

Halmahera and Seram: different histories, but similar butterfly faunas

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Abstract

The islands of Halmahera and Seram in the Moluccas (east Indonesia) have very different geological histories. Their present relative proximity is the result of a long westward journey of Halmahera. It is uncertain when the island emerged, and thus was first able to support a terrestrial fauna. Seram emerged at c.5 Ma at approximately its present location. On the basis of current geological scenarios, expected distribution patterns for terrestrial organisms are proposed. These patterns are tested using information on species distribution, endemism and phylogeny of butterflies.

The butterfly faunas of Halmahera and Seram are remarkably similar for faunas that have never been closer to each other than today. This is attributed to independent colonization by the same species from Sulawesi and particularly from New Guinea. The different geological histories of the two islands are not reflected in their butterfly faunas. Two possible reasons for this are suggested: either the older fauna of Halmahera was wiped out by later colonists, or Halmahera only emerged as recently or even later than Seram.

Endemism in the Moluccas is high (21.3% of the 385 species). Distribution patterns of the endemic species indicate that faunal exchange between the northern and southern islands of the Moluccas has been limited to less than 15% of the 82 endemic species. This is a further indication that the similarity between Halmahera and Seram is not due to a direct exchange of species, but to independent invasions from outside by the same species.

Introduction

Halmahera and Seram are the largest islands of the east Indonesian province of Maluku (Fig.1). This province does not completely coincide with the old notion of Moluccas. Following Vane-Wright and Peggie (1994) the Moluccas have been taken here to include the sub-

provinces of N and C Maluku, but excluding Kepulauan Sula, which biogeographically forms part of the Sulawesi region, and the Banda and Gorong archipelagos. Halmahera is, at 17,400 km², the larger island, but at 16,720 km², Seram is only slightly smaller. The greater part of Halmahera lies north of the equator. Seram is situated well to the south, about 220 km from the southern tip of Halmahera. The island of Obi lies at about one third of this distance from Halmahera to Seram. Halmahera and Seram share the same humid and hot climate, with an average yearly rainfall of 1,500-2,000 mm and lowland temperatures varying between 25°C and 30°C. Monsoons and mountains affect the rainfall, but it is still rather generally distributed throughout the year. The natural vegetation is rain forest. There is still untouched forest left, but, particularly in Halmahera, deforestation is proceeding fast. There is a marked difference in height, the highest peak in Halmahera, Gunung Gamkunoro, reaching an altitude of 1635 m, while Gunung Binaiya, the highest mountain of Seram, ascends to 3027 m. As a consequence, Seram is more diverse in terms of habitat.

Halmahera and Seram are situated more or less halfway between Sulawesi and New Guinea, but smaller islands to the east and west of Halmahera and Seram reduce their degree of isolation from these far larger islands. Between the northeastern tip of Sulawesi and Halmahera, a slightly larger distance than between Halmahera and Seram, there are only two tiny islands, Mayu and Tifore, whereas between Halmahera and New Guinea, also a slightly

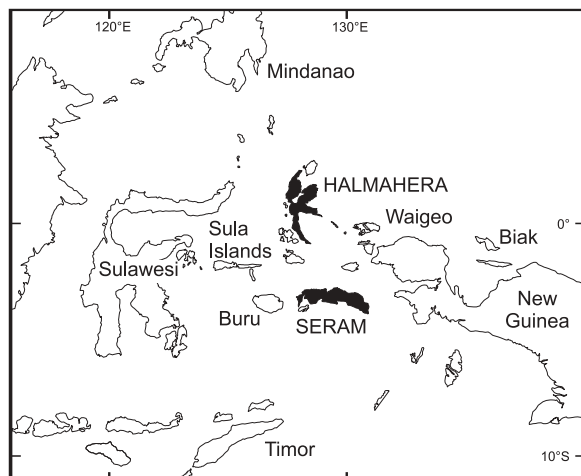


Fig. 1. Location of Halmahera and Seram in east Indonesia.

larger stretch of water than between Halmahera and Seram, there are several islands, such as Gebe, Gag and Waigeo. Seram is separated from New Guinea by about 140 km, but the distance to Sulawesi is considerably greater, about 550 km. There are, however, several islands between Seram and Sulawesi, including Buru, and the Sula and Banggai archipelagos, which could serve as stepping stones.

