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Coleopterology in Laos – an introduction to the nature of the country and its coleopterological exploration

by Michael Geiser & Peter Nagel

Abstract. An introduction to the physical environment of Laos is provided, including vegetation, fauna, conservation and habitat types, intended to serve as general background information for entomological research in that country. An overview of the history of entomological – particularly coleopterological – surveys in Laos is provided, including information about collectors and the places in which their material is deposited. A detailed list of localities surveyed in the course of the seven Laos expeditions undertaken by the Basel Natural History Museum (2003–2012, all organised by Michel Brancucci), is provided, including associated data such as geographical coordinates, altitude and collecting dates. A comparison between existing sampling localities and the available habitats in Laos reveals the coleopterologically least-explored areas, such as the montane rain forests of both the Annamite range along the border to Vietnam, and the Luangprabang range west of the River Mekong, as well as the lowland habitats east and west of the southernmost section of the Mekong.

Key words. Lao PDR – Coleoptera – biogeography – entomological exploration – Laos environment – physical geography – faunistics – history of exploration – conservation

Introduction

The current contribution arises out of the late Michel Brancucci's intention to collate all the data from his expeditions to Laos. This compilation would then have served as a source of information to complement the label data of specimens collected. He was not able to do this himself, but one of us (MG) had the privilege of accompanying him on four of the seven voyages and PN joined one expedition with science students from the University of Basel. Although we are not able directly to transmit Michel Brancucci's close knowledge of the country and its people, or to relate the details of all seven of his expeditions, we have tried our best to present all the relevant data.

An introduction to the nature of any given country is sought after by all entomologists heading for foreign places. Data on climate, habitat structure and diversity, remoteness of certain areas, and uniqueness of particular landscapes, is highly valuable, even essential. A very good, concise work on Laos was published by GRESSITT (1970), in part building on vegetation and soil studies by VIDAL (1960a). Today, almost half a century later, much more detail of all aspects of the natural history of the country is available, while new facts and discoveries continue to be brought to light. The current contribution cannot replace a comprehensive treatment of Laos' environment, which remains to appear. It aims to introduce the reader to the state of contemporary knowledge of selected aspects of the natural history of Lao People's Democratic Republic, with an update of recent references, including the "grey" literature, to relate the history of the entomological exploration of Laos, and to provide detailed data on the expeditions undertaken by Michel Brancucci.

Abbreviations and Conventions

The following institutional and private collections are mentioned in the history section:

BIMH Bishop Museum, Honolulu, H	awaii, USA.
BMNH Natural History Museum, I	London, UK.
CCH Carolus Holzschuh private collection, Villa	ach, Austria.
CKA Klaus-Werner Anton private collection, Emmendinge	n, Germany.
EHUM Entomological Laboratory, Ehime University, Matsuy	yama, Japan.
KMNH Kurashiki Museum of Natural History, Okay	yama, Japan.
MCGD Museo Civico di Storia Naturale "Giacomo Doria", G	enova, Italy.
MMB Moravian Museum, Brno, Czec	ch Republic.
MNHP Muséum national d'Histoire naturelle, P	aris, France.
MTMB Magyar Termeszettudomanyi Muzeum, Budape	est, Hungary.
NHMB Naturhistorisches Museum, Basel,	Switzerland.
NHMW	nna, Austria.
NMPC National Museum, Prague, Czed	ch Republic.
ZISP Zoological Institute, Russian Academy of Sciences, St. Petersh	ourg, Russia.
ZMUC Zoological Museum, University of Copenhage	n, Denmark.
ZSM Zoologische Staatssammlung München, Munic	h, Germany.

Participants in the NHMB Laos expeditions are abbreviated as:

APAny Phanthala
DH David Hauck
EV Elawan Vongphachan
KP Khampheuy Phanthavong
KS Khampaseuth Sisoutham
MB Michel Brancucci
MG Michael Geiser
PP Petr Pacholátko
SX Somphasong Xayalath
VK
ZKZdeněk Kraus

Other abbreviations/acronyms:

NBCA	National Biodiversity Conservation Area
PNBCA	Proposed Biodiversity Conservation Area
NPA	National Protected Area

The transcription of names and localities from the Lao language to English does not appear in any particular standardised format. It goes without saying that locality information on labels attached to specimens is presented strictly in the original version. Whenever current province or district names are mentioned, we follow the official spelling published by LSB (2013b) (see also "http://www.nsc.gov.la/ \rightarrow Statistic \rightarrow Yearbook 2012 \rightarrow Administration").

Although we have put considerable effort into listing all the collectors active in Laos up to 2012, one or two will inevitably have been overlooked. We would therefore very much appreciate any further records from our readers that might enable us to make appropriate changes to our listings in the second special volume of this journal.

The ecology and biogeography of Laos: Basics

Laos is a landlocked, tropical country in the centre of the Indochinese Peninsula, on a north-south extension between approximately 22°30′N and 13°54′N latitude. With a surface area of 236,800 km², it is about the same size as Great Britain, smaller than neighbouring Thailand, Myanmar, China and Vietnam, but slightly larger than Cambodia, which is adjacent to the south. Altitudes in Laos range from about 70 m at the southern tip of the country up to 2818 m at the summit of Mt. Phou Bia in the north. Almost 75% of the country is mountainous (Messerli et al. 2008) and about 40% to 50% of its territory is still covered with forest (see paragraph "Conservation: Forest cover" below). The rugged terrain and considerable extension from north to south generate a high number of habitat types and exceptionally high biodiversity, which makes it a central and important part of the "Indo-Burma hotspot", one of the global biodiversity hotspots designated by Myers et al. (2000).

