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The Biogeography of the Butterfly Fauna of Vietnam With a Focus on the Endemic Species (Lepidoptera)

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<http://dx.doi.org/10.5772/55490>

1. Introduction

Long term studies of Vietnamese Rhopalocera suggest that by using a taxonomic composition analysis of the modern fauna, with ecological and biogeographical characteristics and comparative data with butterfly faunas of adjacent regions, it is possible to offer a plausible account of the history and derivation of the Vietnamese fauna. In former works on the butterfly fauna of Vietnam and of the Oriental tropics generally, we completed the first steps in understanding possible derivation mechanisms for the group. In particular, all Vietnamese butterfly species have been classified according to their global geographical ranges (Holloway, 1973; 1974; Spitzer *et al.*, 1993; Monastyrskii, 2006; 2007), from the most restricted to the most widespread (Methods). A similar approach for notodontid moths in Thailand has been adopted by Schintlmeister & Pinratana (2007). Moreover, depending on the representation of various species distribution range categories, a scheme of biogeographical zonation has been suggested (Monastyrskii, 2006; 2007).

In continuing studies on the specificity and derivation of the modern Vietnam butterfly fauna, aspects of species range configuration and other parameters of butterfly distributions are considered in the current work. For example, it is possible to assign genera to groups according to both their overall range and variation of their species-richness across that range (Holloway, 1969, 1974) or according to representation of particular species range types within the genera (Holloway, 1998). Application of the first approach led to recognition of several generic distribution types within the Oriental Region that provide a foundation for the discussion of species ranges presented in this paper, such as: genera with a species-richness generally distributed from Assam to Sundaland (Indo-Burmese in this paper); genera with their greatest richness in Sundaland (Sundanian in this paper); and genera with a strong centre of richness in western China and the eastern Himalaya (Sino-

Himalayan in this paper). Representation of genera in the third category was low in the analysis by Holloway (1969) because of the inadequacy of data available at that time and also because of the weakness of many generic concepts, but the category is epitomized by the *Zephyrus* group of genera covered by Koiwaya (2007). Though some of the taxonomic concepts in Koiwaya's work need further investigation for the Indochinese fauna, the gross figures indicate that over 30 species in this diverse generic complex occur in northern Vietnam and Laos, but very few penetrate further south than this. This will be seen to hold for the butterfly fauna in this generic category generally except for a small outpost in the Da Lat Mountains. Recent important studies on the biogeographical features of Vietnam, including relatively new geological and palaeontological information, are also considered (Takhtajan, 1986; Holloway & Hall, 1998; Tougaard, 2001; Averyanov *et al.*, 2003).

Consequences of tectonic collisions of the Indian Plate with the Eurasian Plate will have inevitably facilitated the mixing of previously isolated groups of plants and animals (Hall, 1998). This mixing will have promoted competition between taxa and resulted in the relative success of some taxonomic groups and the extinction of others. Further geological events included the rapid growth of the Himalayan mountain range whose development has split the formerly adjoined Asiatic and Southeast Asiatic faunas and floras (Hall, 1998; Sterling *et al.*, 2006). As well as these processes, global cooling and glacial events have also had an impact on the topographic and climatic history of this region and have greatly transformed compositions of many faunas (Tougaard, 2001; Outlaw & Voelker, 2007) including butterflies (Holloway, 1969; 1974). With the appearance of the Arctic ice sheet at the beginning of Pleistocene, large-scale global glaciations began. During this epoch a series of alternating processes of global warming and cooling have resulted in the cyclic reduction and extension of mainland and island areas, and the disappearance and appearance of connecting land bridges (Hanebuth *et al.*, 2000; Voris, 2000). Palynological data for the Late Quaternary in the Indochinese Peninsula are sparse, but suggest that conditions in the Late Glacial Maximum in the Peninsula and in southern China were cooler and drier than at present, with a change to warmer and wetter conditions at about 9000 years B.P. (Maxwell & Liu, 2002). These authors review data from lake sediments in the lowlands of the north-east of both Thailand and Cambodia that indicate development of dense forest with reduced fire activity in the warmer period, with evergreen 'islands' embedded in dry deciduous forest, the latter now strongly influenced by anthropogenic burning.

In accepting the landscape reconstructions of these epochs, as suggested by the Russian geologist Synitsin (1962, 1965) and later confirmed by many authors (e.g. Hall, 1998; 2002), from the beginning of Palaeocene, and perhaps even earlier, a geographically stable area of land has developed in Southeast Asia to form the Indochinese Peninsula. Configuration of this part of the mainland has changed insignificantly since the Mesozoic era. With such relative stability of the mainland, landscapes and climate weakly supported the forming and transforming of floristic and faunistic zonation. As a result the fauna and flora of this area demonstrate small changes even during major global climatic fluctuations. However, of particular relevance to Vietnam and the Indochinese Peninsula generally is the uplift of a series of mountain ranges on the eastern margin of the Peninsula. This uplift

occurred in various eras and epochs, but it has been more intensive during the Neogene. In this period several Asiatic and, in particular, Indochinese mountain systems have reached the elevations seen today (Averyanov *et al.*, 2003; Rundel, 1999). Such factors have impacted on the Vietnamese butterfly fauna, the modern composition and biogeographical structure of which are described below.

2. Methods

2.1. Study area and the collecting of material

The current studies are based on the materials collected in more than 60 sites of Vietnam, including 20 sites in 13 administrative provinces of northern of Vietnam; 30 sites (13 provinces) in central Vietnam and 10 sites (8 provinces) in southern part of the country. Site descriptions are represented in detail in Monastyrskii (2005, 2007). The collecting programme has been carried out from 1994 to 2008, managed by different Vietnamese research organizations and conservation NGO's based in Vietnam. A significant part of the research material has been provided by the collections of the Natural History Museum in London (BMNH) and the National Museum of Natural History in Paris (MNHN). Individuals were collected with different kinds of net allowing catching specimens from different strata within natural forests from the ground to canopies that can be as high as 8 metres. Standard butterfly traps were also operated during field works for collecting fruit-feeding butterfly species (DeVries, 1988; Austin & Riley, 1995; Tangah *et al.*, 2004; Monastyrskii, 2011).

2.2. Taxonomic foundation

Identification work has been carried out using modern taxonomic literature concerning the butterfly fauna of Vietnam (Monastyrskii, 2005; 2007, 2011) and adjacent areas (Corbet, Pendlebury & Eliot, 1992; Ek-Amnuay, 2006 *etc.*). Moreover an important part of the identification process has been based on original comparative work due to demonstrate distinctive characteristics of the local taxa. During this work over one hundred new species and subspecies representing all butterfly families have been described from 1995 up to date.

Biogeographical data can be classified according to (1) gross range types and (2) more topographical and habitat-based data from within Vietnam.

1. Global geographical ranges of Vietnamese butterflies suggested in our previous publications (Monastyrskii, 2006; 2007; 2010b) include nine categories: 1. Endemics of Indochina; 2. Sino-Himalayan species; 3. Indo-Burmese species; 4. Species with an Oriental (particularly Sundanian) distribution; 5. Species with an Indo-Australian distribution; 6. Species with a Palaearctic distribution extending into the Oriental region; 7. Old-World tropical species; 8. Holarctic species extending into the Oriental region; and 9. Cosmopolitan species (Fig. 1)

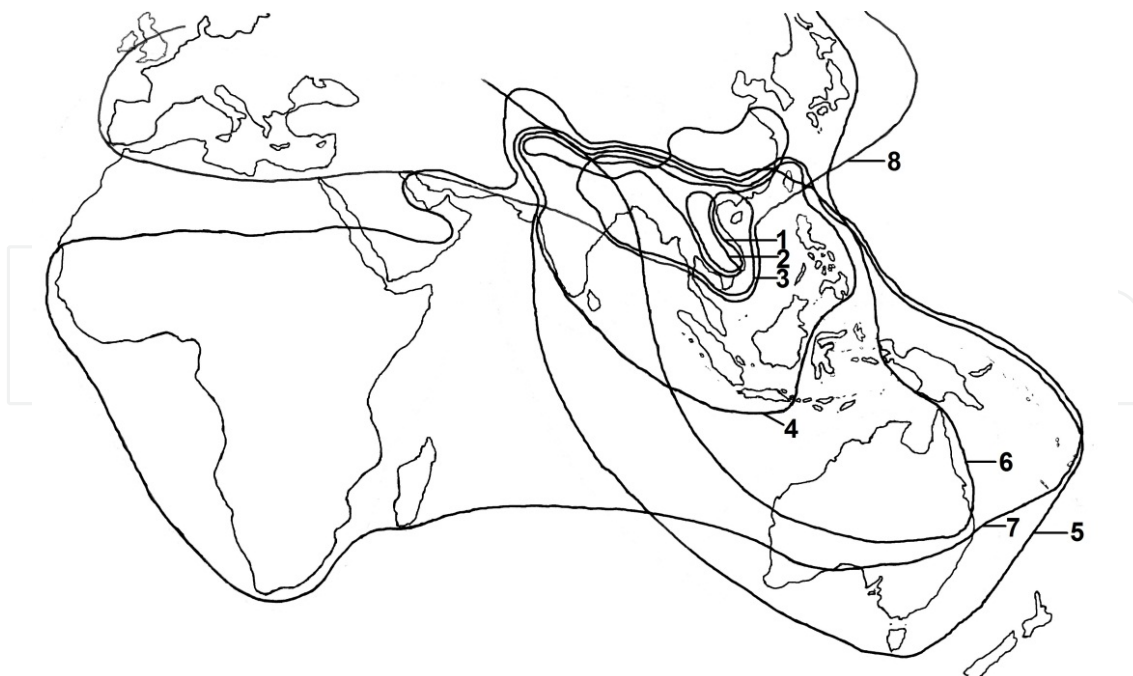


Figure 1. Boundaries of the Vietnamese butterfly biogeographical ranges: (1) Indochinese endemics, (2) Sino-Himalayan species, (3) Indo-Burmese species; (4) Indo-Malayan species, (5) Indo-Australian species, (6) Australo-Oriental-Palaearctic species; (7) Palaetropical species and (8) Holarctic species. The boundary of the sole cosmopolitan species (9) *Vanessa cardui* (Nymphalidae) is not shown.

2. Configurations of butterfly ranges in Vietnam, and in Indochina discussed in the current work, include the following types: **a.** isolated endemic ranges (Fig. 2A): 1. – *Lethe philemon* (Nymphalidae, Satyrinae); 2. – *Heliophorus smaragdinus* (Lycaenidae); 3. – *Euthalia hoa* (Nymphalidae, Limenitidinae) **b.** continuous and mosaic ranges (Fig. 2B): *Ypthima baldus* (Nymphalidae, Satyrinae); **c.** disjunct ranges (Fig. 2C): *Mycalesis unica* (Nymphalidae, Satyrinae); and **d.** vicarious ranges (Fig. 2D): six representatives of *Ypthima sakra* group (Nymphalidae, Satyrinae).