In spite of their relative isolation, Halmahera and Seram have remarkably similar butterfly faunas. Of the 200 species known from Halmahera 58.5% are also found in Seram, while 52% of the 225 butterfly species of Seram is also found in Halmahera. Applying Jaccard's coefficient of similarity (Krebs, 1989), the butterfly faunas of Halmahera and Seram (total fauna 304 species) are exactly as similar ($S_j = 0.39$) as the butterfly faunas of Spain and Northwest Africa (total fauna 243 species; data from Tennent, 1996, and Vives Moreno, 1994), which are, however, only 15 km apart, and not 220 km like Halmahera and Seram. Knowing that the two islands have very different geological histories, it is of interest to investigate the possible causes of this similarity. The history of the areas is taken as a starting point rather than something to be derived from the distribution of organisms. Thus, the present contribution is not concerned with the relationship of areas, but with the history of existing faunas and how this may have been affected by the history of the areas. Since the areas concerned (Halmahera, Seram, Sulawesi and New Guinea) have never been connected by land, similarities between any two of the areas in

terms of shared taxa must be the result of long distance dispersal, and not of range fragmentation. A fauna typically consists of species exhibiting a spectrum of range sizes, from narrow endemics to wide-ranging or even cosmopolitan species. A study of the history of a fauna should address all elements of this fauna, and not just the narrow endemics. This will be elaborated further in the section below on Methods.

Wallace (1869) claimed a predominantly New Guinea origin for the avifauna of the Moluccas, but later students (*e.g.*, Bowler and Taylor, 1993) stressed the strong Asian representation in the bird faunas of the Moluccas and New Guinea, and Gressitt (1982) estimated that 60-95% of the Papuan fauna (depending on the group of animals under study) had Oriental origins. The present paper is not concerned with such larger scale distributional histories, but investigates only the biogeographic links in the butterfly faunas of Halmahera and Seram, and with Sulawesi and New Guinea. Even so, this may help to understand the biogeographic history of the whole of the Moluccas.

Methods

In biogeographic studies of the last 15 years, an approach has dominated in which the history of areas is considered the crucial factor in the distribution of life. This approach originated from the work of Croizat (*e.g.*, 1962). The coupling of phylogenetic data to geological history, the basis of cladistic biogeography, has led to very fruitful research, partly thanks to the development of computer hardware and software able to evaluate large amounts of data (*e.g.*, the COMPONENT program of Page, 1993). In this approach areas are considered related in terms of a shared biological history (as expressed in the phylogenies of the studied organisms). It leads to a hypothesis of area history, which can be corroborated or falsified by geological data. This approach, though robust, does not deal with faunas, but with informative taxa. In this context, informative means that taxa may reflect the history of the areas where they occur. The more widespread a taxon is, the less informative it is in this sense. As a consequence, cladistic biogeography may reveal and explain historical patterns of areas and distributions, but only part of the distributional history of the fauna as a whole, which indeed is a mixture of old and new species, with old and new distributional patterns.

There are some practical problems in the application of the method, particularly in the detection and meaning of areas of endemism, and in the synchrony of speciation patterns. By its procedure, cladistic biogeography is an inductive method. It leads to hypotheses which can only be tested by evidence from outside, *e.g.*, geology. This can be a mutually beneficial enterprise. However, if the geological history is well-established or if there are competing geological hypotheses, it may be more effective to apply a hypothetico-deductive method, meaning that on the basis of geological knowledge, hypotheses of distributional patterns are formulated, which then can be tested against actual patterns. Such patterns can, but need not, be phylogenetic, and no part of the fauna is excluded beforehand. The author has applied this approach before (*e.g.*, de Jong and Congdon, 1993; de Jong and Treadaway, 1993; de Jong, 1997a), and it will be followed here.

The overall question to be answered in this contribution is: are the different geological histories of Halmahera and Seram reflected in different distributional patterns in the butterfly faunas of these islands? If not, what possible causes could there be? Problems not addressed here include the origin of the faunas of Sulawesi and New Guinea. After a short explanation of the geological histories of Halmahera and Seram, the patterns to be tested are formulated.

Geological history of Halmahera and Seram

Halmahera consists of a younger western volcanic part and an eastern part. The two parts collided between 3 and 1 Ma (Hall and Nichols, 1990). The oldest rocks in the basement of eastern Halmahera are of Cretaceous or greater age (see Hall *et al.* 1995, for a summary of the geology of the Halmahera region). The island originated far east of its present position as part of an arc system bordering the Pacific plate. The Halmahera islands have a stratigraphic record which indicates that for most of the Cenozoic they were submerged although with a prolonged, albeit discontinuous, volcanic arc history and were at least locally emergent for short intervals (Hall, 1987; Hall *et al.*, 1995 and references therein). The east Philippine islands (the east Philippine arc of Hall, 1996) also belonged to this arc system. Halmahera and surrounding islands (*e.g.*, Waigeo, Biak, Yapen and parts of present-day northern New Guinea, such as the Gaultier Mountains) formed a broadly continu-

ous arc during the Oligocene (Hall, 1998 this volume).