Landscape features. The topography of Laos is dominated in the east by the north-west – south-east Annamite mountain chain (Xai Phou Luang in Lao, Day Truong Son in Vietnamese) and in the west by the valley and floodplains of its largest river, the Mekong (Mae Nam Khong). The country consists of three basic physiogeographical units: the Northern Highlands, the Annamite Range and the Mekong plains. The Northern Highlands consist mainly of rugged mountainous terrain, but also include the large Vientiane Plain by the Mekong and the lower section of the Nam Ngum river. The Annamite Range is generally less rugged (outside its karst areas) and the Mekong plains consist of the alluvial floodplain of the Mekong between Pakxan and the Cambodian border, including adjacent low-lying areas (such as the east of Savannakhet) (see Duckworth et al. 1999) (Fig.1). Notable landscape features include large plateaus (the Xieng Khouang Plateau, the Nakai Plateau, the Bolaven Plateau) and spectacular tropical karst areas (around Vang Vieng and Viang Xai in the northern highlands, as well as in southern Borikhamxay and Khammuane provinces). Geological data appears in DGM (2013), while a summary is provided by Robichaud et al. (2001: Annex 4).

With a total population of 5.6 million in 2005 and an estimated 6.5 million in 2012 (LSB 2013a,b), the average population density for the whole country has been calculated at 26 (2005) and 28 (2012) people per km². The most densely populated administrative areas are the Vientiane Prefecture, comprising the capital city (178 people per km², figures based on the 2005 population census, LSB 2013b), and the provinces of Champasack (39 people per km²) and Savannakhet (38 people per km²), while the least densely populated provinces are Attapeu (11 people per km²) and Sekong (11 people per km²) in the south and Phongsaly (10 people per km²) in the north (Fig. 2) (see also maps of population density in GoL 2006, LSB 2013a [province level, 2005], Encyclopaedia Britannica 2013 [province level, 2005], CIESIN 2009 [district level, 2000], UNOSAT 2008 [sub-district level, 2004]). Some 90% of the territory of Laos is populated at a level of fewer than fifty people per km2 and 35% contains fewer than five people per km2 (MESSERLI et al. 2008). This is an extremely low population density, especially when compared to neighbouring regions (people per square kilometre, United Nations data, 2010 database): Laos 27, Myanmar 77, Cambodia 79, Yunnan prov. of China 120, Thailand 129, Vietnam 268. The population density is one factor to be considered in the

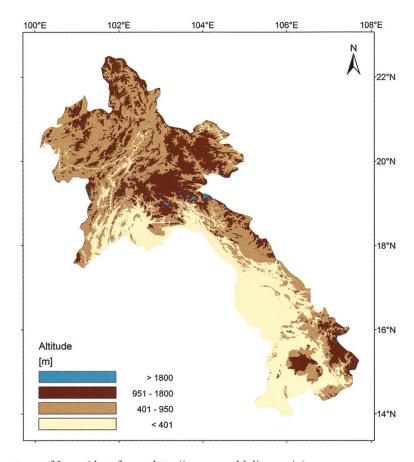


Fig. 1. Altitude pattern of Laos (data from http://www.worldclim.org/">http://www.worldclim.org/).

assessment of the remoteness of areas. Human impact on natural habitats is generally higher in areas of high population density. However, even in such areas, islands of natural habitat may occur as well as, conversely, extensive destruction of forest habitats in areas of low population density.

The Northern Highlands are dominated by a large number of interconnected mountain ranges, often as high as 1800 m in parts (Fig. 1). The upper course of the Mekong and the Nam Ou, its main tributary, form deeply-incised valleys with their beds at between 250 and 450 m. The main mountain range west of the Mekong valley, with its maxima at 2077 m (Doi Lo), 2079 m (Doi Luangprabang) and 2102 m (Phu Soaydao or Phu Soi Dao) at the Thai border in Xayabury Province, is referred to as the Luangprabang Range. The high mountains extending along the Vietnamese border to the Chinese province of Yunnan are an extension of the Annamite Range. The Xieng Khouang (or Phouane, Phou Ane, colonial French name Tran-Ninh) Plateau includes the Plain of Jars and is situated in the middle of the Northern Highlands, bordered by the Phou Bia massif in the south-west (the highest point in Laos, at 2818m [Messerli et al. 2008], 18°59'N 103°09'E, is the summit of Mt. Phou Bia, Vientiane Province), and high mountains towards the eastern border to Vietnam (second- and third-highest mountains in Laos, Xiengkhuang province: Phu Xamxum [Phou Samsoum] 2620 m, 19°08'N / 103°48'E; Phu Xao 2590 m, 19°09'N / 103°28'E, together with the massif of Phu

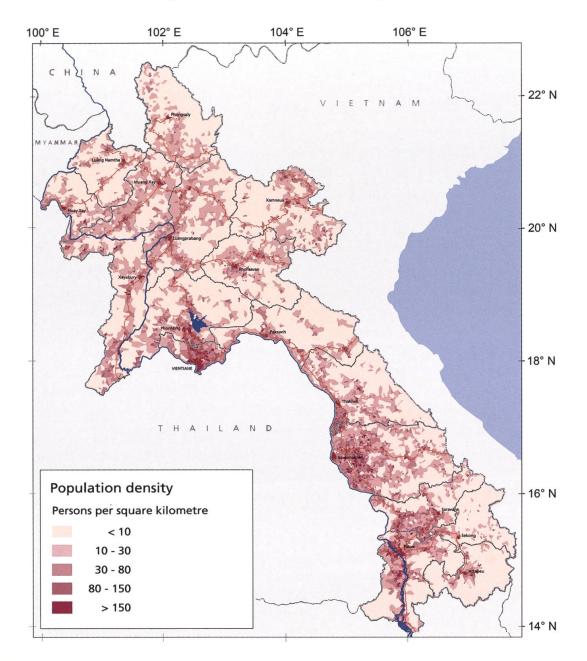


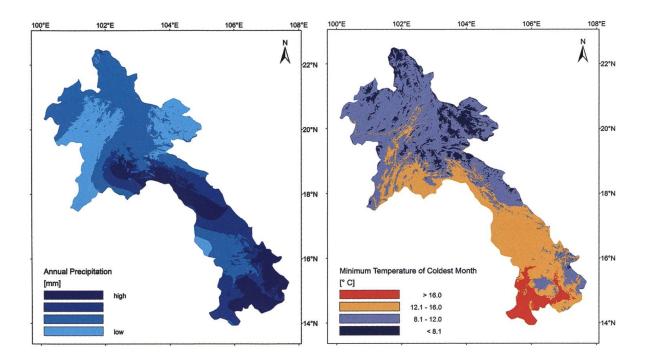
Fig. 2. Human population density of Laos (map reproduced with changes in layout from MESSERLI *et al.* 2008, by courtesy of Swiss National Centre of Competence in Research (NCCR) North-South, Switzerland, the Department of Statistics (DOS) and the Lao National Mekong Committee Secretariat (LNMCS)).