The great diversity of isolation factors can be demonstrated by the schematic landscape profiles drawn in the north-south direction across the entire Vietnam territory (Fig. 4); they reveal considerable variation in the altitudes. One profile (I) runs along the principal mountain ranges (above 2000 m) of Hoang Lien Son in the north and Truong Son in the central part of Vietnam (including Kon Tum and Da Lat Plateaux). The other profile (II) runs across the plains and low mountains (0–500 m) along the coastline. According to this diagram, there are two types of isolating barriers in Vietnam. Firstly, there are significant fluctuations in altitude in the north-south mountain ranges, isolating mountain faunas of the Truong Son Range (Da Lat and Kon Tum Plateaux, the northern Truong Son) and the Hoang Lien Son Range (the southern part of Yunnan Mountains). The relative position of altitude belts and the previously proposed subdivision of biogeographical provinces associated with them are shown in Fig. 1. Secondly, these mountain ranges themselves separate the coastal zone, itself also hilly, from other lowlands of the Indochinese Peninsula, which are found west of Profile I in the diagram.

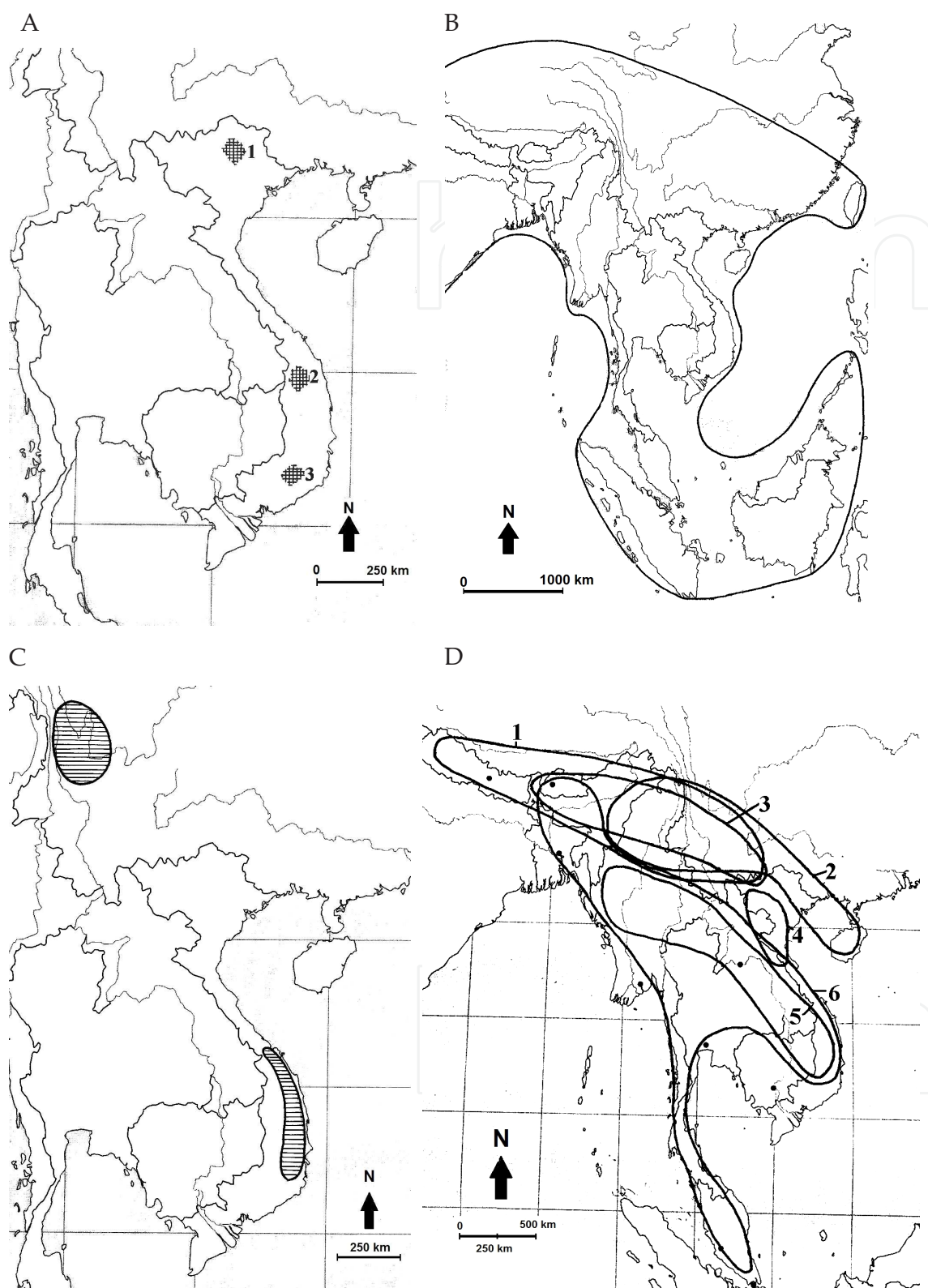


Figure 2. The main types of configurations of the butterfly ranges in Vietnam: A – Isolated (1 – *Lethe philemon*; 2 – *Heliophorus smaragdinus*; 3 – *Euthalia hoa*); B – Continuous (*Ypthima baldus*); C – Disjunct (*Mycalesis unica*); D – Vicarious (*Ypthima sakra* group): 1 – *Y. sakra*; 2 – *Y. atra*; 3 – *Y. persimilis*, 4 – *Y. pseudosavara*; 5 – *Y. evansi*; 6 – *Y. dohertyi*

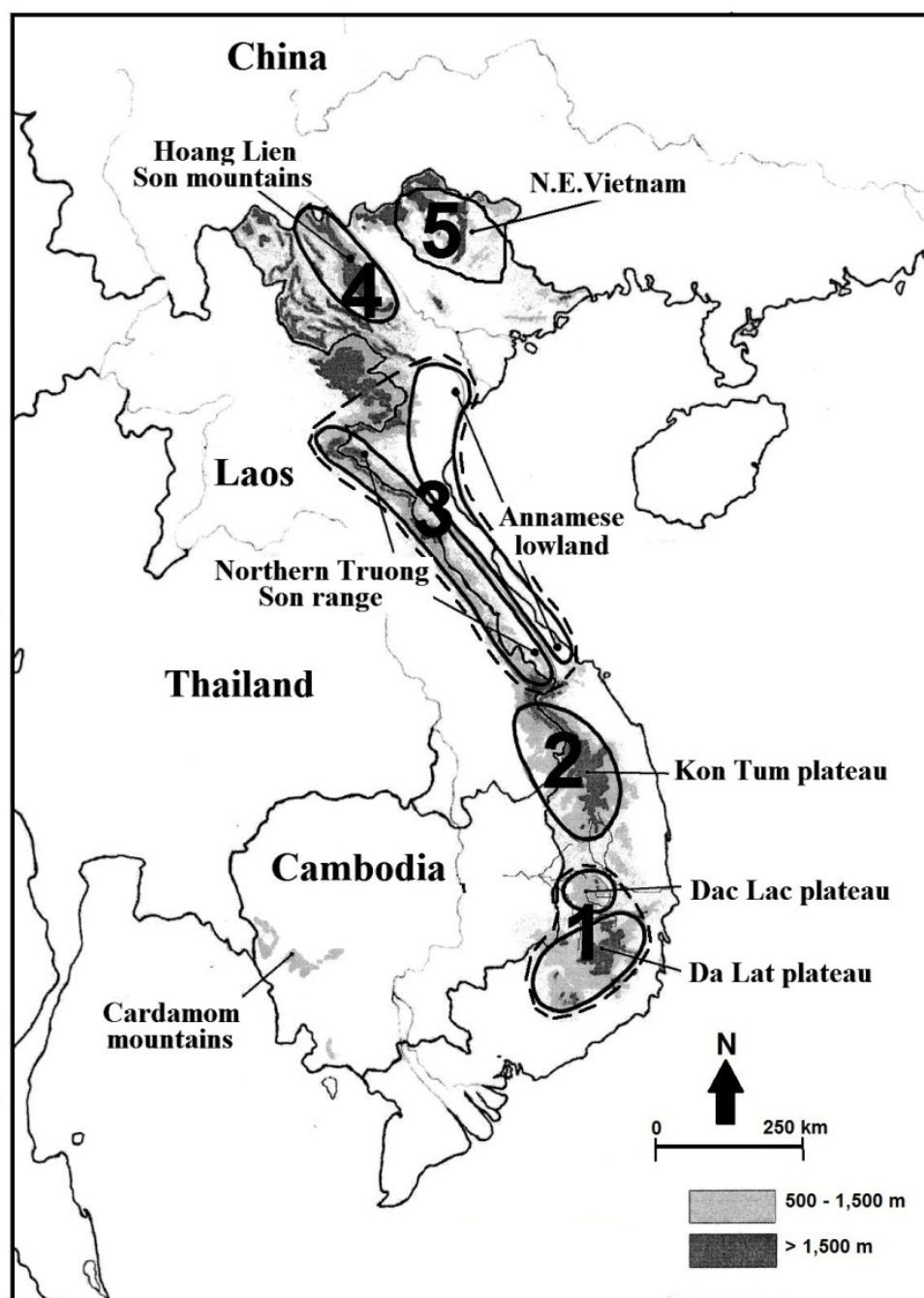


Figure 3. Butterfly endemism centres in Vietnam

3. Ranges of endemic Vietnamese butterflies

There are over 1100 butterfly species currently known from Vietnam. Approximately seven percent of all species are considered as endemic to the Indochinese Peninsula (Vietnam, Laos, Cambodia and eastern Thailand) (Monastyrskii, 2010a). These distinctive species, listed in the Appendix, are restricted to within the Peninsula border and have not yet been found in adjacent areas (Figs. 5-7).

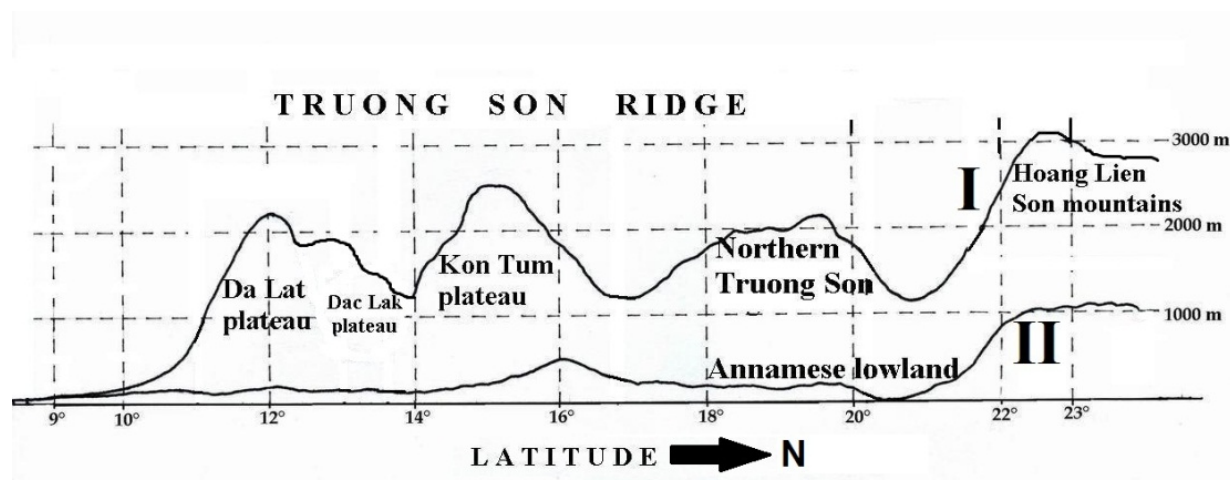


Figure 4. North-south Profiles of the Vietnamese landscapes through the main areas of endemism (indicated): I - Main ridges above 2000m; II - Lowland landscapes (0-500m) along the shoreline

The majority of endemic butterfly species range over isolated mountain massifs of the central Vietnamese Highlands and some areas in the northern part of the country (Fig. 3). Most of the smaller number of endemics that occur in the most southerly of these isolated montane areas, such as the Kon Tum and Da Lat (including small Dac Lac plateau) plateaus, are unknown in other parts of the Peninsula although there is a relatively small and lower altitude massif of mountains in western Cambodia called the Cardamom Mountains. However, according to preliminary studies, this area supports a much lower number of endemic butterfly taxa.