It is not certain from the literature when the islands of the Halmahera arc emerged. In a Late Eocene reconstruction of the New Guinea-Bismarck region, Struckmeyer *et al.* (1993) supposed that in the Halmahera arc parts of Halmahera, Waigeo and Gaultier were dry land. At the time, the northern half of New Guinea was little more than a number of allochthonous terranes carrying partly widely separate, submerged or emerged islands (see Boer, 1995, for a summary). The terranes successively accreted to the northern craton of the Australian plate, starting with the Sepik terrane, about 25 Ma, while the Arfak terrane, supposed to have originally been part of the Halmahera arc, only accreted to New Guinea at 2 Ma according to Pigram and Davies, 1987 (cf. Hall, 1998 this volume). Accretion and uplift finally shaped present-day New Guinea but, at the time of origin of Halmahera, New Guinea did not exist in its present form. What did exist were some emergent islands of the Sepik terrane (Central New Guinea) to the southwest of the Halmahera arc while the Kemum terrane, with a relatively large emergent part (according to Struckmeyer *et al.*, 1993) and the Misool terrane, with a small emergent part, were located far to the west. The Kemum terrane forms the greater part of the present-day Bird's Head of New Guinea, situated to the east of Misool.

According to Rangin *et al.* (1990) and others, at 10 Ma Halmahera lay approximately 800 km southeast of its present position. Between 8 and 4 Ma it (or rather the still separated western and eastern parts) passed by the Bird's Head. It reached its present position recently, and is still moving westward. During its entire life Halmahera has never been close to any part of Sulawesi; it has always been closer to, or associated with, terranes that finally accreted with New Guinea. Furthermore, the east Philippine islands have always been closer to Halmahera than to Sulawesi (see reconstructions in Hall, 1996).

The origin of Seram is still a matter of debate, although it is not doubted that its roots are Australian. Some authors suppose that it formed a microcontinent with Buru. This block probably rifted from the Australian continent, possibly from as far east as central Papua New Guinea (*e.g.*, Pigram and Panggabean, 1984), or from northwestern Australia (*e.g.*, Daly *et al.*, 1991). According to Hall (1996), Seram moved eastward relative to the Bird's Head, from 12-4 Ma,

and northward to its present position relative to the Bird's Head, from 4-0 Ma. Biogeographically the uncertainties about the early evolution of Seram are not important. According to Audley-Charles (1986, 1993), there was no land between the coast of Australia-New Guinea and Sulawesi before the Miocene emergence. As shown by sedimentary rocks, Seram was beneath the sea until about 6 Ma. Fortuin and de Smet (1991) estimate the time of emergence of Seram at 5 Ma. It emerged by uplift, and it has never been connected to other land areas, a deep marine trough separating it from New Guinea and Misool. Nevertheless, New Guinea was the closest land area. According to the reconstructions by Hall (1996), at 5 Ma Buru and the Sula archipelago, which at present form the connecting link with Sulawesi, were still far to the north of Seram.

Patterns to be expected

Based on different geological histories and different or similar ages for the terrestrial faunas of Halmahera and Seram, the following biogeographic patterns can be expected.

General

Different histories are supposed to lead to different faunas. Conversely, do similar faunas have similar histories? The similarity between faunas can be expressed in several ways. It is usually measured at the species level, but in addition there are other ways of measuring similarity. One way is similarity above the species level, as will be explained below. The other way is by comparing what is here called distribution profiles, a breakdown of a regional fauna according to distribution patterns. It is an overall comparison from which some conclusions can readily be drawn. Faunas of historically different areas are supposed to have different distribution profiles. In other words, Halmahera and Seram would be predicted to have different profiles, unless the early history of Halmahera has not left any traces, because of extinction or because Halmahera was submerged (pattern A).

Age

In the absence of fossils or other clues to (relative or absolute) age, we must resort to more

indirect clues. Supposing that some part of (proto-)Halmahera has always remained sub-aerial, a greater age and longer period of isolation could have had the following effects on the fauna of Halmahera relative to Seram:

B1: Presence of older species. This can only be checked in monophyletic groups with endemic representatives in Halmahera, Seram and at least one other area.

B2: Higher endemism. Apart from speciation rate, degree of endemism depends on diversity of habitats and degree of isolation, either in time or in space. Since Seram has more diverse habitats due to higher altitudes, it could be expected to have more endemics than Halmahera, if other things, including age and degree of isolation, were equal. If Halmahera has an equal or higher endemism than Seram, either it is older or it has been more strongly isolated in space, or both.

B3: Reduced similarity to New Guinea. Due to speciation and extinction, not only in Halmahera but in New Guinea as well. This would also apply to Sulawesi if Halmahera had originated in its present position, which we know it did not. Clearly this pattern only makes sense if proto-Halmahera was close enough to proto-New Guinea to exchange organisms.