Xailaileng [Phu Xaylailèng] 2711 m, 19°12′ N / 104°11′E at the Lao-Vietnamese border, the peak of which is usually listed as part of the Vietnamese register; data retrieved from maps, see LSB 2013b for slightly differing data). The plateau itself lies at altitudes of between 900 m and 1300 m. The landscape around Vang Vieng, approximately 100 km north of Vientiane, is dominated by spectacular limestone formations, including caves, as is the area around Viang Xai, in eastern Houaphanh province.

Near Vientiane, the Mekong river valley becomes a broader alluvial plain, fed further downstream by a number of major tributaries (from north to south: Nam Ngum, Nam Kading, Xe Bangfay, Xe Banghiang, Xe Don and others, comprising the Xe Kong that merges with the Mekong only in Cambodia). Its altitude decreases gently from around 200 m near Vientiane to about 70 m south of Pakse, at the Cambodian border. Here, the valley once more opens out into a large plain and the river becomes very wide, with cataracts, and breaks up into several arms enclosing islands.

The border between the central and southern parts of Laos and Vietnam follows the watershed of the Annamite Range to a greater or lesser extent. While the Vietnamese north-eastern part slopes steeply towards the coastal plain, the south-westerly incline in Laos is more gentle, covering a wider area until merging into the Mekong Plain. The Annamite Range is interrupted by lower altitude areas (around 300 m) in Savannakhet Province, then reaches slightly more than 2000 m again in the south-eastern provinces of Sekong and Attapeu, before running on into South Vietnam. Major parts of the central province of Khammuane consist of a large limestone area, the Khammouan Karst, containing large numbers of caves (see DGM 2013). Large parts of the Nakai Plateau in Khammuane province have only recently been flooded by the Nam Theun 2 Reservoir (see Fig. 6). A major topographical feature of southern Laos is the volcanic Bolaven Plateau, reaching altitudes of between 700 and 1600 m (mostly around 1000 m) and occupying major parts of Champasack Province. This is separated from the southern part of the Annamite Range by the large valley of the Xe Kong (Sekong) river.

Climate. The climate is tropical-seasonal and dominated by the south-western, wet summer monsoon. The resulting rainy season, providing more than 90% of the annual precipitation, normally lasts from May to October. The large majority of the rain falls on the south-western slopes of the mountains, while most of the Mekong Plain and the leeward aspects of mountains receive markedly less (Fig. 3). The country's average annual rainfall ranges from 1650 mm to 1950 mm (NIEMAN & KAMP 2009) or 1300 mm to 2300 mm (Encyclopaedia Britannica 2013) (differences in data arising out of the basic number of meteorological stations sampled and the sampling years). With regional differences, the mean annual rainfall is between 900 mm and more than 3700 mm (SAYPASEUTH 2011, cf. NHOYBOUAKONG et al. 2012). The basin east of Savannakhet (NIEMAN & KAMP 2009), the north-west including the north-south oriented valleys of the Mekong and Nam Ou (NHOYBOUAKONG et al. 2012) and some leeward sides of mountain chains in the north and north-east generally receive the least rainfall (VIDAL 1960a). Among the lowest annual rainfall data are 397 mm (2004) and 1080 mm (1998), from the Savannakhet meteorological station (annual mean 1976 - 2011: 1396 mm) (LSB 2013b). The highest average annual precipitation was recorded on the Bolaven Plateau (4100 mm, Encyclopaedia Britannica 2013), and mean annual rainfall of over 3000 mm occurs in many parts of the Annamite Range from Mount Bia in the north to the southeasternmost corner of the country (see NHOYBOUAKONG et al. 2012). In terms of longterm average for the whole country, the months with highest precipitation are July and August and the driest are January and February (World Bank 2013). Extra-seasonally high daily rainfall often occurs during September and October in the west of the central parts of the Annamite Range. This is due to extension of typhoons originating over the



Figs 3–4. 3 – Mean annual rainfall in Laos (reference see Fig.1). 4 – Minimum temperature of coldest month in Laos (reference see Fig. 1).

sea, moving westward towards the Vietnamese coast and only partially blocked by the Annamite Range. The dry season lasts from late October/November to April/May.

Drought-prone areas are situated largely in the southern parts of Xayabury Province, in all of Vientiane Province and Prefecture, and the lowland belt along the Mekong from Borikhamxay down to the Cambodian border. In some years, drought may even occur on the Bolaven Plateau, which is usually very humid. Drought spells in June/July can have a severe impact on crop yields (SAYPASEUTH 2011). The risk of drought is at its lowest in the eastern parts of Khammuane, Savannakhet and Saravane provinces along the Vietnamese border (JICA 2010). The last-named areas have relatively low seasonality compared to other parts of the Andaman chain (EPPRECHT *et al.* 2008, p. 71). Flooding is mostly associated with heavy and persistent downpours arising out of the extensions of typhoons in the South China Sea in September and October.

The mean annual temperature of the country is 26.5°C–27.5°C (NHOYBOUAKONG *et al.* 2012), varying year on year from 22.4°C to 29.1°C (NIEMAN & KAMP 2009), with May as the warmest month on long-term average for the whole country and December and January the coldest (World Bank 2013). The highest temperatures during April can exceed 40°C, with a maximum of 44°C recorded at Luangprabang (WEISCHET & ENDLICHER 2000) and Savannakhet (SAYPASEUTH 2011). Monthly T_{max} averages of about 33°C to 34°C in April and May were recorded at both meteorological stations in 2011 (LSB 2013). The relative air humidity peaks at 60% to 70% during this pre-monsoon

period (WEISCHET & ENDLICHER 2000). The phenology and mortality rates of insect populations are strongly influenced by minimum temperatures which, therefore, have considerable impact on their spatial and temporal distribution. In some high-altitude areas, above 1200 m, frost sometimes occurs late at night (NIEMAN & KAMP 2009) with a minimum of -3°C recorded at the end of December near Phonsavan (SAYPASEUTH 2011) (Fig. 4).

