</i>	(212143)	<i>iadera</i>	(2231F3)	<i>augias</i>	(22442)
<i>minor</i>	(212144)	<i>Quedara monteithi</i>	(2231G)	<i>ancilla</i>	(22443)
<i>similis</i>	(212145)	<i>Isma bononia</i>	(2231H1)	<i>ohara</i>	(22444)
<i>palawana</i>	(212146)	<i>binotatus</i>	(2231H2)	<i>hilda</i>	(22445)
<i>Gerosis limax</i>	(212211)	<i>eralia</i>	(2231H3)	<i>Cephrenes acalle</i>	(2245)
<i>corona</i>	(212212)	<i>Pyroneura flavia</i>	(2231I1)	<i>Prusiana prusias</i>	(2246)
<i>Tagiades japetus</i>	(2122211)	<i>agnesia</i>	(2231I2)	<i>Parnara bada</i>	(22511)
<i>gana</i>	(2122212)	<i>liburnia</i>	(2231I3)	<i>kawazoei</i>	(22512)
<i>parra</i>	(2122213)	<i>derna</i>	(2231I4)	<i>Borbo cinnara</i>	(2252)
<i>ultra</i>	(2122221)	<i>niasana</i>	(2231I5)	<i>Pelopidas agna</i>	(22531)
<i>trebellius</i>	(2122222)	<i>toshikoe</i>	(2231I6)	<i>mathias</i>	(22532)
<i>Mooreana princeps</i>	(212231)	<i>Plastingia naga</i>	(2231J1)	<i>conjuncta</i>	(22533)
<i>trichoneura</i>	(212232)	<i>pellonia</i>	(2231J2)	<i>Polytremis lubricans</i>	(2254)
<i>Odontoptilum angulatum</i>	(21231)	<i>viburnia</i>	(2231J3)	<i>Baoris oceia</i>	(2255)
<i>pygela</i>	(21232)	<i>Salanoemia sala</i>	(2231K1)	<i>Caltoris brunnea</i>	(22561)
<i>leptogramma</i>	(21233)	<i>similis</i>	(2231K2)	<i>bromus</i>	(22562)
<i>Aeromachus musca</i>	(22111)	<i>Xanthoneura telesinus</i>	(2231L)	<i>cormasa</i>	(22563)
<i>plumbeola</i>	(22112)	<i>Lotongus calathus</i>	(2231M)	<i>philippina</i>	(22564)
<i>Thoressa justini</i>	(22121)	<i>Zela excellens</i>	(223211)		

Table A2. Single-step priority-areas analysis for Philippine hesperiid genera, using Williams' WORLDMAP Version 3.04.

Diversity measure: TAXON RICHNESS (1)				Diversity measure: TAXON RICHNESS (2)			
choices step	island	diversity increment%	cumulative%	choices step	island	diversity increment%	cumulative%
1	Palawan	84.91	84.91	1	Mindanao	84.91	84.91
2	Mindanao	11.32	96.23	2	Palawan	11.32	96.23
3	Luzon	1.89	98.11	3	Luzon	1.89	98.11
4	Tawitawi	1.89	100.00	4	Tawitawi	1.89	100.00

Diversity measure: ENDEMISM WEIGHT				Diversity measure: DISPERSION			
choices step	island	diversity increment%	cumulative%	choices step	island	diversity increment%	cumulative%
1	Palawan	74.84	74.84	1	Mindanao	88.69	88.69
2	Luzon	15.62	90.46	2	Palawan	8.47	97.16
3	Mindanao	4.77	95.23	3	Luzon	1.42	98.58
4	Tawitawi	4.77	100.00	4	Tawitawi	1.42	100.00

Table A3. Single-step priority-areas analysis for Philippine hesperiid species, using Williams' WORLDMAP Version 3.04.