Topographic origin and subsequent history

The differences between Halmahera and Seram in history could have led to the following different patterns:

C1: There has not been much difference between Halmahera and Seram in the degree of isolation from Sulawesi. When Seram emerged from the sea it was probably closer to Sulawesi than Halmahera, then to the north of the Bird's Head, but Buru and the Sula islands were still so far to the north that they could not function as stepping stones between Sulawesi and Seram. When they reached that position, Halmahera also reached its present position. Consequently, the expected pattern is a comparable degree of similarity between the faunas of Halmahera and Sulawesi on one hand, and between those of Seram and Sulawesi on the other.

C2: If Halmahera was sub-aerial from Eocene times and it received butterflies at such an early date, the butterfly fauna would not have been very different from the fauna found on other islands of the Halmahera arc, like Waigeo and Gaultier, and after emergence also Biak, Yapen and Arfak. An indication for the existence of such a fauna would be distribution patterns in-

volving some of these areas and excluding other areas.

C3: Whatever the time of emergence, Halmahera has always been closer to New Guinea than to Sulawesi; consequently, it can be expected that the similarity of the Halmahera fauna with the New Guinea fauna should be much greater than with the Sulawesi fauna.

C4: Since Seram emerged much closer to New Guinea than to other areas of dry land, it can be expected to carry a fauna that is much more similar to the fauna of New Guinea than to the fauna of Sulawesi.

C5: If the fauna of Seram actually came from New Guinea, the ties with New Guinea are older than with Sulawesi, since Buru and the Sula archipelago could only act as stepping stones at a much later date. Consequently, among the New Guinea links would be older species than among the Sulawesi links. This can only be tested in cases of endemics in the three areas forming a monophyletic or paraphyletic group. Biogeographically it seems an unlikely pattern.

C6: Halmahera and Seram have never been closer to each other than nowadays, and have never been connected directly or indirectly. Similarity between the two islands can be expected to involve mainly widespread species (at least covering New Guinea, in addition to Halmahera and Seram), and species only occurring in Halmahera and Seram are not to be expected, unless by chance dispersal.

The expected patterns are based on the supposition that butterflies have existed in the area at least since the origin of Halmahera. The supposition may be self-evident, but the presence of the butterflies is not. The oldest fossil butterfly remains are about 50 Ma old (de Jong, 1997b) but the butterflies as a taxon must be much older. Undoubtedly, when (proto-) Halmahera and surrounding islands emerged in the Tertiary, the butterflies as a group already existed, but the young islands may have been too isolated for the first butterflies to reach them at a very early date.

Patterns actually found

Distribution profile

Table 1 gives the number of species per butterfly family in Halmahera and Seram, and the number of species also occurring in Sulawesi and New Guinea. In Tables 2 and 3 these numbers have been broken down to distribution pat-

Table 1. Number of butterfly species in Halmahera and Seram, with the numbers of these species also occurring in Sulawesi and/or New Guinea.

| | Sulawesi | Halmahera | Seram | New Guinea |
|--------------|----------|------------|------------|------------|
| Hesperiidae | 19 | 25 | 32 | 30 |
| Papilionidae | 10 | 20 | 17 | 13 |
| Pieridae | 12 | 23 | 30 | 12 |
| Lycaenidae | 34 | 54 | 72 | 60 |
| Nymphalidae | 38 | 78 | 74 | 62 |
| Total | 113 | 200 | 225 | 177 |

terns, and for each distribution pattern the percentages of the species relative to the total number of species in Halmahera and Seram, respectively, are given. In Fig. 2 the percentages of Tables 2 and 3 are represented graphically in a distribution profile, which allows a quick comparison of the faunas of Halmahera and Seram. Although there are slight differences in the percentages, the profiles for the two islands are remarkably similar, suggesting a largely similar biogeographic history for the butterflies. It is also clear that a greater part of the faunas (55.6% in Seram, 59.8% in Halmahera) is widespread, *i.e.*, involving at least three areas. This is to be expected in islands that were colonized by long distance dispersal over about the same length of time. The profiles further show that the Sulawesi connection excluding New Guinea is much weaker (Halmahera 26 species or 13.3%, Seram 27 species or 12.2%) than the New Guinea connection excluding Sulawesi (Halmahera 70 species or 35.3%, Seram 76 species or 33.7%). It not only agrees with the supposition that Halmahera and Seram have always been closer to New Guinea, but also shows that the degree of isolation with respect to Sulawesi and New Guinea has been about the same for the two islands (see above, expected general pattern).