In summary, there are two main seasons and one short season: a wet, warm rainy season from May to October; a cool, dry season from November to February; and a hot, dry season from March to April (Weischet & Endlicher 2000). These changes of temperature and rainfall over the year are reflected in the phenology of insects: the highest diversity of beetles is found in April and May, while some large-bodied species occur later, between June and August (Rondon 1970).

Agriculture. The soils are predominantly acidic and poor in minerals and organic matter, largely inappropriate to intensive agricultural use. More fertile soil is found in the alluvial areas (NIEMAN & KAMP 2009). Agriculture in Lao PDR takes three main forms: lowland agriculture (predominantly irrigated rice cultivation); highland agriculture (predominantly shifting cultivation in the form of rotational slash-and-burn ("swidden") agriculture, including rain-fed upland rice cultivation); and an expanding specialised crop sector (ICEM 2003). The potentially cultivable land is estimated at 25% of Laos' land resources (data from FAO, 2000, see ICEM 2003). Published figures for the actual agricultural land as a percentage of the total land area are between 7% and 10% for 2010/2011 (MAF 2012, World Bank 2013), low compared with adjacent countries (World Bank 2013). Rice cultivation (mainly paddy rice) takes up the majority of agricultural use of land (more than 75% according to ICEM 2003, slightly more than 60% based on data for 2010/2011 of MAF 2012) and pasture another 15% (ICEM 2003) or 2% (MAF 2012). In 2011, the spatially dominant crop other than rice was maize, with a total of 0.6% (1345km²) of the country or 6% to 8% of the agricultural land (APCAS 2012).

Plantations, generally small-scale, include teak, rubber and eucalyptus. Freshwater fish-farming is widespread and much of the livestock consists of cattle (NIEMAN & KAMP 2009). Cattle number 1.7 million head for the whole country, mainly distributed in the provinces of Savannakhet and Vientiane. Water buffaloes are mainly found in the southern provinces of Savannakhet and Champasack (1.2 million head in 2012 for the whole country) (LSB 2013b). The Bolaven Plateau has coffee plantations above 800 m with tea in second place (NIEMAN & KAMP 2009).

The centre of origin of the glutinous rice types is reported to lie within the region comprising Laos and northern Thailand (STEA-PMO 2004). Glutinous rice is grown on more than 90% of the rice producing area of Laos (MAF 2012).

Vegetation. The natural vegetation of Laos has been described in detail by VIDAL (1960b), with local information added by LEHMANN *et al.* (2003) and a field guide to trees by VAN SAM *et al.* (2004). The vegetation of Indochina as a whole has been addressed by VIDAL (1997) and MACKINNON & MACKINNON (1986) (see also MACKINNON 1997) (Fig. 5). The woodland and forest canopy vegetation of Indochina is dominated by trees of the family Dipterocarpaceae. They are represented by species of

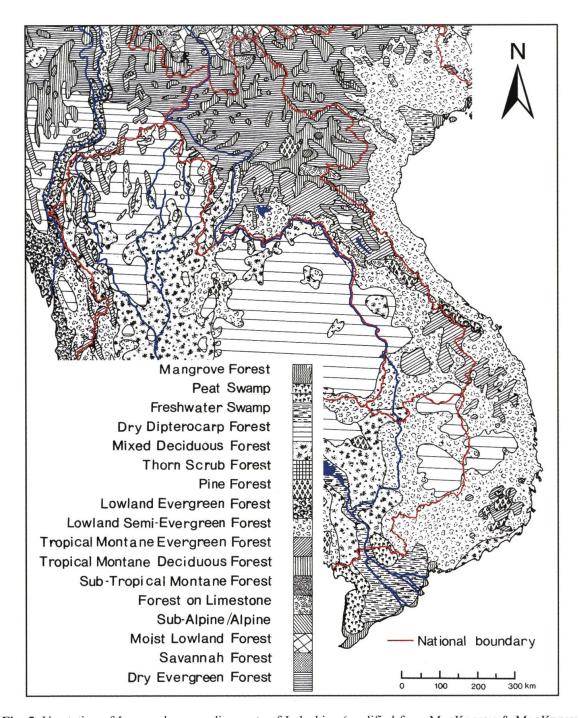


Fig. 5. Vegetation of Laos and surrounding parts of Indochina (modified from MACKINNON & MACKINNON 1986).

six genera, all of which are non-endemic and their range also takes in larger parts of Sundaland (WHITMORE 1990).

Most of the Mekong valley is covered in a species-rich deciduous monsoon forest, dominated by dipterocarps. The mountainous areas contain a mosaic of humid and semi-humid forest types, including subtropical montane forests in the north. Some of these

evergreen montane forests are exceptionally species-rich, and may have become Pleistocene refugia for forest-dwelling species while most of Laos had a drier, more savannah-like climate (METCALFE et al. 2001, MEIJAARD & GROVES 2006, CANNON et al. 2009). Mountain-tops and ridges in the Annamite Range are often dominated by species of Fagaceae (*Castanopsis* and *Lithocarpus*), while the Luangprabang Range is one of the original habitats of the teak tree *Tectona grandis*.

Pine forests, largely *Pinus merkusii* and *P. kesiya*, occur in pockets all over the Annamite Range, but mostly on the Xieng Khouang Plateau and the upper Xe Kong catchment in the south. Possibly the only extensive old-growth pine stands in the country (including specimens of the rare Dalat pine *Pinus dalatensis*) are found on the Nakai Plateau (Duckworth *et al.*1999, Nguyen & Thomas 2005, Thomas & Phan 2013).

A number of the higher mountain tops in the northern Annamites (from Houaphanh to Borikhamxay/Khammuane, including Nakai Nam Theun NBCA) are covered in Fokien cypress *Fokienia hodginsii*, a peculiar gymnosperm species. Natural montane grassland areas occur in parts of the Xieng Khouang Plateau and in Attapeu Province (Thong Kai Ohk) (VIDAL 1960b).