In Vietnam, endemic butterfly taxa consist mainly of geographically isolated populations. These species and subspecies are usually separated for hundreds or even thousands of kilometres from their nearest relatives. However, in Vietnam there are often very short distances (up to a few tens of kilometres) between isolated species populations and other parts of the range of a taxon. Such cases demonstrate that even small gaps, characterised by specificity of landscapes and habitats, are enough to break the process of genetic interchange and to promote development of separate taxa.

The concentration of endemic butterfly species is much higher in: the Da Lat and Dac Lac plateaus (Lam Dong and Dac Lac provinces) (1); Kon Tum plateau (Gia Lai and Kon Tum provinces) (2); northern Truong Son range and Annamese lowlands (Nghe An, Ha Tinh, Quang Binh and Quang Tri provinces) (3); Hoang Lien Son range (4); and the eastern region of N. Vietnam (Bac Kan and Lang Son provinces) (5) (Fig. 3) (Monastyrskii, 2007). These Vietnamese endemic butterfly species exhibit links to relatives distributed in different biogeographical zones. A number of Vietnamese endemic species have closely related species among representatives of the Sino-Himalayan and Sundanian faunas (Figs. 5 and 6). Another group of endemic taxa belongs to the local autochthonous Indo-Burmese fauna (Holloway, 1973) (Fig. 7). Distribution of the endemic butterfly species in Vietnam and their range features is described below.

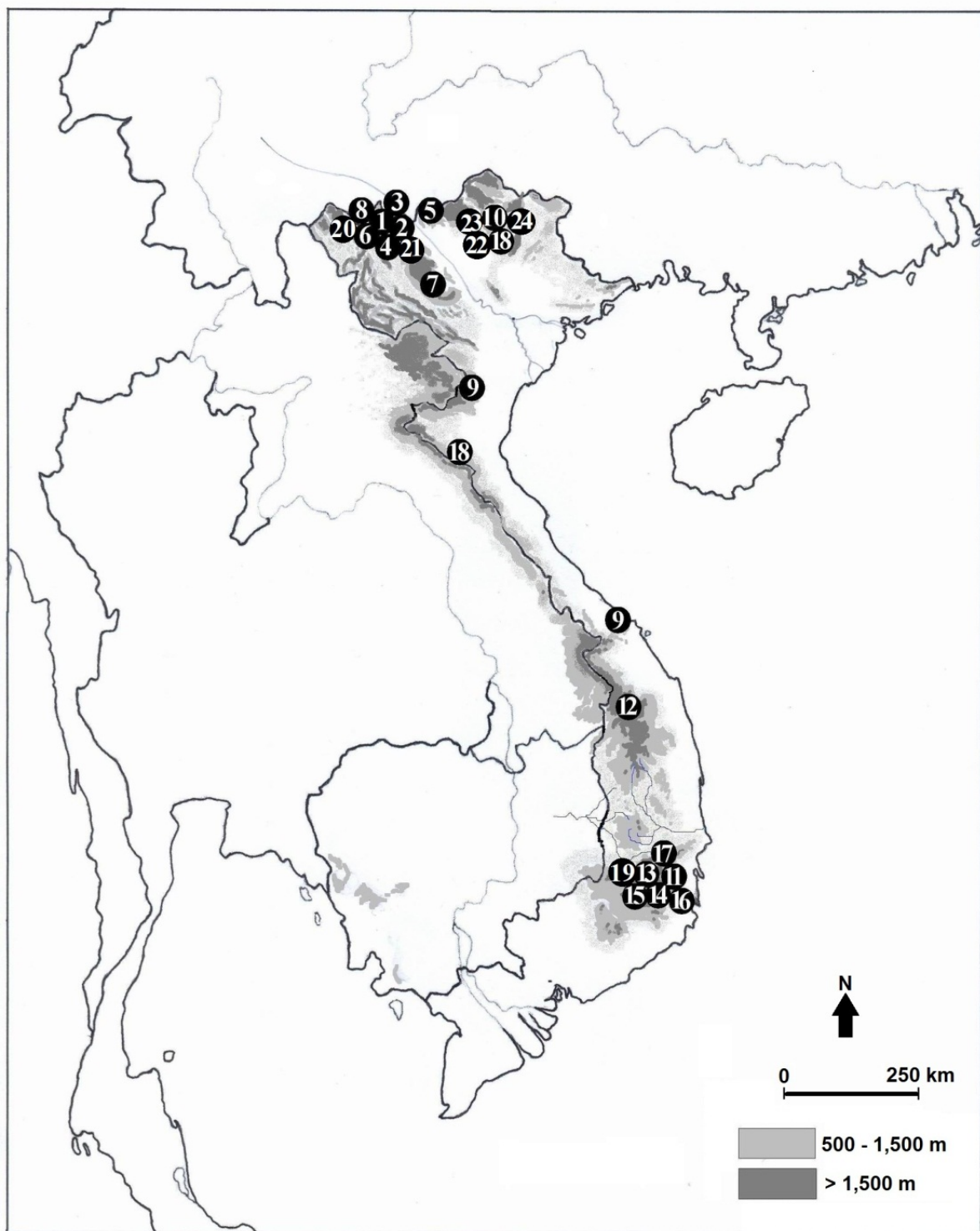


Figure 5. Endemic butterfly taxa of Indochina showing link with Sino-Himalayan fauna: 1- *Ypthima frontieri*; 2 – *Euthalia khambounei*; 3 – *Euaspa nishimurai*; 4 – *Shirozuozephyrus masatoshii*; 5 – *Proteuaspa akikoe*; 6 – *Chrysozephyrus vietnamicus*; 7 – *Lethe berdievi*; 8 – *Chrysozephyrus hatoyamai*; 9 – *Chrysozephyrus wakaharai*; 10 – *Calinaga funeralis*; 11 – *Euthalia hoa*; 12 – *Heliophorus smaragdinus*; 13 – *Euaspa minaei*; 14 – *Neptis transita*; 15 – *Chilasa imitata*; 16 – *Phaedyra armariola*; 17 – *Euthalia strephonida*; 18 – *Mycalesis inopia*; 19 – *Shirozuozephyrus alienus*; 20 – *Coladenia koiwaii*; 21 – *Praescobura chrysomaculata*; 22 – *Celaenorrhinus victor*; 23 – *Scobura eximia*; 24 – *Celaenorrhinus phuongi*

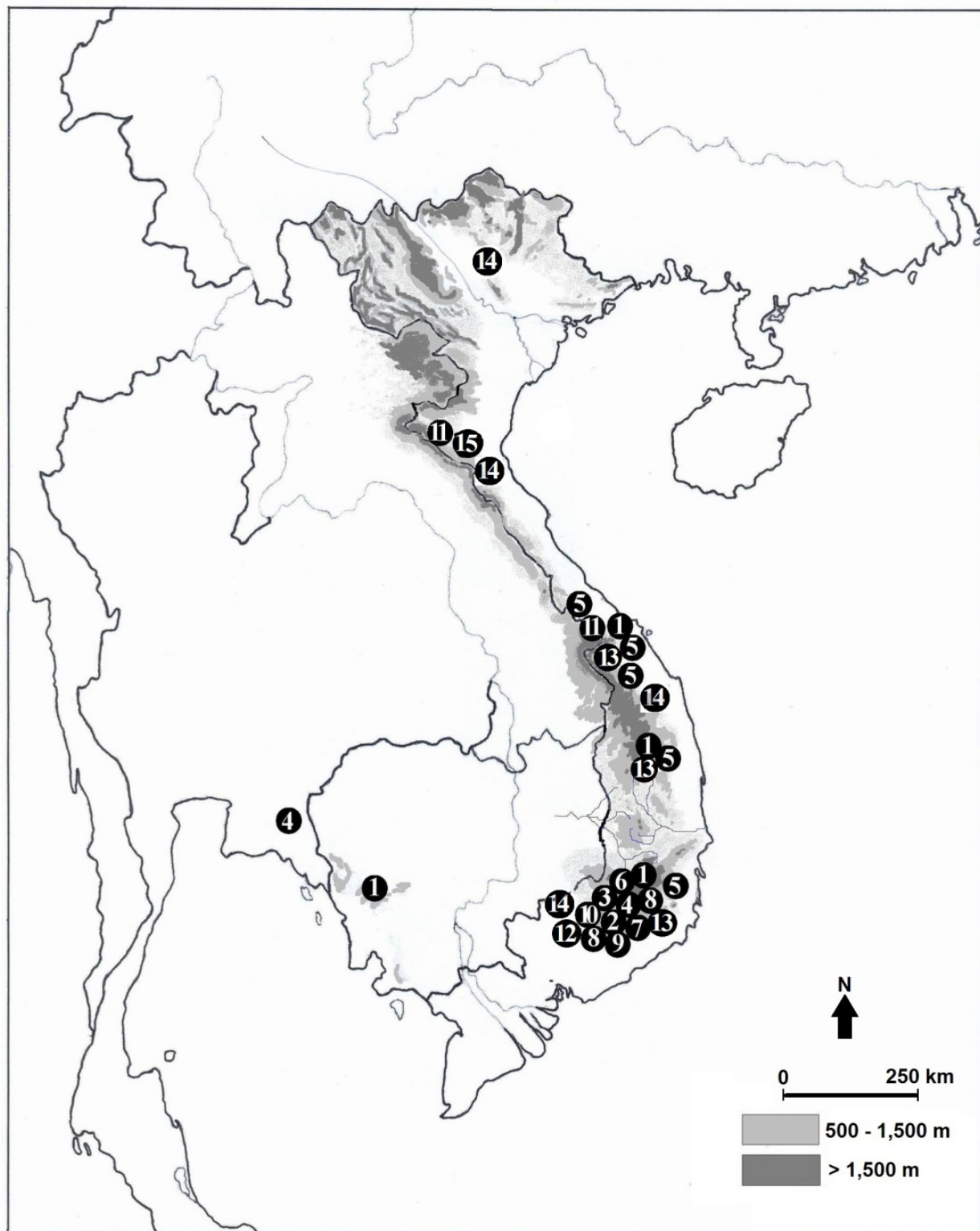


Figure 6. Endemic butterfly taxa of Indochina showing link with Sundanian fauna: 1- *Delias vietnamensis*; 2 – *Disco-phora aestheta*; 3 – *Cyllogenes milleri*; 4 – *Euploea orontobates*; 5 – *Zeuxidia sapphirus*; 6 – *Ypthima daclaca*; 7 – *Dera-mas cham*; 8 – *Tanaecia stellata*; 9 – *Tajuria sekii*; 10 – *Tajuria shigehoi*; 11 – *Elymnias saola*; 12 – *Eurema novapallida*; 13 – *Faunis bicoloratus*; 14 – *Suada albolineata*; 15 – *Neomyrina* sp.