Similarity at the species level

Many coefficients are available to express the similarity of two regional faunas, or two samples in general (Krebs, 1989). Applying Jaccard's coefficient (proportion of shared species relative to total number of species in the two areas) we find that the butterfly faunas of Halmahera and Sulawesi, and those of Seram and Sulawesi are equally similar, in both cases $S_j = 0.04$. The same

Table 2. Numbers and percentages of non-endemic butterfly species of Halmahera, divided over the seven possible distribution patterns. For coding of distribution patterns, see Fig. 2.

| Halmahera | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|--------------|-----|-----|------|-----|-----|----|----|
| Hesperiidae | 4 | 0 | 1 | 2 | 1 | 8 | 9 |
| Papilionidae | 2 | 2 | 1 | 2 | 1 | 4 | 3 |
| Pieridae | 1 | 2 | 1 | 2 | 0 | 3 | 5 |
| Lycaenidae | 1 | 1 | 12 | 3 | 6 | 11 | 10 |
| Nymphalidae | 3 | 3 | 11 | 6 | 2 | 18 | 22 |
| total | 11 | 8 | 26 | 15 | 10 | 44 | 49 |
| percentage | 5.6 | 4.1 | 13.3 | 7.7 | 5.1 | 22 | 25 |

applies to the similarity of the butterfly faunas of Halmahera and New Guinea on one hand, and that of Seram and New Guinea on the other, in both cases the coefficient being $S_j = 0.08$. Thus we find that the butterfly faunas of Halmahera and Seram are (a) equally similar to the faunas of Sulawesi and New Guinea respectively (contra expected pattern B3, but in agreement with expected pattern C1), and (b) have a much greater similarity to New Guinea than to Sulawesi. The latter finding is not surprising since the New Guinea fauna is much richer (estimated to be at least 800 species) than the Sulawesi fauna (470 species). However, New Guinea is a very large island and many of its species occur further away from Halmahera than

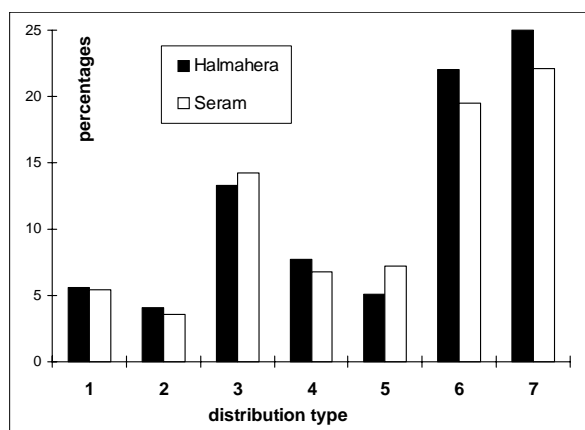


Fig. 2. Distribution profiles for Halmahera and Seram. The distribution types are numbered 1-7, meaning Halmahera or Seram with: 1, Sulawesi; 2, Seram, respectively Halmahera; 3, New Guinea; 4, Sulawesi and Seram, respectively Halmahera; 5, Sulawesi and New Guinea; 6, New Guinea and Seram, respectively Halmahera; 7, Halmahera, Seram, Sulawesi and New Guinea. The frequency of the distribution types is given as percentages of the fauna of Halmahera and Seram, respectively, without endemics.

Table 3. Numbers and percentages of non-endemic butterfly species of Seram, divided over the seven possible distribution patterns. For coding of distribution patterns, see Fig. 2.

| Seram | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|--------------|-----|-----|------|-----|-----|------|------|
| Hesperiidae | 1 | 0 | 9 | 2 | 2 | 8 | 9 |
| Papilionidae | 0 | 2 | 2 | 2 | 2 | 4 | 3 |
| Pieridae | 2 | 2 | 1 | 2 | 2 | 3 | 5 |
| Lycaenidae | 6 | 1 | 13 | 3 | 8 | 11 | 10 |
| Nymphalidae | 3 | 3 | 7 | 6 | 2 | 18 | 22 |
| total | 12 | 8 | 32 | 15 | 16 | 44 | 49 |
| percentage | 5.4 | 3.6 | 14.2 | 6.8 | 7.2 | 19.5 | 22.1 |

the average Sulawesi species. Thus, the greater similarity of the Moluccan islands to New Guinea than to Sulawesi appears to be the result not only of the richer New Guinea fauna but of the shorter distance. This is in agreement with expected patterns C3 and C4.

Similarity above the species level

Similarity at the species level may be reduced by extinction and speciation after the dispersal event. Since Halmahera and Seram have endemic species, it is clear that speciation has occurred in the islands. Finding their sister species either in New Guinea or Sulawesi would strengthen the ties with these areas. For this we need phylogenetic studies. Phylogenetic information on the endemics is available for very few species only. These cases will be discussed. In some other cases an approximation can be made by checking the overall distribution of the genus; if it occurs only either east or west of the Moluccas, we can be reasonably sure that the sister species of the relevant endemic also occurs only east or west of the islands. These will be discussed here as well.