The natural forest cover has largely been replaced due to human influence, leaving only about 20% of habitats as primary (still one of the largest proportions in Southeast Asia) (Mackinnon 1997). Most of the primary forest cover is found in the south of the country and in the eastern half of the central provinces of Borikhamxay and Khammuane. The landscape in northern Laos is now a small-scale mosaic of villages, rice-fields (mainly "mountain rice" grown on slopes), pastures, plantations (e.g. rubber tree *Hevea brasiliensis*), fragments of secondary forest and bamboo thickets as an early succession stage of forest regrowth. Primary forests are still to be found, but only in remote places or deep within protected areas. On the Bolaven Plateau, increasingly large areas are being used for coffee and tea plantations. The Mekong valley is the most densely populated area and is used mostly for agriculture, with larger areas of primary forest remaining in only a few protected areas (e.g. Nam Kading NPA in Borikhamxay and Xe Pian NBCA in Champasack Province).

The flora of Laos is less known than that of most other Asian countries, largely because of a lack of herbarium material collected in the country (Newman *et al.* 2007). Major reference works comprise the published fascicles of the "Flore du Cambodge, du Laos et du Viêtnam", the "Flora of Thailand" and the "Flora of China". DINERSTEIN & WIKRAMANAYAKE (1993) (see also MACKINNON 1997, GROOMBRIDGE & JENKINS 2002) report 8286 vascular plant species for Laos. A more recent checklist of the vascular plants, however, lists 4624 native plants and 226 introduced, cultivated and naturalized plants (Newman *et al.* 2007). Another estimate is 8000 to 11,000 species of flowering plants (MAF & STEA 2003). The number of plant species in the entire Indo-Burma hotspot has been estimated at 13,500 (MITTERMEIER *et al.* 2004).

Inland waters. The relatively high rainfall over nearly all of the country and the largely hilly terrain make for abundant streams and provide a major freshwater habitat. Much of the country belongs to the catchment area of the River Mekong (80%). Only in the Houaphanh Province and Xiengkhuang Province do a number of rivers drain into the South China Sea *via* Vietnam (Fig. 6).

The main river is the Mekong, which runs along or near the border of Laos with neighbouring Myanmar and Thailand, entering Cambodia in the very south. The monsoon climate leads to wide seasonal variation in flow rates, resulting in large parts of the river bed becoming exposed towards the end of the dry season and creating an important and particular habitat for wildlife (Duckworth *et al.* 1999). Large, slow-moving streams such as the Nam Theun/Nam Kading (central Laos), Xe Banhiang (Savannakhet prov.) and Xe Kong (Attapeu prov.) are rare and highly threatened (Robichaud *et al.* 2001). The country is particularly rich in small, often swift-running forest streams, sometimes with spectacular waterfalls. The Mekong Khone Falls in southern Champasack Province are among the widest rapids in the world. Farmland ditches and irrigation canals make up the country's artificial linear water bodies.

Among the natural lakes is Nong Fa (Nong Fatomkleen) in Attapeu Province, a crater lake at an altitude of about 1150 m. Other lakes are at much lower altitudes, such as Khoun Kong Leng, a ground-water lake in the Karst formation of Khammuane Prov. near Thakhek, and Nong Luang and other shallow floodplain lakes east of Savannakhet. Natural standing water habitats are also created by partly or completely cut-off river sections in floodplains, by permanent or seasonal pools, and by phytotelmata (water-filled holes in trees or similar water-filled structures provided by epiphytes and other plants, and the pitchers of *Nepenthes*).

There are hot springs and mineral springs in Xiengkhuang, Houaphanh and Oudomxay provinces in the north, and southern Borikhamxay in the central part of the country.

Among the artificial lakes is the large Ang Nam Ngum reservoir (Vientiane prov.) at an altitude of about 210 m, covering 370 km², created the early 1970s. The Houay Ho Dam reservoir covers 37 km², has been in operation since 1999, and lies at 890 m about 30 km north-west of the town of Attapeu on the edge of the Bolaven Plateau. The Nam Theun 2 reservoir on the border of the Nakai Nam Theun NBCA has been in full operation since 2010, has a maximum water surface area of 450 km² and lies at an altitude of about 550m (Fig. 6). There are several other dams and more are proposed, largely for hydro-electricity production (map: http://www.international-rivers.org/files/attached-files/lao_dams_map.jpg, table: http://www.international-rivers.org/files/attached-files/laohydro2010_sept_final.pdf, see also ALLEN *et al.* 2008, p.15). Smaller dams are numerous and their reservoirs are often used for pisciculture, while the paddy-fields also serve as an important habitat for fish-farming. Perennial and seasonal ponds or waterholes are numerous, and are used for fish cultivation, water storage for people and livestock, and irrigation.

There are important wetlands along the Mekong Plain, consisting of seasonal swamps and grassland. These include the two Ramsar sites in Savannaketh and Champasack provinces (see "Conservation: Protected areas" section below). More intensive and/or larger rice paddy areas are situated to the north and east of Vientiane, to the west and south of Phonsavan, to the south of Thakhek, all around Savannakhet, to the west of Saravane, the west of Pakxe and east of Attapeu (Messerli *et al.* 2008: map A4).

Fauna. The fauna of Laos is among the most species-rich in Asia. A certainly-outdated database (DINERSTEIN & WIKRAMANAYAKE 1993), adapted by MACKINNON (1997) and CLARKE (2000), gives the following species numbers: mammals: 200, birds 609, reptiles 66, amphibians 37, fish 244, swallowtail butterflies 39. However, new species are being recorded at a surprisingly high rate in Laos and the greater region (see Thompson *et al.* 2011). The figures are adjusted as far as possible below. The fauna also includes some spectacular endemics or near-endemics, such as the antelope-like Saola *Pseudoryx nghetinhensis*, an elusive bovid, some of the world's largest freshwater fish such as the giant catfish *Pangasianodon gigas*, and possibly the largest spider of all, the giant huntsman Spider *Heteropoda maxima* Jaeger, 2001, from a cave in the Khammouan Karst (over 46mm body length and about 30cm leg-span, JAEGER 2001).