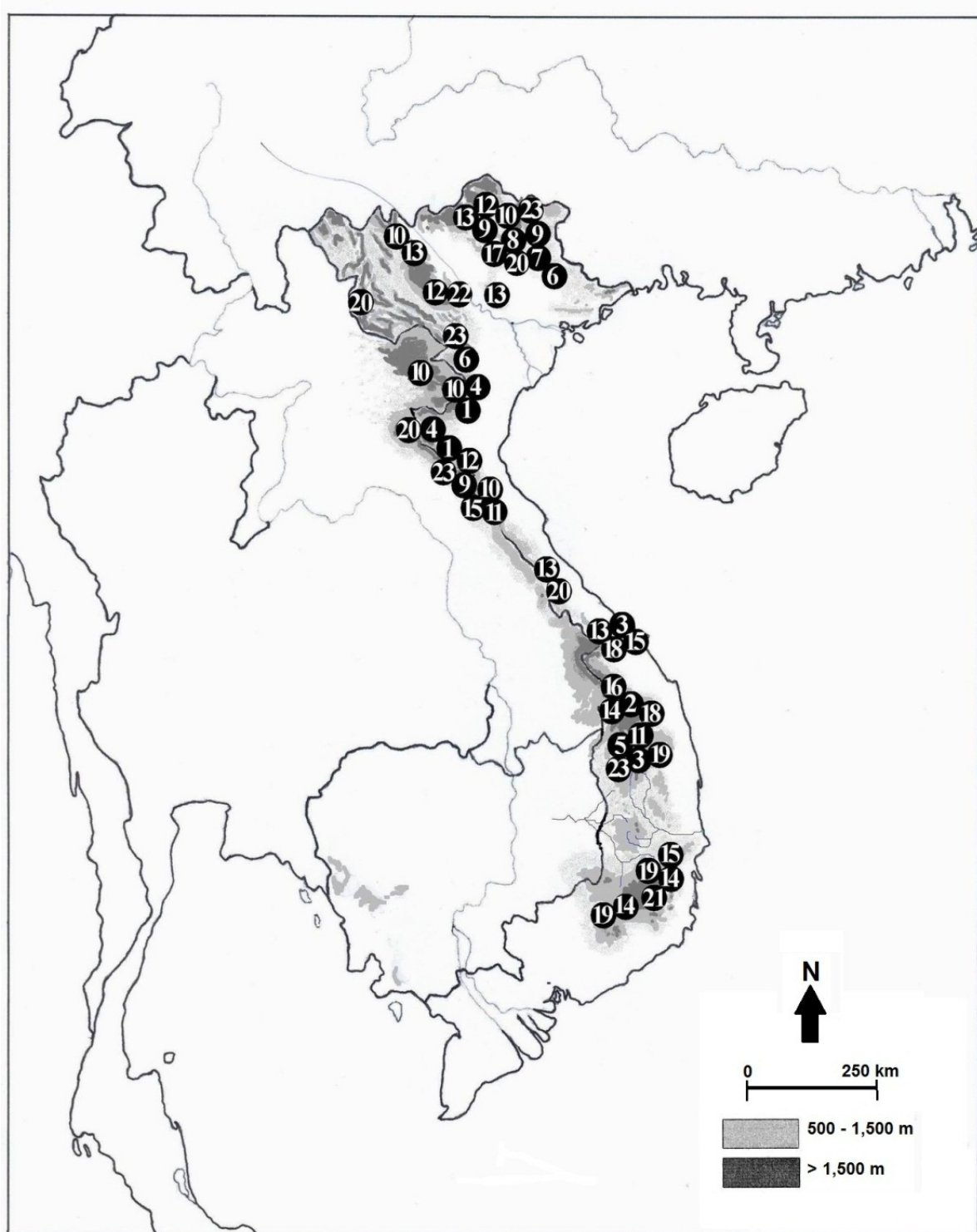


Figure 7. Endemic butterfly taxa of Indochina showing link with Indo-Burmese fauna: 1 – *Halpe paupera*; 2 – *Lethe melisana*; 3 – *Aemona simulatrix*; 4 – *Ypthima pseudosavara*; 5 – *Lethe konkakini*; 6 – *Lethe philesanoides*; 7 – *Lethe huongii*; 8 – *Lethe philemon*; 9 – *Lethe philesana*; 10 – *Graphium phidias*; 11 – *Dodona katerina*; 12 – *Aemona implicata*; 13 – *Aemona tonkinensis*; 14 – *Dodona speciosa*; 15 – *Pintara capiloides*; 16 – *Aemona kontumei*; 17 – *PentHEMA michallati*; 18 – *Stichophthalma eamesi*; 19 – *Stichophthalma uemurai*; 20 – *Stichophthalma mathilda*; 21 – *Aemona falcata*; 22 – *Aemona berdyevi*; 23 – *Taxila dora*

3.1. Endemics of the Da Lat plateau

There are twenty nine endemic butterfly species recorded within the border of Da Lat plateau. Twenty species have not been recorded outside of this mountain region so far. Additionally, several other species show distinct subspecific differences on the plateau (Monastyrskii, 2010a). The Da Lat endemics show a diversity of phylogenetic relationships with representatives of other biogeographic regions.

The endemic swallowtail *Chilasa imitata*, nymphalids *Euthalia hoa*, *E. strephonida*, *Phaedyra armariola*, *Neptis transita*, and lycaenids *Euaspa minaei* and *Shirozuozeephyrus alienus* (Fig. 5) are related to species from Tibet, E. Himalayas, W. & C. China (Monastyrskii & Devyatkin 2003; Monastyrskii, 2005; Koiwaya & Monastyrskii, 2010). Some endemic species of the Da Lat plateau and their Sino-Himalayan relatives are separated by hundreds to thousands of kilometres (Appendix).

Ranges of some other relatives of endemic taxa are located in close proximity to the Da Lat plateau. For example, the closest relation to the recently described *Chilasa imitata* (Papilionidae) is *Ch. epycides*, which is widely distributed from Nepal, Tibet and W. China to Kon Tum plateau, and only occupies habitats above 1,000 – 1,500m. The continuous range of *Euthalia strephon* extends widely from Tibet to the Kon Tum plateau, while the closely-related endemic species *E. strephonida* is restricted to the Da Lat plateau.

Another group of endemic butterfly species of the Da Lat plateau includes taxa of Sundanian derivation. These are pierid *Delias vietnamensis*, nymphalids *Tanaecia stellata*, *Cyllogenes milleri*, *Faunis bicoloratus*, *Zeuxidia sapphirus*, *Discophora aestheta* and *Ypthima daclaca*, lycaenids *Tajuria sekii*, *T. shigehoi*, *Deramas cham* and hesperiids *Suada albolineata* (Fig. 6). These species occur far from their relatives living in the Malay Peninsula and Sunda Islands (Appendix).

Most (8 out of 12) of the endemics of Sundanian origin mentioned above have only been found in the Da Lat plateau. However, an exception is the pierid *Delias vietnamensis* which has also been found in other isolated mountain areas of Indochina (Fig. 5). The only species of Sundanian origin found in a locality other than Da Lat is the nymphalid *Elymnias saola* in the northern Truong Song Ridge.

Endemic butterfly taxa of the Da Lat plateau that demonstrate links with the faunas of Malaya and Sundaland (Fig. 6) are the most remarkable feature of the local fauna, with more than 60% of butterfly species found in the Da Lat plateau characterised by Sundaland derivation. The majority of these species still maintain this link with the archipelago through the Malay Peninsula. For this reason endemism of butterfly taxa in the Da Lat plateau should be noted as a rather unusual event. For example, the satyrid *Cyllogenes milleri*, recently discovered in Da Lat plateau of Vietnam, has a sole relative *C. woolletti* in northern Borneo. Both species are quite similar and suggest confirmation of the former land connection bridge between the mainland and the Greater Sunda Islands (Voris, 2000). It is notable that in comparison with endemic butterfly taxa of Sino-Himalayan origin, endemic butterfly taxa of the Sundanian fauna are mainly located at lower elevations, thus demonstrating the segregation on biogeographic lines of butterfly groups that have come into contact during climatic fluctuations in the last Ice Age.

The list of nationally endemic butterfly species found in the Da Lat plateau is extended by including taxa of Indo-Burmese origin (Fig. 7). Some of these species also occur on the Kon Tum plateau, for example *Stichophthalma uemurai* and *Dodona speciosa*.

3.2. Endemics of the Kon Tum plateau

There are sixteen endemic butterfly species belonging to families Pieridae (1), Nymphalidae (10), Riodinidae (3), Lycaenidae (1) and Hesperiidae (1) (Appendix). Generally, the biogeographical pattern of endemics of the Kon Tum plateau is similar to that of the Da Lat plateau (Figs. 5-7). In comparison with the Da Lat plateau, at higher elevations of the Kon Tum Mountains (above 1,500m) there are only two endemic butterfly species showing relationship with the Sino-Himalayan fauna, for example two lycaenids *Heliophorus smaragdinus* and *Chrysozephyrus wakaharai*, even though the total number of Sino-Himalayan species is rather high (over 16%). Strong morphological differences are becoming apparent in local populations of Sino-Himalayan species; these populations may well be described as new subspecies when additional material has been obtained.

The number of endemic butterfly species demonstrating a Sundanian origin is also less than on the Da Lat plateau. As in Da Lat, these endemics are distributed mainly at middle elevations (900-1,400m), for example *Delias vietnamensis*, *Elymnias saola*, *Zeuxidia sapphirus*. Endemic butterfly species of Indo-Burmese origin on the Kon Tum plateau are noticeably predominant (Fig. 7). Many of them are geographically unique and to date have only been found in this area and in the neighbouring Da Lat plateau and the northern Truong Son range: nymphalids *Lethe melisana*, *L. konkakini*; *Aemona kontumei*, *A. simulatrix*, *Stichophthalma uemurai*, *S. eamesi*; riodinids: *Dodona speciosa*, *D. katerina*; and hesperiid: *Pintara capiloides*.

3.3. Endemics of the northern Truong Son ridge

To the north of the Kon Tum plateau (northern Truong Son ridge and Annamese lowland (3)) the number of endemic butterfly species (26 species) is similar but with a different biogeographical pattern of endemism (Fig. 5-7). For example, the number of endemics (3 species) revealing a link with the Sundanian fauna is significantly reduced (*Elymnias saola*, *Zeuxidia sapphirus*, *Neomyrina* sp.) (Fig. 6) and the number of endemic species of Sino-Himalayan origin is also not high (*Papilio doddsi*, *Mycalesis inopia*, *Chrysozephyrus wakaharai*) (Fig. 5). The majority of endemic species belong to the local Indo-Burmese fauna (73% of all endemics) (Fig. 7). Six endemics are unique to this territory.