Ornithoptera croesus Wallace, 1859. The species occurs on Halmahera, Bacan, Ternate, Tidore and Morotai. The occurrence on Sanana in the Sula archipelago, from where only a single female is known, needs checking (Collins and Morris, 1985), but is almost certainly erroneous (Vane-Wright, pers. comm., 1997). The taxon is on the verge of specific distinctness from *O. priamus* (Linnaeus, 1758) (S Moluccas and New Guinea), and the two, together with *O. aesacus* (Ney, 1903) (Obi) and *O. urvillianus* (Guérin-Méneville, 1830) (Bismarck archipelago, Bougainville, Solomon Islands), can be considered to form a superspecies (Parsons,

1996). Thus, biogeographically, *O. croesus* is linked with New Guinea (directly or through S Moluccas), and not with Sulawesi.

Troides criton (C. and R. Felder, 1860). According to Tsukada and Nishiyama (1980), *T. criton* (Halmahera, Bacan, Obi) forms an unresolved trichotomy with *T. plato* Wallace, 1865 (Timor) and *T. haliphron* (Boisduval, 1836) (Sumba to Tanimbar, S Sulawesi). Together they form an unresolved trichotomy with *T. riedeli* (Kirsch, 1885) (Tanimbar) and *T. vandepolli* (Snellen, 1890) (Java, Sumatra). Although with the present distribution area of this group of species we must assume extinction in the greater part of Sulawesi to understand how *T. criton* could ever reach the northern Moluccas, the absence of any related species in New Guinea indicates that the link is to the west and not to the east.

Papilio deiphobus Linnaeus, 1758. According to Tsukada and Nishiyama (1980) this widespread Moluccan endemic forms part of an unresolved monophyletic group of seven species, distributed throughout the Oriental region, including Sulawesi and the Lesser Sunda Islands as far east as Timor. No relatives occur in New Guinea.

Papilio beringi Niepelt, 1924. Hancock (1983) believes this endemic of Halmahera to be a natural hybrid between *P. tydeus* (C. and R. Felder, 1860) and *P. fuscus* Goeze, 1779, whereas Racheli and Haugum (1983) reassessed its specific status in accordance with Tsukada and Nishiyama (1980). If considered a proper species, it belongs to a supposedly monophyletic group of eight species with a distribution from the Moluccas eastward. In this case it is clearly one of the New Guinea links of Halmahera.

Papilio gambrisius Cramer, 1777 (S Moluccas), and *P. tydeus* C. and R. Felder, 1860 (N Moluccas). Hancock (1983) showed the two species (Fig.3) to be sister species. Together they have as a sister species *P. aegeus* Donovan, 1805, which is distributed from New Guinea and satellite islands to Australia and the Pacific. The three species together have as sister group two species from the Solomon Islands and Admiralty Island, respectively. They all belong to the *aegeus* group of nine species, which together have an eastern distribution; the Moluccas and islands around Tanimbar being the western outposts.

Graphium stresemanni Rothschild, 1916. This species is either an endemic of Seram, with *G. batjanensis* Okano, 1984 (Bacan and, probably,

Halmahera) as sister, or the two taxa are conspecific. Its or their sister is *G. weiskei* Ribbe, 1900 from southeastern New Guinea (or the whole of New Guinea; Collins and Morris 1985). These taxa combined have as sister *G. macleayanum* Leach, 1814 from E Australia, Tasmania, Lord Howe Island and Norfolk Island (extinct now, Holloway, pers. comm. 1997; recently also known from New Guinea; Collins and Morris, 1985), and sister to all these taxa is *G. gelon* Boisduval, 1859 from New Caledonia.

Hypochrysops. The genus includes 57 species in 20 species groups (Sands, 1986). Except one species, *H. coelisparus* Butler, 1883, in S Thailand, Malaysia, Sumatra and some smaller islands, and a yet undescribed species from Sulawesi, the genus is restricted to the Australian region (including the Moluccas). Six species are endemic to the Moluccas. *H. chrysanthis* C. Felder, 1865, endemic to Seram and Ambon, forms a species group together with *H. coelisparus* and an Australian species, and thus has links to the west and to the east. All other Moluccan species have only links to the east, except that further knowledge of the Sulawesi species may disturb this pattern.

Luthrodes. This genus contains, in addition to the Moluccan endemic, *L. buruana* Holland, 1900 (Obi, Seram, Buru), only a single species in New Guinea and surrounding islands, and in Timor.

Phyliris. A large genus of 63 species, mainly endemics of New Guinea, but one species is restricted to Seram and Ambon, and another to Obi and S Moluccas; there are no species west of the Moluccas.