Fauna: mammals. The number of species of mammals occurring in Laos is given by WCMC (1992) and Groombridge & Jenkins (2002) as only 172 and 173 respectively, even fewer than the 200 species reported by Dinerstein & Wikramanayake (1993). However, based on another compilation, over 100 species of large mammals, about 10 insectivores (gymnure, moles, shrews), nearly 90 species of fruit bats and insectivorous bats and more than 30 Muridae (mice, rats, pygmy dormice, voles, bamboo rats) have been reported for the country (Duckworth *et al.* 1999). This is still certainly an underestimate and only about half of the nearly 470 land mammal species reported for mainland Southeast Asia (Francis 2008). Ecoregion-based figures are available from http://worldwildlife.org/pages/wildfinder.

Spectacular recent discoveries, even of relatively large mammals, serve to underline our lack of knowledge of the biodiversity of Laos. Such records include endemics of the Annamite Range such as the Saola *Pseudoryx nghetinensis* Dung *et al.*, 1993, the giant muntjac *Muntiacus vuquangensis* Tuoc *et al.*, 1994, the small dark muntjac *Muntiacus truongsonensis* Giao *et al.*, 1998, the Annamite striped rabbit *Nesolagus timminsi* Averianov *et al.*, 2000 and, restricted to the limestone areas of the Khammuane province, the long-eared gymnure *Hylomys megalotis* Jenkins *et al.*, 2005. The rock rat is an example of micro-endemism, in which distinct populations become restricted to isolated limestone blocks (NICOLAS *et al.* 2012). It is the single extant representative of the family Diatomyidae, otherwise known only from the fossil record.

Among the larger mammals, Indochinese tigers *Panthera tigris corbetti* Mazák and Asian elephants *Elephas maximus* L. were, until recently, found throughout the country, but have become increasingly rare and may now be restricted to one or a few protected areas. Irrawaddy dolphins *Orcaella brevirostris* (Owen) are still found in the Mekong in the southernmost parts of Champasack Province, while two species of rhinoceros (Javan rhinoceros *Rhinocerus sondaicus* Desmarest and the Sumatran rhinoceros *Dicerorhinus sumatrensis* (G. Fischer)) are now extinct in Laos. The kouprey *Bos sauveli* Urbain, a forest-dwelling ox, is now IUCN-listed as critically endangered, possibly extinct on Laotian territory, as well as in the other parts of its former range in Cambodia, Vietnam and Thailand (Duckworth *et al.* 1999, Timmins *et al.* 2008). Laos is home to a range of diurnal primates: five species of macaque *Macaca* spp., possibly three species of langurs *Trachypithecus* spp., at least one species of douc *Pygathrix nemaeus* L., two gibbons

Hylobates spp. and four crested gibbons Nomascus spp. (Duckworth et al. 1999, Francis 2008, cf. IUCN data).

Fauna: birds. The number of bird species reported or provisionally reported for Laos has been estimated at 481 (WCMC 1992), 487 (GROOMBRIDGE & JENKINS 2002) and 609 (DINERSTEIN & WIKRAMANAYAKE (1993), yet appears to be about 700 with 100 more likely to occur (DUCKWORTH et al. 1999, WICE 2013). It was only recently that an unmistakable new species was discovered and finally described in 2009, the bare-faced bulbul *Pycnonotus hualon* Woxvold et al., 2009. This species is apparently endemic to Laos and seems to prefer vegetation at the top of limestone outcrops. Another new species from the same general area is the limestone leaf warbler *Phylloscopus calciatilis* Alström et al., 2010.

Further elements of the Lao bird fauna of international note include the globally-threatened white-winged duck *Cairina scutulata* (S. Müller) (only five to ten pairs were recorded in Laos, from the western Nakai Plateau in 1995–1996, before the Nam Theun 2 reservoir started to fill: see Asian Development Bank 2004), white-shouldered ibis *Pseudibis davisoni* (Hume), giant ibis *Thaumatibis gigantea* (Oustalet), Siamese fireback *Lophura diardi* (Bonaparte), the crested argus *Rheinardia ocellata* (Elliot), with the tail feathers reaching nearly 2 m in the male, green peafowl *Pavo muticus* L. and other key species of birds such as the Alexandrine parakeet *Psittacula eupatria siamensis* Kloss. The globally endangered greater adjutant *Leptoptilos dubius* (Gmelin) appears to be extinct in Laos (Duckworth *et al.* 1999, BirdLife International 2012).

Fauna: reptiles. WCMC (1992) reported 66 species of reptiles for Laos. Among more than 110 species of reptile listed by DUCKWORTH at al. (1999), the species attracting the most attention appears to be the Siamese crocodile Crocodylus siamensis Schneider, mainly because of its rapid and massive decline in the recent past. It used to inhabit, in some numbers, rivers, lakes and other wetlands, yet recent records are very rare (DUCKWORTH at al. 1999). What is presumably the largest remaining population in Laos consists of about 75 specimens in Savannaketh Province, mainly at the Xe Champhone Ramsar site (IUCN 2011), where reintroduction attempts are currently under way. Snakes are represented by about 60 species, including the widespread flowerpot snake Ramphotyphlops braminus (Daudin), at 6–16 cm long one of the smallest snakes in the world, and at the other pole, the reticulated python Python reticulatus Schneider, one of the largest. Poisonous species such as three species each of krait Bungarus spp. and cobra Naja spp. and six pit vipers Trimeresurus s.l. spp. are also known from Laos. The turtles are represented by two or three species of box turtle Cuora spp. and soft-shelled turtle (Trionychidae). Among the lizards, possibly more than one species of flying lizards Draco spp. live in Laos (Duckworth et al. 1999, Nguyen et al. 2009).

Fauna: amphibians. While earlier WCMC (1992) databases give just 37 species of amphibians for the country, Duckworth et al. (1999) listed some 60 species. New species have recently been described, among them the endemic Laos warty newt Laotriton laoensis (Stuart et Papenfuss) (described as Paramesotriton in 2002) from the north. The Laos knobby newt Tylototriton notialis Stuart et al. was described in 2010 from Khammuane province and two new frog species were reported in the same year

(see Thompson *et al.* 2011). Molecular approaches and call analyses will certainly reveal many more species of frogs than are currently known to science.