3.4. Endemics of Hoang Lien Son range

The fauna of Hoang Lien Son range (the Fansipan massif) is considered as a part of the Southern Chinese mountain fauna (Monastyrskii, 2007). The massif includes southern ridges of the Yunnan Mountains with peaks reaching 3,000 m and above. The butterfly species composition of the Hoang Lien Son massif and the butterfly range structure in this area are distinctive and significantly differ from the populations of the other regions of the Indochinese Peninsula (Monastyrskii, 2007, 2010a). The species characterized by Sino-Himalayan ranges (44.3%) are

predominant, extending to the Chinese provinces of Yunnan and Sichuan. At the same time the butterfly species endemism in this area is rather low. There are fourteen endemic species (3.6%) ranges of which are restricted by the massif. Nine species are relatives of representatives with the Sino-Himalayan ranges, for example, nymphalid *Euthalia khambouni*, lycaenids *Euaspa nishimurai*, *Chrysozephyrus vietnamicus*, *C. hatoyamai*, *Shirozuozeephyrus masatoshii*, and hesperiid *Praescobura chrysomaculata*; five endemic species demonstrate a link with Indo-Burmese fauna: *Graphium phidias*; *Aemona tonkinensis*, *A. berdyevi*, *A. implicata* and *Taxila dora*,

3.5. Endemics of N.E. Vietnam

A total 26 species, inhabiting eastern areas of N. Vietnam (east of the Red River), are endemic to the Indochinese Peninsula. Fifteen species extend south to the territories of northern Truong Son ridge and Annamese lowland (Appendix), and four of these endemics are found to west of the Red River. The ranges of eleven endemic species are bounded only by the eastern areas of North Vietnam.

3.6. Summary

It is evident from the data in Appendix that all except one of the Sundanian species is in Da Lat plateau, with little extension to the north. The Indo-Burmese species are dispersed more or less evenly from the north to south with definite localization. The Sino-Himalayan endemic species are concentrated in the two most northerly areas of endemism with disjunction also in Da Lat (Table 1); all seven of the Sino-Himalayan endemics in Da Lat are also exclusive to that area.

Centres of endemism in Vietnam	Biogeographical provinces (Monastyrskii, 2007)	Average latitude of area studied	Total no. endemic species of Vietnam	Biogeographical elements		
				Sino-Himalayan (total of 26 endemic to Vietnam)	Indo-Burmese (total of 35 endemic to Vietnam)	Sundanian (total of 15 endemic to Vietnam)
Hoang Lien Son	Sikang-Yunnan	22°	14	9	5	0
N. & N.E. Vietnam	South Chinese	21°	26	7	18	1
Nothern Truong Son	North Annamese	18°	26	4	19	3
Kon Tum plateau	Central Annamese	14,5°	16	2	9	5
Da Lat plateau	Da Lat	11,5°	28	7	9	12

Table 1. Dispersion of the biogeographical elements of the butterfly species endemics in Vietnam

Each of the five centres of butterfly endemism in Vietnam contains species unique to it (Table 2).

Centres of endemism in Vietnam	Biogeographical provinces (Monastyrskii, 2007)	Average latitude of area studied	Total no. of unique endemic species	Biogeographical elements		
				Sino-Himalayan (total of 26 endemic to Vietnam)	Indo-Burmese (total of 35 endemic to Vietnam)	Sundanian (total of 15 endemic to Vietnam)
Hoang Lien Son	Sikang-Yunnan	22°	10	9	1	0
N. & N.E. Vietnam	South Chinese	21°	11	5	6	1
Nothern Truong Son	North Annamese	18°	6	1	4	1
Kon Tum plateau	Central Annamese	14,5°	6	2	4	0
Da Lat plateau	Da Lat	11,5°	19	7	4	8
Total			52	24	19	10

Table 2. Uniqueness of the butterfly species endemics in the Centres of endemism in Vietnam

This unique component is highest in the Hoang Lien Son massif (71%) and almost has high in the Da Lat plateau (66%). Amongst the former, 90% is of Sino-Himalayan affinity, whereas, in contrast, 42% of the latter is of Sundanian affinity.

It is also clear that there is a diversity of faunistic complexes that differ in origin, age and relationships, with the north-south grain of the landscape structure (Fig. 3) being a important factor in the development of this diversity, the topography providing both barriers to, and corridors for, butterfly dispersal.

The percentage of Indochinese endemic butterfly species noticeably decreases from the north of Vietnam to the south. There is a strong positive correlation between the latitude (X) and the percentage of species represented (Y): $r = .532$, $P < 0.05$ (Fig. 8) (Monastyrskii, 2010b).

4. Continuous and mosaic ranges of Vietnamese butterflies

Continuous ranges are typical of a number of Vietnamese butterflies, particularly eurybiont (or opportunistic) species. Many of these species are distributed throughout the country and also extend beyond its borders. High migratory activity, diffuse population boundaries and a high intensity of genetic flow are all contributing factors to increased similarity between populations of different species. Examples of such similarity may be seen among representatives of the families Papilionidae (genera *Papilio* and *Graphium*); Pieridae (genera *Appias*, *Prioneris* and *Catopsilia*); Danainae, and some groups of widely distributed Nymphalinae

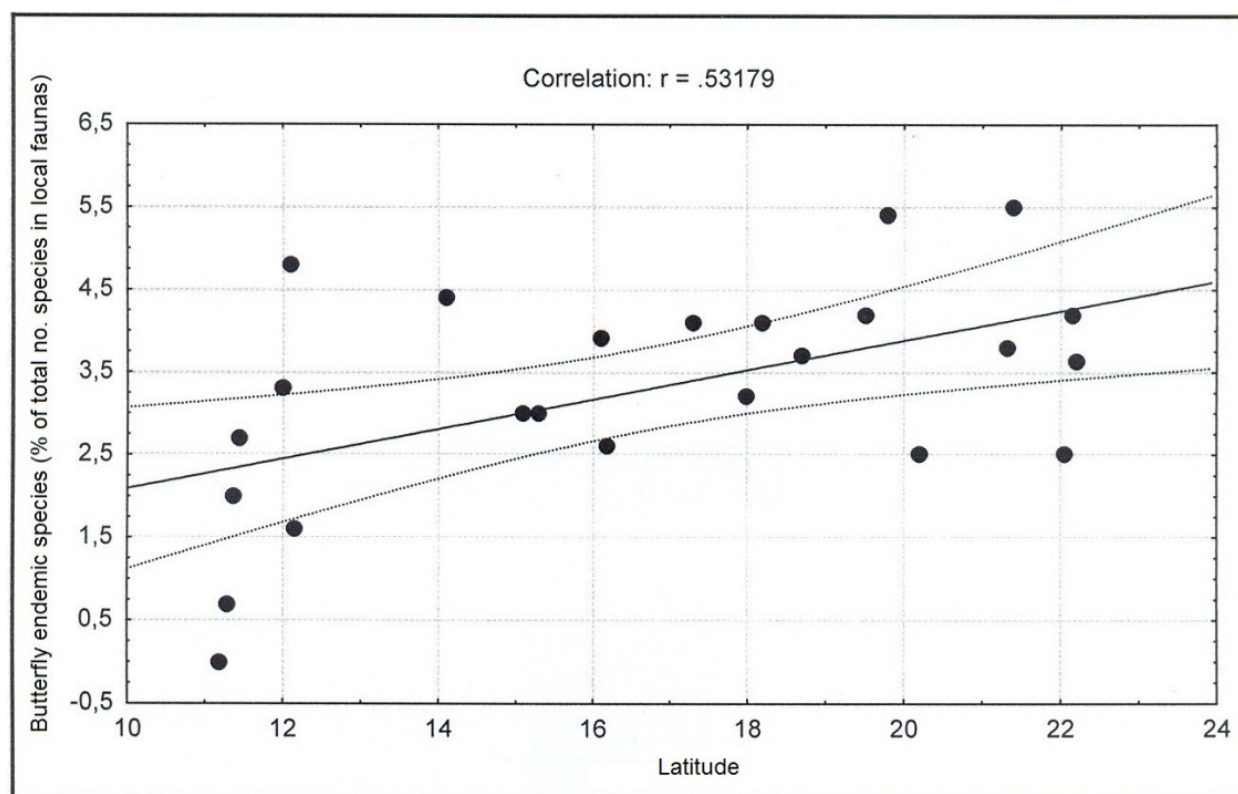


Figure 8. Correlation between the latitude (x-axis) and percentage endemism (y-axis) in localised inventories of Vietnamese butterflies (Monastyrskii, 2010b)

(genera *Kaniska*, *Junonia* and *Vanessa*) and also some other taxa that are characterised by long distance migrations. Conversely, the continuous ranges of stenotopic species have specific configurations corresponding with the geography of habitats and often demonstrate a mosaic character. These species often demonstrate a clinal variability of morphological characters; this is seen particularly in some other Papilionidae (*Byasa*, *Chilasa*, *Teinopalpus* and *Meandrusa*), Pieridae (*Delias*), and the majority of Satyrinae, Amathusiinae, Nymphalinae and Lycaenidae.

Clinal variability is exemplified by the widespread satyrine *Ypthima baldus* (Fig. 9). In populations of male *Ypthima baldus* the length of the forewing fluctuates insignificantly in central and southern parts of Vietnam while in the north this character depends greatly on habitats and landscapes. Populations occupying the northern mountainous regions (from Hoang Lien Son to the northern part of the Truong Son ridge) have a shorter forewing length though in Vu Quang (northern Truong Son ridge) this character varies widely. In terms of pattern of Vietnamese landscapes (Figs. 2, 3), the northern mountainous region maintains a continuous belt-like zone of intergradation between mountain and lowland habitats.

Mosaic ranges are exemplified by the very local, montane, seasonal amathusiine species *Faunis aerope* (Fig. 10) which is distributed in habitats above 1,500m, and where geographical population gaps can be large or small. Habitat isolation and high stenotopic behaviour have influenced morphology of the species' male genitalia. The pattern of the clasp apex from different sites of N. and C. Vietnam is illustrated in figure 10. Males from the central part of

the country have a rather broad clasp, the apex of which is covered by several rows of much larger spines. Even populations of males from different localities of N. Vietnam are characterised by constant differences in the apical structure of the clasp (Monastyrskii, 2004).