Ariadne. The Moluccas form the easternmost locality for this genus, which contains 10 species. The single Moluccan endemic, *A. obscura* Felder, 1865, is found on Halmahera, Bacan and Buru.

Mynes. Another genus of 10 species, but this one does not occur west of the Moluccas (with the exception of one species in Flores and Timor). One Moluccan endemic, *M. plateni* Staudinger, 1877, occurs on Bacan and Halmahera.

Sumalia. An Oriental genus of five species. Although the genus does not occur in Sulawesi, the Moluccan endemic, *S. staudingeri* Ribbe, 1898, from Seram and Ambon can have only western links.

Taenaris. A typical genus (25 species) of the Papuan sub-region, with only a single species (*T. horsfieldii* Swainson, 1820) in the Oriental region (Malaysia, Java, Borneo, Palawan). The

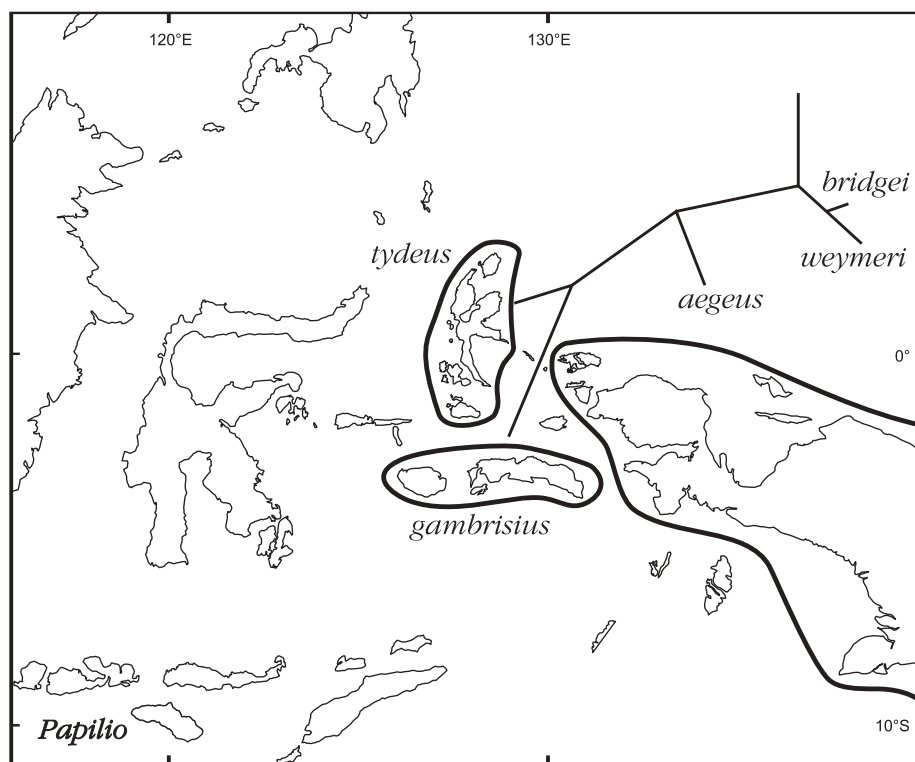


Fig.3. Phylogeny and distribution of the *Papilio aegeus* group (after Hancock, 1983).

five Moluccan species belong to three species groups (Stichel, 1912), which have only representatives to the east of the Moluccas.

Suniana. The three species in this genus are restricted to the Australian region, with one species extending to Timor, and another to Sumba. One species, *S. subfasciata* Rothschild 1915, is endemic to Seram and Ambon. The second Moluccan species, *S. sunias* Felder, 1860, is found in the N Moluccas, and as far east and south as Fiji and New South Wales in Australia. The genus is sister to another genus, *Ocybadistes*, with similar distribution (de Jong, 1990).

In addition to the genera dealt with here, there are other widespread genera which do not occur east of the Moluccas, but lack endemic species in the Moluccas, e.g., *Erionota*, *Iraota*, *Discolampa*, *Lethe*. Similarly, there are a number of eastern genera which do not occur west of the Moluccas, but lack endemic species in the Moluccas, e.g., *Netrocoryne*, *Hypochlorosis*, *Praetaxilia*, *Eutraeropsis*, *Apaturina*, *Tellerio*. The relevant species have been included in the similarity assessments of the regional faunas.

In summary, of the endemic species of the

Moluccas (at least for those which occur in Halmahera or Seram), four show exclusively western links, while 21 indicate a relationship with New Guinea. Halmahera and Seram differ slightly in the proportions: west-east scores 3-10 for Halmahera, and 3-12 for Seram, but the numbers are too low to attach much meaning to. In some cases, like *Papilio gambrisius/tydeus*, direct links between Halmahera and Seram are apparent. These results reinforce the conclusions based on similarity at the species level. For all other endemics there is currently no clue as to the geographic link.