Fauna: fish. The fish fauna is particularly species-rich in SE Asia. The number of reported indigenous fish species in Laos' fresh waters increased from about 220 in 1996 to 465 in 2000 (Allen et al. 2012, based on data by Kottelat 2001). Currently, a total of 545 native fish species have been scientifically confirmed for the country (Froese & Pauly 2013), most of them from the Mekong and its tributaries (see Kottelat 2001). This represents about half of the fish species diversity for the Indo-Burma hotspot. The whole Mekong drainage within the hotspot area is home to some 500 species (Allen et al. 2012). New species continue to be discovered, increasingly from small headwater streams and rapids as well (Tordoff et al. 2012, based on data provided by Kottelat 2001). It has been reported that perhaps over 25% of fish species recorded from the Dakchung Plateau in Sekong province appear to be endemic to it (Tordoff et al. 2012, based on data provided by Kottelat). In general, the majority of endemics with small ranges live in headwaters (Allen et al. 2012).

Among the most impressive fish species in Laos are the giant catfish *Pangasianodon gigas* Chevey, one of the three largest freshwater fish in the world (originally from Bokeo to Champasack provinces, currently only in the south), and the giant carp *Catlocarpio siamensis* Boulanger from the River Mekong, both once abundant, now critically endangered. The giant freshwater whipray *Himantura polylepis* (Bleeker) can reach a length of 2.4 m and has been reported in the Mekong near the Cambodian border. Some of the formerly economically important fish from the Mekong, such as the Laotian shad or Mekong herring *Tenualosa thibaudeaui* (Durand) and the Isok barb or Jullien's golden carp *Probarbus jullieni* Sauvage populations have declined dramatically and are now regarded as endangered (FROESE & PAULY 2013).

Within the Laos borders, only the eastern parts of Huaphanh and Xiengkhuang provinces have catchment areas that do not drain into the Mekong and therefore harbour a zoogeographically different fauna, i.e. the northern Annam and Song Hong freshwater ecoregions (see ABELL *et al.* 2008, see Fig.6).

Fauna: insects. An account on the insects of Laos is planned for the "Sonderband Laos II" of this journal, which will also consider the contributions in the current two volumes. Summaries on the insects of the Indomalayan region and the Indochinese subregion have been provided by HOLDHAUS (1927, 1928), FRANZ (1970), and KRYZHANOVSKY (2002).

Conservation issues. Habitat conversion, including cash-crop plantations and unsustainable logging, poaching for bush meat and the illegal wildlife trade pose the greatest risks to the natural biotic resources of the country (Duckworth *et al.* 1999, Nooren & Claridge 2001).

Conservation: forest cover. The original forest cover in Laos has been estimated at more than 99% of the total land area, comprising 68% evergreen forest, 23% mixed deciduous forest and 7% dry dipterocarp forest (MacKinnon & MacKinnon 1986, MacKinnon 1997, p.111), while the figures for recent decades vary widely in the light of various definitions and databases. Data originating 1980s – 2000 range from 47% to 80% forest cover (ICEM 2003). Most sources agree that the figures published for

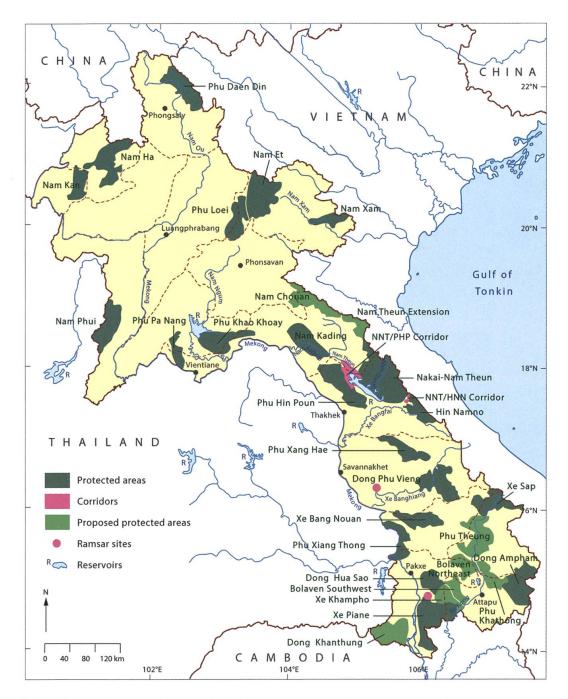


Fig. 6. Distribution of protected areas, selected rivers, main reservoirs for hydro-electric projects, and province boundaries, as broken lines (original).

general forest cover have actually to be divided by at least two in order to designate mature or original, primary forest (ICEM 2003). Data for 2004/2005 indicate 70% forest cover when defined as 10% canopy cover and 5 m minimum tree height, but 41.5% when based on 20% canopy cover and 10 m minimum tree height (MRC 2010). Further examples of figures for forest cover for 2005 and 2010 are 67%, 68% and 70% (FAO 2005, 2010, MRC 2010, World Bank 2013). MACKINNON (1997) estimated that 17% of

the original forest survives, while a more recent figure is 6% (FAO 2005, MRC 2010). The deforestation rate was estimated at 2% between the beginning and the end of the 1980s (MACKINNON 1997), yet deforestation rates may have been as high as 20% in certain districts during 1993–1997, especially in the north (World Bank & STEA 2006).

Conservation: protected areas. The first protected areas in Laos have only been legally implemented in 1993. At that time, 18 pieces of land were officially declared National Biodiversity Conservation Areas (NBCA). More were added in 1995, 1996 and 2008, and there are currently 21 established NBCAs, with a further 10 proposed (CLARKE 2000, WREA 2010) (Fig. 6). The 21 officially declared NBCAs, plus two corridors established in 2000, cover 14.9% of the country, which places Laos among the south-east Asian countries with the highest proportion of land under legal protection (STEA-PMO 2004, WREA 2010). A National Biodiversity Conservation Area (NBCA) is an environmentally protected area in Laos that corresponds to IUCN Category VI – Managed Resource Areas (ICEM 2003). Some 276 Provincial and District Protected Areas exist in addition to the national protected areas (ICEM 2003, WREA 2010), and a number of sacred heritage sites also contribute to conservation. Two wetlands of international importance have recently (2010) been established within the framework of the Ramsar Convention (http://www.ramsar.org/): the Beung Kiat Ngong wetlands in Champasack Province (IUCN 2012) and the Xe Champhone wetlands in Savannaketh Province (IUCN 2011). Despite this extensive legal conservation framework, actual implementation of protection measures remains a considerable challenge.