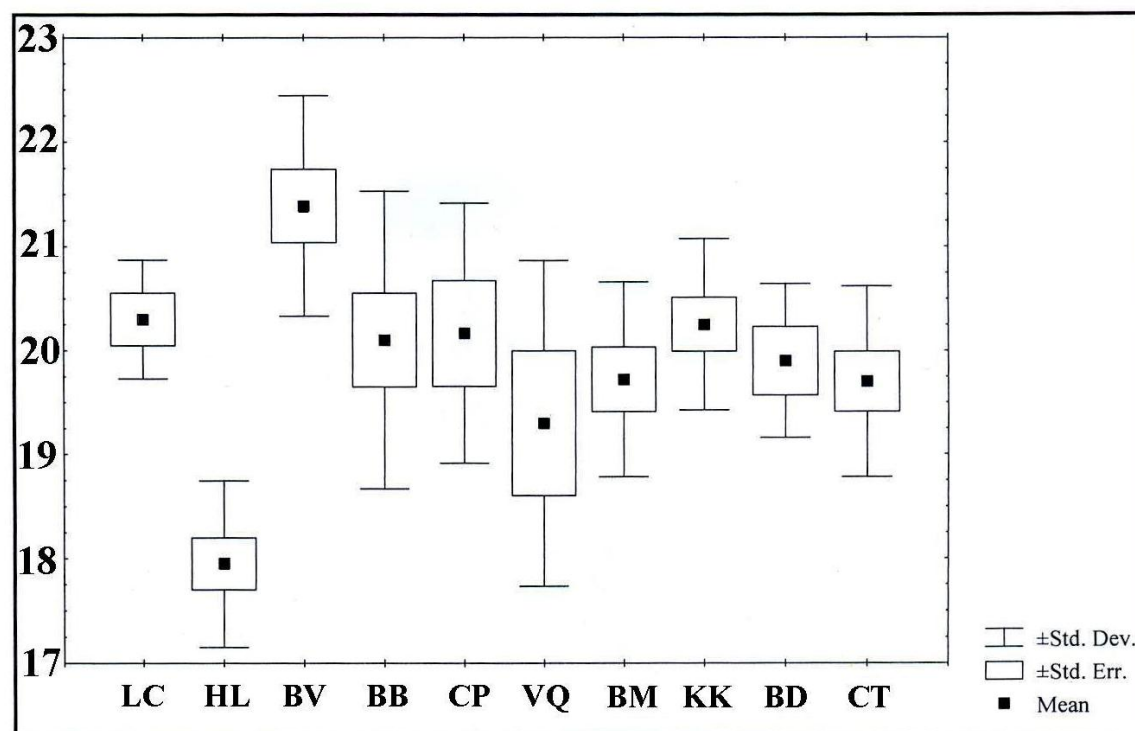


Figure 9. Cline variability of the forewing length in *Ypthima baldus* (Nymphalidae, Satyrinae); x – areas studied from north to south (from left to right) and latitude: LC – Lai Chau (22,3°N); HL – Hoang Lien (22,1°N); BV – Ba Vi (21,05°N); BB – Ba Be (22,2°N); CP – Cuc Phuong (20,1°N); VQ – Vu Quang (18,2°N); BM – Bach Ma (16,05°N); KK – Kon Ka Kinh (14,3°N); BD – Bi Doup (12,0°N); CT – Cat Tien (11,3°N); y – length of the forewing (in mm.) Std. Dev. – the standard deviation; Std. Err. – the standard error; mean – average

It is well known that continuous variability occurs in a latitudinal manner (Mayr, 1969; 1970). In Vietnam there are many butterfly species with geographically separate populations which vary in distinct characteristics such as colour and wing patterns, size and the development of some organs. Species are sometimes distributed very widely and occur in different kinds of landscapes and habitats. In such cases it is difficult to make conclusions regarding contact zones between subspecies. In other cases distinctive butterfly populations are divided by insuperable natural barriers. This latter variability is rather typical of populations of many Vietnamese butterflies.

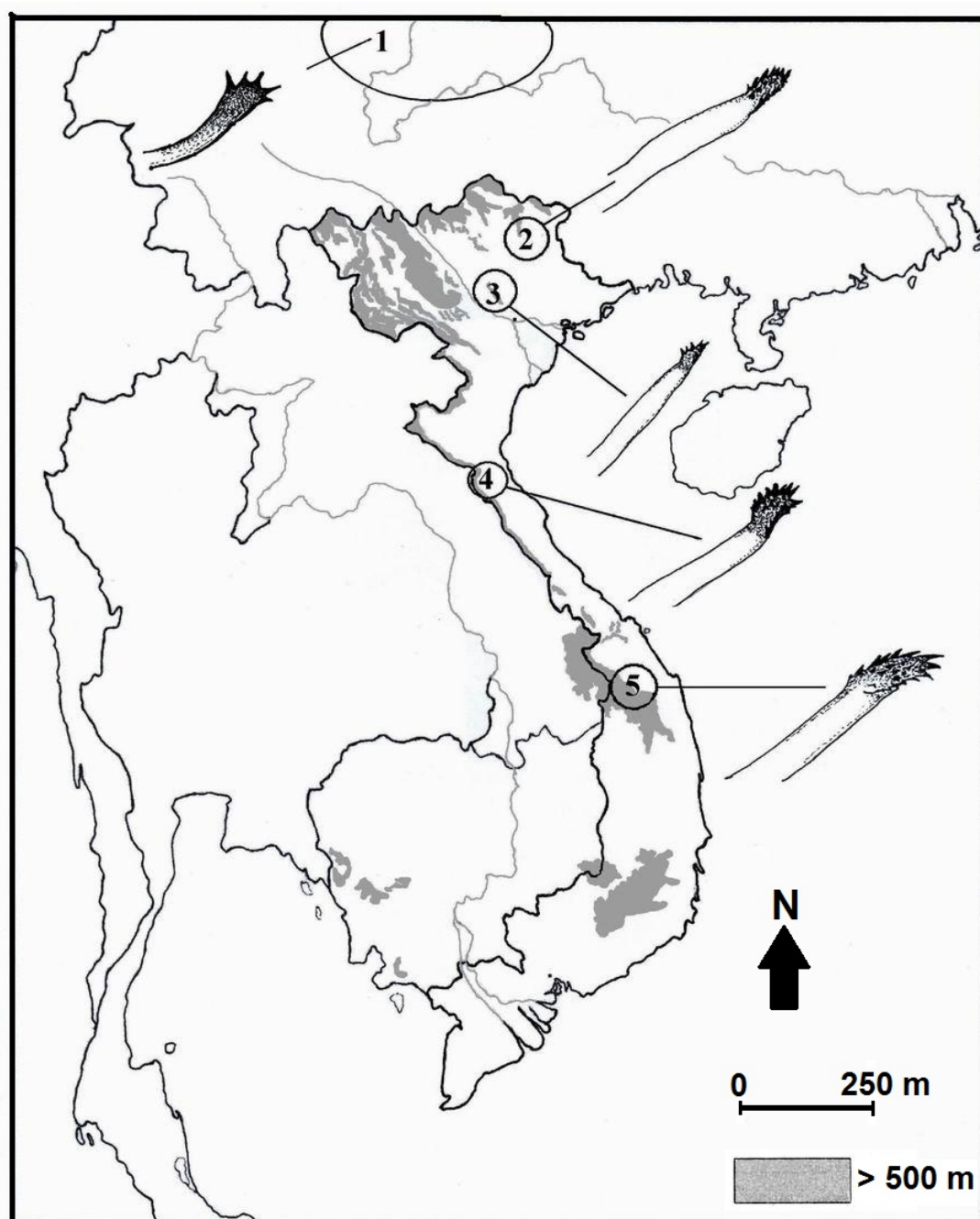


Figure 10. The pattern of the clasp apex in the males of *Faunis aerope* (Nymphalidae, Amathusiinae) from different sites of N. and C. Vietnam: 1 – ssp. *aerope* (C. & S. China); 2, 3 – ssp. *excelsa* (N. Vietnam); 4 – ssp. *excelsa* (northern Truong Son); 5 – ssp. *centrala* (the Kon Tum plateau).

5. Disjunct ranges of Vietnamese butterflies

Geographical gaps between populations of species caused by natural factors are not rare occurrences in the butterfly faunas of Indochina and Southeast Asia. Disjunctions observed differ in their distance and direction.

5.1. Distances of disjunctions

In some cases disjunctions between populations may only be a few tens of kilometers, but strong factors such as climate, river basins and montane ridges become geographical barriers which may cause and maintain divergence. For example, populations of many montane species are separated between the Da Lat and Kon Tum plateaus and also between the Kon Tum plateau and the northern Truong Son ridge and S. Yunnan mountain system. The Indo-Burmese swallowtail *Meandrusa lachinus* is distributed from Nepal to Indochina and consists of a number of subspecies, three of which are found in Vietnam. The subspecies *M. l. sukkity* is distributed from N.E. Thailand to C. Laos and the central Vietnamese Kon Tum plateau. This taxon does not cross the lower Dac Lac plateau and water barriers such as the Song Ba and Song Da Rang rivers; nor does it overlap populations of the distinctive subspecies *M. l. helenusoides* which is restricted to Da Lat plateau. There are many other examples similar to that of *M. l. sukkity* that are known.

In the majority of cases the natural disjunctions between Vietnamese populations of butterflies can occur over several hundreds or thousands of kilometres. Reasons for disjunctions between butterfly populations may also include human activity such as burning. For example, lowland forest habitats in coastal areas of Vietnam have been cleared leading to fragmented butterfly populations clinging to isolated habitats. It is now almost impossible to gather data on the nature of the original forests, though some information from palynology is becoming available (Maxwell & Liu, 2002). It is therefore difficult to reconstruct the possible composition of the original butterfly fauna. Altered coastal climate and remaining fragments of coastal forests with their plant communities point to the high diversity of mosaic habitats in recent time. It is also possible, however, that disjunctions were a natural characteristic of the local species ranges in these previously coastal forests. Nevertheless, logging of timber and other kinds of human activity may have intensified these gaps and exacerbated difficulties in explaining these geographical differences in the modern context.

5.2. Directions of disjunctions

These examples may be extended by disjunctions occurring over a few thousands of kilometres. Likewise the butterfly taxa of Indochina demonstrate links with butterfly faunas distributed in different directions from Vietnam (similar elements in the notodontid moth fauna of Thailand were indicated by Schintlmeister & Pinratana (2007): Yunnan; Pacific; Himalayan; Sundanian), with range disjunctions also along the same geographical orientation:

1. W. and C. China:

The majority of disjunctions in the Sino-Himalayan ranges is observed between populations of northern Vietnam (e.g. Hoang Lien Son mountains) and northern part of central Vietnam (northern Truong Son ridge) and populations of W. China and E. Himalaya: Nymphalidae: *Euthalia confucius*, *E. strephon*, *Mycalesis unica*, *Lethe ocellata*, *L. umedai*; Lycaenidae: *Euaspa milionia*, *Euaspa hishikawai*, *Howarthia kimurai*, *Teratozephyrus kimurai*, *Chrysozephyrus tytleri*, *Chrysozephyrus intermedius*, *Kawazoezephyrus jiroi*, *Yamomotozephyrus kwangtungensis* etc.

2. S.E. China, Taiwan and Hainan:

Examples of these taxa include swallowtail *Teinopalpus aureus*, nymphalid *Athyma minensis*, groups such as the Lycaenidae Hairstreaks *Zephyrus*, including *Ravenna nivea*, *Yamomotozephyrus kwangtungensis*, representatives of the genera *Chrysozephyrus* and *Euaspa*, and also some unique Hesperiididae that have long been regarded as endemics of S.E. China.