Diversity measure: TAXON RICHNESS				Diversity measure: ENDEMISM WEIGHT			
choices step	island	diversity increment%	cumulative%	choices step	island	diversity increment%	cumulative%
1	Mindanao	58.55	58.55	1	Palawan	58.86	58.86
2	Palawan	28.29	86.84	2	Mindanao	19.87	78.73
3	Luzon	3.95	90.79	3	Luzon	5.57	84.30
4	Tawitawi	2.63	93.42	4	Samar	3.94	88.25
5	Samar	1.97	95.39	5	Tawitawi	3.08	91.32
6	Negros	1.32	96.71	6	Leyte	2.37	93.69
7	Leyte	1.32	98.03	7	Negros	2.37	96.06
8	Mindoro	0.66	98.68	8	Mindoro	1.58	97.63
9	Marinduque	0.66	99.34	9	Dumaran	1.58	99.21
10	Dumaran	0.66	100.00	10	Marinduque	0.79	100.00

## Diversity measure: DISPERSION

choices step	island	diversity increment%	cumulative%
1	Mindanao	68.86	86.86
2	Palawan	21.56	90.42
3	Luzon	2.88	93.29
4	Tawitawi	1.92	95.21
5	Samar	1.44	96.65
6	Negros	0.96	97.60
7	Leyte	0.96	98.56
8	Mindoro	0.48	99.04
9	Dumaran	0.48	99.52
10	Marinduque	0.48	100.00

Table A4. Single-step priority-areas analysis for Philippine hesperiid subspecies, using Williams' WORLDMAP Version 3.04.

Diversity measure: TAXON RICHNESS (1)				Diversity measure: TAXON RICHNESS (2)			
choices step	island	diversity increment%	cumulative%	choices step	island	diversity increment%	cumulative%
1	Palawan	58.55	44.95	1	Mindanao	58.55	44.95
2	Mindanao	28.29	74.75	2	Palawan	28.29	74.75
3	Luzon	3.95	81.82	3	Luzon	3.95	81.82
4	Tawitawi	2.63	86.36	4	Tawitawi	2.63	86.36
5	Samar	1.97	89.90	5	Samar	1.97	89.90
6	Negros	1.32	92.93	6	Negros	1.32	92.93
7	Leyte	1.32	94.95	7	Leyte	1.32	94.95
8	Mindoro	0.66	95.96	8	Mindoro	0.66	95.96
9	Marinduque	0.66	96.97	9	Marinduque	0.66	96.97
10	Sibutu	0.66	97.98	10	Sibutu	0.66	97.98
11	Sibuyan	0.51	98.48	11	Sibuyan	0.51	98.48
12	Babuyan	0.51	98.99	12	Babuyan	0.51	98.99
13	Busuanga	0.51	99.50	13	Busuanga	0.51	99.50
14	Dumaran	0.51	100.00	14	Dumaran	0.51	100.00

Diversity measure: ENDEMISM WEIGHT				Diversity measure: DISPERSION			
choices step	island	diversity increment%	cumulative%	choices step	island	diversity increment%	cumulative%
1	Palawan	47.02	47.02	1	Mindanao	59.05	59.05
2	Mindanao	17.09	64.12	2	Palawan	22.75	81.80
3	Luzon	8.73	72.85	3	Luzon	5.60	87.40
4	Tawitawi	5.77	78.62	4	Tawitawi	3.15	90.55
5	Negros	5.34	83.96	5	Samar	2.45	93.00
6	Samar	4.56	88.52	6	Negros	2.10	95.10
7	Leyte	2.91	91.43	7	Leyte	1.40	96.50
8	Mindoro	1.94	93.37	8	Sibutu	0.70	97.20
9	Sibutu	1.94	95.31	9	Mindoro	0.70	97.90
10	Marinduque	1.46	96.77	10	Marinduque	0.70	98.60
11	Babuyan	0.97	97.74	11	Busuanga	0.35	98.95
12	Busuanga	0.97	98.71	12	Sibuyan	0.35	99.30
13	Dumaran	0.97	99.68	13	Dumaran	0.35	99.65
14	Sibuyan	0.32	100.00	14	Babuyan	0.35	100.00

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Page numbers only refer to the text in the chapters 'Annotated list of the HesperIIDae' and 'Biogeography'. Further references, for instance to figures and tables, can be found there.

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