Patterns of endemism

Most of the 82 endemic Moluccan species occur in two or more islands. The distribution is not random. Dividing the Moluccas into northern and southern groups of islands along a line between Seram and Obi (as done by Vane-Wright and Peggie, 1994), we find that 34 of the endemics occur only in the northern islands, 47 only on the southern islands, and 12 species (14.6%) on both sides of the dividing line. Moreover, four of the 12 widespread endemics occur north of the

line only in Obi, the southernmost island of the northern group. The pattern of endemism, thus, supports the division of the Moluccas into a northern and a southern group. This agrees well with the finding that the distribution pattern of the Moluccan endemics is non-random. Apparently, faunal interchange has been easier within the northern islands and within the southern islands, than it has been between these two island groups.

Only five (13.9%) of the 36 endemic Moluccan species in Halmahera are restricted to this island. For Seram these figures are 6 (13.6%) of the 44 endemic Moluccan species. Since there are only eight endemics occurring in both Halmahera and Seram, Halmahera has 28 endemics not occurring in Seram, and Seram has 36 endemics not occurring in Halmahera. This strengthens the impression that the line between Obi and Seram dividing the Moluccas into northern and southern islands, is not imaginary. It is in agreement with expected pattern C6.

Even if we suppose that all endemics occurring in Halmahera, except those also occurring in Seram, actually originated in Halmahera, and do the same for Seram, then Seram is still a richer centre of origin for endemics than Halmahera. This agrees with the expected pattern for faunas of comparable age, but differing in diversity of habitats (see expected pattern B2), and not with an older age for the Halmahera fauna.

Phylogenetic patterns

The little information available on the phylogeny of endemic species has already been discussed above. The only case known in which a monophyletic group of three endemic species can be distinguished, one in Halmahera, one in Seram, and the third in New Guinea (with possible extensions further south and east), is *Papilio gambrisius-tydeus-aegeus*. Since the two Moluccan species are sister species, they have the same age. A comparable case could be *Graphium stresemanni-batjanensis-weiskei*, depending on taxonomic decisions and exact distributions. Therefore, there is no phylogenetic evidence of an older age for the Halmahera endemics relative to the Seram endemics (see expected pattern B1). Similarly, there is no evidence for older connections between Seram and New Guinea than between Seram and Sulawesi (see expected pattern C5). The genera *Delias*, *Arhopala*, *Hypochrysoptis*, *Jamides* and *Taenaris*

are potential sources for this kind of information, since they all have endemics in Halmahera, Seram and New Guinea. Up to now, however, the great morphological similarity in these genera has frustrated attempts to analyse these taxa phylogenetically.

Halmahera arc pattern

This pattern could either involve species or monophyletic groups of species restricted to the former islands of the Halmahera arc (see expected pattern C2). As discussed in the previous paragraph, phylogenetic information is still too meagre to be of much help. The author knows of only one species with such a distribution, *Euploea morosa* Butler, 1866, which is found in the northern Moluccas, Misool, Biak and Numfoor. With eleven other *Euploea* species, this species forms an almost completely unresolved monophyletic group (Ackery and Vane-Wright, 1984). The existence of only one species (among the 196 species of Halmahera) showing this pattern is considered insufficient evidence for support. The nominate subspecies of *Erysichton palmyra* Felder, 1860 is found in the N and S Moluccas, Numfoor and Biak, but the species as a whole is widespread in the Papuan and Australian regions, and its sub-specific differentiation needs re-examination.

Conclusions

Despite distance and different histories, Halmahera and Seram have remarkably similar butterfly faunas. This can be attributed to similar positions relative to New Guinea and Sulawesi, which acted as source areas. New Guinea, with a much larger fauna than Sulawesi, contributed many more species. As shown by the pattern of endemism within the Moluccan islands, direct exchange between the northern and southern Moluccas apparently played a minor role. In the butterfly fauna there are no traces evident of the older history of Halmahera, but a number of possibly informative genera have not yet been analysed phylogenetically. As far as available evidence goes, we can only conclude that Halmahera remained submerged for most of its life and did not emerge before Seram, or traces of an older butterfly fauna have been wiped out by later immigrants. In both cases, the butterfly fauna of Halmahera, like that of Seram, is younger than that of New Guinea or Sulawesi.

Consequently, exchange will have been largely unidirectional, *i.e.*, into the Moluccas, although at a later stage exchange in the opposite direction may have taken place. With regard to the regional links of the faunas of the northern and southern Moluccas the conclusions generally agree with those of Vane-Wright and Peggie (1994) who studied the butterflies of the whole of the Moluccan islands with a different objective, and applied a slightly different approach.

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