3. Burma and N.E. India:

Euthalia iva; *Cyllogenes janetae*, *Penthema michallati*.

4. Malay Peninsula and Sunda Islands:

Delias malayana, *Elymnias panthera*, *Zeuxidia masoni*, *Papilio prexaspes* and *Kallima albobasata*.

Natural causes of disjunctions between butterfly populations are important in understanding the evolutionary processes that have resulted in the taxonomic composition of the modern fauna, and also for the prediction of its future transformations. In Vietnam populations of many butterfly species have lost links with the main part of their ranges, and have adapted to new natural conditions. This adaptation has been accompanied by the appearance of new taxonomic units (new species and subspecies). Fig. 11 shows range disjunctions for some species belonging to the genus *Ypthima*, for example *Y. norma* (1); *Y. watsoni* (2) and *Y. sarcaposa* (3), which are all distributed in the Indochinese subregion.

Some butterfly species in Vietnam are distributed mainly according to climatic factors. Changes in local climate appear to influence strongly the distribution of those butterfly species that are restricted to Vietnam's mountain areas. Survey reports suggest that some N. Vietnam/ S. Yunnan montane butterfly species (e.g. *Neorina neosinica* and *Teinopalpus imperialis*) also occur in the highlands of the Kon Tum plateau – montane habitats that are separated by hundreds of kilometres. This pattern might reflect the fragmentation of a once broader range that these butterflies occupied when montane habitats extended to lower elevations during cooler glacial periods. During the warmer eras, the species may have become isolated when these habitats receded to higher altitudes. Such cycles of habitat change may also have led to varying degrees of divergence in some groups of butterflies. Today this scenario presents a suitable explanation for range disjunctions for many separate montane butterfly taxa in Vietnam.

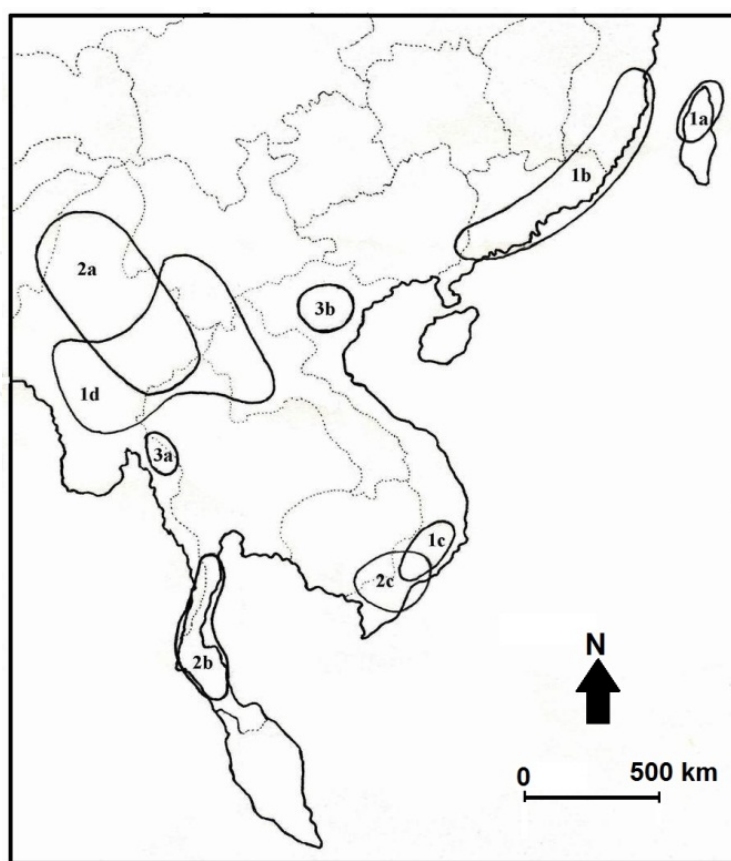


Figure 11. Disjunct ranges of some *Ypthima* species (Nymphalidae, Satyrinae): *Y. norma* (1); *Y. watsoni* (2) and *Y. sarcaposa* (3)

6. Vicarious ranges of Vietnamese butterflies

Examples of geographically vicarious butterfly species found in Vietnam are provided by stenotopic taxa representatives. Notable chains of vicariants include species belonging to the genera *Aemona* and *Stichophthalma* (Nymphalidae, Amathusiinae) (Figs. 12, 13). The range of *A. berdyevi* (1) in the north of the country (Hoang Lien Son mountains) is the vicariant of *A. oberthueri* ranging through the mountain areas of W. China (Sichuan and N. Yunnan) (Fig. 12). N. Vietnam and northern part of C. Vietnam is ranged by the sympatric taxa *A. tonkinensis* (2) and *A. implicata* (3) which are similar in size and wing colour pattern but have very distinctive genitalia. Ranges of these species reach the central highlands where they cede similar habitats to *A. kontumei* (4) and *A. simulatrix* (5). The southern Da Lat plateau is occupied by *A. falcata* (6) which has a distinctive wing pattern and genitalia (Fig. 12).

Ranges of *Stichophthalma* species in Vietnam follow a similar pattern (Fig. 13). During a recent new revision of Vietnamese *Stichophthalma*, the taxonomic status of some taxa has been changed (Monastyrskii & Devyatkin, 2008). The range of the Yunnan species *S. howqua iapetus* has borders with that of *S. mathilda* (4), *S. suffusa tonkiniana* (2) and *S. fruhstorferi* (3). The montane taxon *S. mathilda* reaches the central Vietnamese highlands (Gia Lai province); both other taxa, *S. s. tonkiniana* and *S. fruhstorferi*, are distributed through the lowlands of N. Vietnam

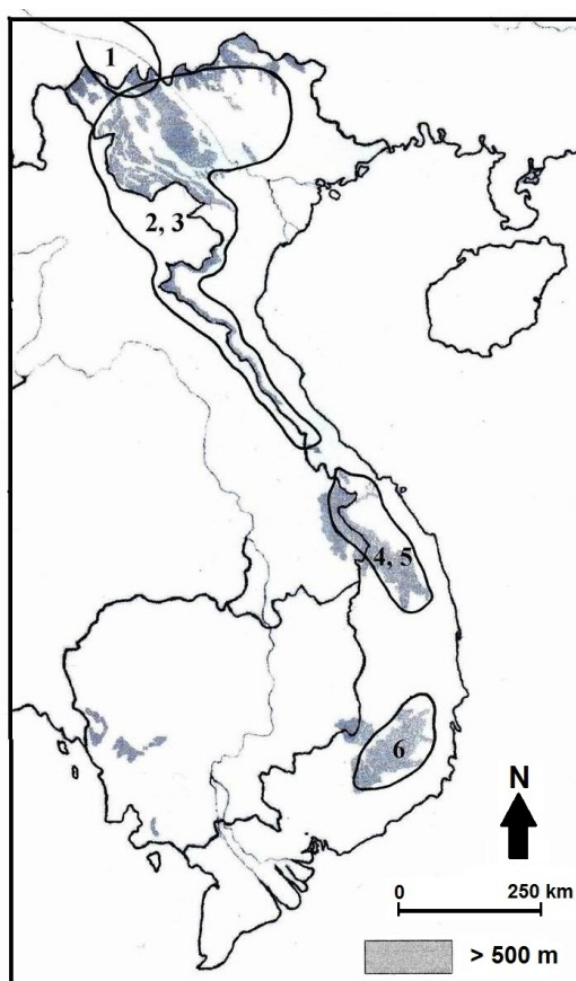


Figure 12. Vicarious ranges of the *Aemonia* spp. (Nymphalidae, Amathusiinae): 1. *A. berdiewi*; 2. *A. tonkinensis*; 3. *A. implicata*; 4. *A. simulatrix*; 5. *A. kontumei*; 6. *A. falcata*.

and northern part of C. Vietnam. The greater part of the Kon Tum plateau is populated by *S. eamesi* (5) where it overlaps with the range of *S. uemurai* (6), a species that covers the entire Da Lat plateau. The next vicariant species is *S. cambodia* (7) which ranges through the mountains of W. Cambodia and E. Thailand.

The ranges of these six species of *Aemonia* and seven species of *Stichophthalma* found in Vietnam and adjacent countries coincide with floristic provinces proposed by Takhtajan (1986). These provinces belong to the Indomalayan subkingdom characterised by remarkably high levels of endemism including 16 endemic families of vascular plants and a great number of endemic genera and species.

Sometimes the pattern of vicarious ranges appears to have been modified by subsequent dispersals, leading to overlap of what were probably previously allopatric species. An example is mapped in Fig. 2d: the *Ypthima sakra* group of species. In a northern centre of diversity, three species (*Y. sakra*, *Y. atra*, *Y. persimilis*) partially overlap in the eastern Himalayas, and this overlap zone extends to N. Vietnam. To the south, these species are replaced by one very

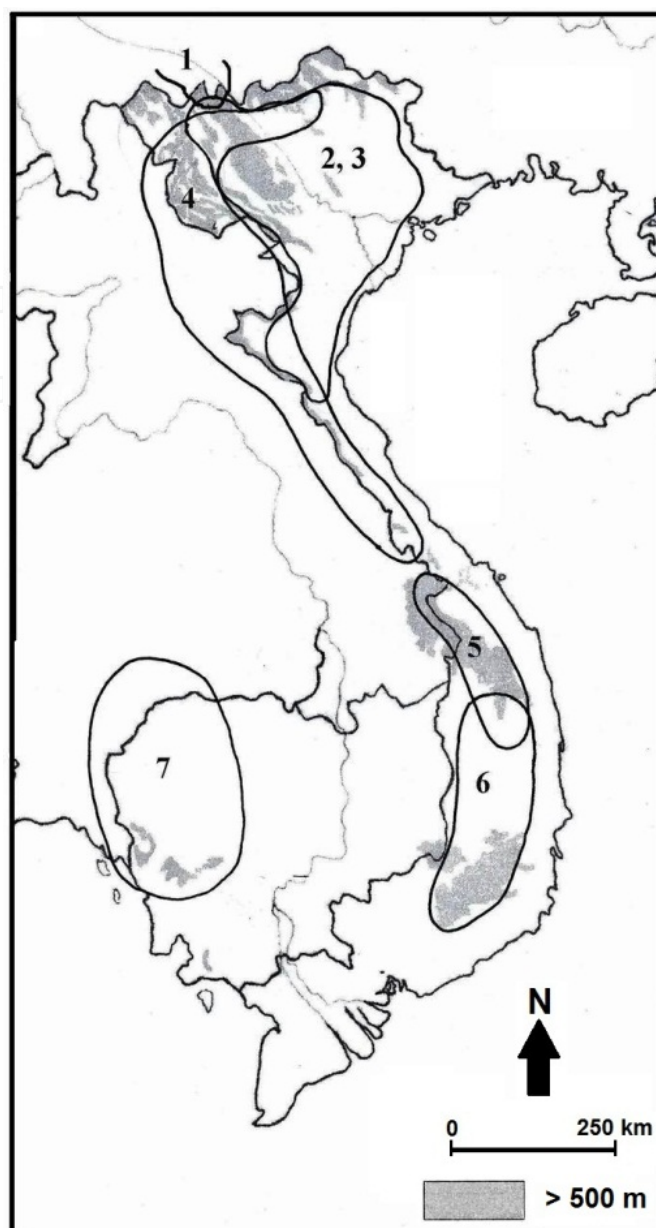


Figure 13. Vicarious ranges of the *Stichophthalma* spp. (Nymphalidae, Amathusiinae): 1. *S. howqua iapetus*; 2. *S. suffusa tonkiniana*; 3. *S. fruhstorferi*; 4. *S. mathilda*; 5. *S. eamesi*; 6. *S. uemurai*; 7. *S. cambodia*.

localised species, *Y. pseudosavara*, that is entirely allopatric, and a species pair, where one member, *Y. evansi*, has a range completely nested within that of the other, *Y. dohertyi*.

7. Conclusion

Analysis shows that Vietnamese butterflies are characterised by various range configurations, including endemic, continuous, mosaic, disjunct and vicarious. This diversity of pattern suggests that the Vietnamese butterfly fauna is in a continuous state of evolutionary develop-

ment in response to changes in topography and climate, possibly at least partially cyclic, younger patterns being progressively overlain on older ones, with various links to the adjacent Sino-Himalayan, Sundanian and Indo-Burmese faunas. Thus, it is plausible that the north-south ranges of mountains in the east of the Indochinese Peninsula, mostly in Vietnam, may have provided both a route whereby Sino-Himalayan elements were able to penetrate further south in cooler periods, and also a refuge in the very south, perhaps in more clement maritime conditions of the eastern margin of the much expanded area of Sundaland (Voris, 2000) where Sundanian humid forest elements were able to persist when the interior became much drier. The current altitudinal segregation of Sino-Himalayan versus Sundanian endemics in Da Lat is consistent with this hypothesis. Such a scenario might be assessed further by conducting rigorous phylogenetic studies of those butterfly groups with vicariant endemism within the Indochinese Peninsula, particularly *Aemona* and *Stichophthalma*, and also of those groups such as that of *Ypthima sakra*, where considerable overlap of species ranges occurs.

Appendix

Species	Family	Centres of endemism in Vietnam					Nearest relatives	
		Hoang Lien Son	N. and N.E. Vietnam	Northern Truong Son ridge	Kon Tum plateau	Da Lat and Dac Lac plateaus	Species	Distribution
1	2	3	4	5	6	7	8	9
<i>Chilasa imitata</i>	Papilionidae					+	<i>Ch. epycides</i>	Sino-Himalayan
<i>Papilio doddsi</i>	Papilionidae		+	+			<i>P. dialis</i>	Sino-Himalayan
<i>Graphium phidias</i>	Papilionidae	+	+	+			-	Indo-Burmese
<i>Delias vietnamensis</i>	Pieridae				+	+	<i>D. georgina</i>	Sundanian
<i>Eurema novapallida</i>	Pieridae					+	<i>E. lacteola</i>	Sundanian
<i>Euploea orontobates</i>	Nymphalidae					+	-	Sundanian
<i>Cyllogenes milleri</i>	Nymphalidae					+	<i>C. woolletti</i>	Sundanian
<i>Elymnias saola</i>	Nymphalidae			+	+		<i>E. casiphone</i>	Sundanian
<i>Penthema michallati</i>	Nymphalidae		+				<i>P. lysarda</i>	Indo-Burmese
<i>Lethe berdievi</i>	Nymphalidae	+					<i>L. christophi</i>	Sino-Himalayan
<i>L. melisana</i>	Nymphalidae				+		-	Indo-Burmese
<i>L. konkakini</i>	Nymphalidae				+		<i>L. latiaris</i>	Sino-Himalayan
<i>L. philemon</i>	Nymphalidae		+				-	Indo-Burmese

Species	Family	Centres of endemism in Vietnam					Nearest relatives	
		Hoang Lien Son	N. and N.E. Vietnam	Northern Truong Son ridge	Kon Tum plateau	Da Lat and Lac plateaus	Species	Distribution
1	2	3	4	5	6	7	8	9
<i>L. philesana</i>	Nymphalidae		+	+			-	Indo-Burmese
<i>L. philesanoides</i>	Nymphalidae		+	+			-	Indo-Burmese
<i>L. huongii</i>	Nymphalidae		+				-	Indo-Burmese
<i>Ragadia critias</i>	Nymphalidae			+	+	+	-	Indo-Burmese
<i>Mycalesis inopia</i>	Nymphalidae		+	+			-	Sino-Himalayan
<i>Ypthima frontierii</i>	Nymphalidae	+					<i>Y. megalomma</i>	Sino-Himalayan
<i>Y. pseudosavara</i>	Nymphalidae		+	+			<i>Y. savara</i>	Indo-Burmese
<i>Y. daclaca</i>	Nymphalidae					+	<i>Y. pandocus</i>	Sundanian
<i>Faunis bicoloratus</i>	Nymphalidae				+	+	<i>F. canens</i>	Sundanian
<i>Aemona tonkinensis</i>	Nymphalidae	+	+	+			-	Indo-Burmese
<i>A. kontumei</i>	Nymphalidae				+		-	Indo-Burmese
<i>A. simulatrix</i>	Nymphalidae				+		-	Indo-Burmese
<i>A. implicata</i>	Nymphalidae	+	+	+			-	Indo-Burmese
<i>A. falcata</i>	Nymphalidae					+	-	Indo-Burmese
<i>A. berdyevi</i>	Nymphalidae	+					<i>A. oberthuri</i>	Indo-Burmese
<i>Stichophthalma fruhstorferi</i>	Nymphalidae		+	+			<i>S. cambodia</i>	Indo-Burmese
<i>S. uemurai</i>	Nymphalidae				+	+	<i>S. cambodia</i>	Indo-Burmese
<i>S. mathilda</i>	Nymphalidae		+	+			<i>S. louisa</i>	Indo-Burmese
<i>S. eamesi</i>	Nymphalidae				+		<i>S. louisa</i>	Indo-Burmese
<i>Zeuxidia sapphirus</i>	Nymphalidae			+	+	+	<i>Zeuxidia spp.</i>	Sundanian
<i>Discophora aestheta</i>	Nymphalidae					+	<i>Discophora spp.</i>	Sundanian
<i>Neptis transita</i>	Nymphalidae					+	<i>N. noyala</i>	Sino-Himalayan
<i>Phaedyma armariola</i>	Nymphalidae					+	<i>P. aspasia</i>	Sino-Himalayan
<i>Tanaecia stellata</i>	Nymphalidae					+	<i>T. godartii</i>	Sundanian
<i>Euthalia hoa</i>	Nymphalidae					+	<i>T. thibetana</i>	Sino-Himalayan

Species	Family	Centres of endemism in Vietnam					Nearest relatives	
		Hoang Lien Son	N. and N.E. Vietnam	Northern Truong Son ridge	Kon Tum plateau	Da Lat and Lac plateaus	Species	Distribution
1	2	3	4	5	6	7	8	9
<i>E. khambounei</i>	Nymphalidae	+						Sino-Himalayan
<i>E. strephonida</i>	Nymphalidae					+	<i>E. strephon</i>	Sino-Himalayan
<i>Calinaga funeralis</i>	Nymphalidae		+				<i>Calinaga spp.</i>	Sino-Himalayan
<i>Dodona katerina</i>	Riodinidae			+	+		<i>D. dipoea</i>	Indo-Burmese
<i>D. speciosa</i>	Riodinidae				+	+	-	Indo-Burmese
<i>Taxila dora</i>	Riodinidae	+	+	+	+		-	Indo-Burmese
<i>Deramas cham</i>	Lycaenidae					+	<i>D. jasoda</i>	Sundanian
<i>Heliophorus smaragdinus</i>	Lycaenidae				+		<i>H. tamu</i>	Sino-Himalayan
<i>Euaspa minaei</i>	Lycaenidae					+	<i>E. hishikawai</i>	Sino-Himalayan
<i>E. nishimurai</i>	Lycaenidae	+						Sino-Himalayan
<i>Proteuaspa akikoe</i>	Lycaenidae		+					Sino-Himalayan
<i>Chrysozephyrus wakaharai</i>	Lycaenidae			+				Sino-Himalayan
<i>Ch. vietnamicus</i>	Lycaenidae	+						Sino-Himalayan
<i>Ch. hatoyamai</i>	Lycaenidae	+						Sino-Himalayan
<i>Shirozuozeephyrus alienus</i>	Lycaenidae					+	<i>S. hayashi</i>	Sino-Himalayan
<i>Sh. masatoshii</i>	Lycaenidae	+						Sino-Himalayan
<i>Neomyrina sp.</i>	Lycaenidae			+			-	Sundanian
<i>Tajuria sekii</i>	Lycaenidae					+		Sundanian
<i>Tajuria shigehoi</i>	Lycaenidae					+	<i>T. luculenta</i>	Sundanian
<i>Rapala persephone</i>	Lycaenidae					+	<i>R. hades</i>	Indo-Burmese
<i>Celaenorrhinus inexpectus</i>	Hesperiidae		+				<i>C. maculosa</i>	Indo-Burmese
<i>C. victor</i>	Hesperiidae		+				<i>C. dayaoensis</i>	Sino-Himalayan
<i>C. incestus</i>	Hesperiidae			+			<i>C. maculosa</i>	Indo-Burmese
<i>C. kuznetsovi</i>	Hesperiidae			+			<i>C. oscula</i>	Taiwan

Species	Family	Centres of endemism in Vietnam					Nearest relatives	
		Hoang Lien Son	N. and N.E. Vietnam	Northern Truong Son ridge	Kon Tum plateau	Da Lat and Dac Lac plateaus	Species	Distribution
1	2	3	4	5	6	7	8	9
C. phuongi	Hesperiidae		+				<i>maculosa</i> group	Sino-Himalayan
Darpa inopinata	Hesperiidae		+	+			<i>D. striata</i>	Indo-Burmese
Coladenia tanya	Hesperiidae		+	+				Indo-Burmese
C. koiwaii	Hesperiidae	+					-	Sino-Himalayan
Pintara capiloides	Hesperiidae			+		+	other <i>Pintara</i>	Indo-Burmese
Tagiades hybridus	Hesperiidae			+			<i>T. gana</i> , <i>T. parra</i>	Indo-Burmese
Thoressa similissima	Hesperiidae		+	+				Indo-Burmese
Aeromachus cognatus	Hesperiidae					+		Indo-Burmese
Halpe frontieri	Hesperiidae		+				<i>H. nephele</i>	Indo-Burmese
Halpe paupera	Hesperiidae			+				Indo-Burmese
Halpe annamensis	Hesperiidae					+	<i>H. zema</i>	Indo-Burmese
Scobura eximia	Hesperiidae		+					Sino-Himalayan
Suada albolineata	Hesperiidae		+	+	+	+	<i>S. swerga</i>	Sundanian
Quedara flavens	Hesperiidae		+				<i>Q. albifascia</i>	Indo-Burmese
Praescobura chrysomaculata	Hesperiidae	+					<i>Scobura</i>	Sino-Himalayan

(Species marked with bold are restricted by the territory of Vietnam)

Table 3. Indochinese butterfly endemics and their distribution and nearest relatives.

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