Conservation: natural habitats. The following habitat types of high international importance have been recognized in Laos (Robichaud et al. 2001, ICEM 2003): the evergreen forests of the Annamite Mountains and foothills, the central Indochina limestone karst, the dry dipterocarp forests of the Mekong Plain, Bolaven plateau, the Northern Highlands, and the River Mekong together with other rivers and streams. This is a more generalised classification when compared with the WWF terrestrial ecoregions (Wikramanayake et al. 2002) (Fig. 9) which specify for Laos the Luangprabang montane rain forests, the rain forests of the northern and southern Annamites, the moist deciduous forests of northern Thailand-Laos and the Northern Khorat Plateau, the dry evergreen forests of south-eastern Indochina and the dry forests in the south of central Indochina, as well as the subtropical forests of northern Indochina in the north of the country. Almost all of the WWF ecoregions for Laos are considered globally outstanding in terms of species richness (Wikramanayake et al. 2002).

Most of these habitats are represented in one or more of the officially protected areas, although a detailed current analysis is lacking and important gaps may exist. Mackinnon (1997) claims a lack of sufficient protection especially of pine forests, subtropical broadleaf forest and other drier forest types. The extensive floodplains of the Nam Theun at the Nakai Plateau, for example, have been destroyed as wetland and special freshwater habitats by the flooding of the reservoir of the Nam Theun 2 hydroelectric power plant. About half of the terrestrial habitats of the plateau disappeared with the impoundment (see EAMP 2005, Asian Development Bank 2004).

The remaining natural habitats (forested and non-forested areas) have been estimated at almost 30% of the total land area of the country in 1985 and less than 20% in 1995 (MACKINNON 1997).

Conservation: protection of species. Rare, endemic and near-endemic plant and animal species are particularly highly endangered by uncontrolled logging, for example of the Fokien cypress *Fokienia hodginsii*, and by illegal hunting for the food, wildlife and quack medicine trade, such as the Saola (*Pseudoryx nghetinhensis*). The latter is the flagship species for Laos (MITTERMEIER *et al.* 2004) and requires particular attention.

Key indicator species for the ecological integrity of the landscapes of Laos include well-known, mostly large or otherwise conspicuous mammals or birds characterized by their unequivocal demand for large areas of intact habitat to maintain viable populations. One outstanding example is the Asian elephant. Laos was once known as Lan Xan, "the Land of a Million Elephants". Recent reviews estimate today's total elephant population at 600 to 800 wild specimens scattered all over the country (Khounboline 2011). The two largest populations appear to be the 132 individuals reported from Nam Theun NBCA in the central Annamites and approximately 100 individuals reported from Nam Pouy NBCA in the Luangprabang range. However, these populations may possibly prove too small to remain viable in the long term (Khounboline 2011).

Some of the most spectacular extinctions have occurred only recently: The two rhinos in the 1940s and 1950, the kouprey last seen in 1980 in southern Laos, and the hog deer *Axis porcinus* Zimmermann last reported around 1990 in southern Laos (Duckworth *et al.* 1999). Other extinct species listed by MAF & STEA (2003) and repeated by WREA (2010) (such as Schomburgk's deer, the Asian tapir and the red panda) have probably never been native to Laos in historical times (see IUCN data).

There are 56 further vertebrate species (mammals, birds, reptiles) that probably fall below the number of 50 breeding pairs or 500 individuals that might be considered a practical guideline for survival (see Franklin & Frankham 1998) or for assessment of a minimum viable population if there is no other existing information (Primack 2002, MAF & STEA 2003).

Biogeography. Laos forms part of the Indochinese division of the Indochinese subregion of the Indomalayan region if one follows the classification by CORBET & HILL (1992) for mammals. The Indochinese division thus defined comprises the mainland and offshore islands from Bangladesh through Myanmar, Thailand, Laos, Vietnam and the southern provinces of China (from Yunnan to Zheijiang), with the Malay Peninsula excluded. A more recent study of zoogeographical regions, also based on mammals, results in a slightly different demarcation of the "Indo-China" region (KREFT & JETZ 2010; for further discussion see HOLT *et al.* 2013, KREFT & JETZ 2013).

Although it is not supported by strictly scientific arguments, we prefer the term "Indomalayan" region (UDVARDY 1975) to "Oriental" region (WALLACE 1876), largely for the reasons cited by CLARK *et al.* (1988) and because it is more descriptive of the area covered.

HOLDHAUS (1927, 1928) and FRANZ (1970) use the term "Oriental region", which comprises the Indochinese subregion with mainland Southeast Asia, the southern slopes of the Himalayas, and Taiwan, and also excludes the Malay Peninsula. The zoogeographical transition area north and south of the Isthmus of Kra has recently been the subject of studies of sphingids (BECK *et al.* 2007) and mammals (WOODRUFF & TURNER 2009). The Indochinese subregion also harbours Palaearctic elements, mainly

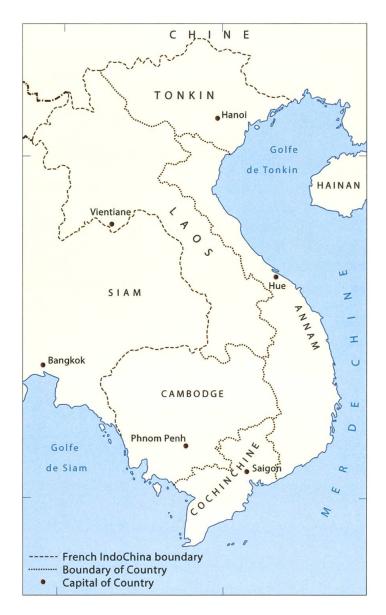


Fig. 7. French Indochina (1885–1956) (after GRESSITT 1970).

distributed in the mountains at increasing altitudes towards the south. This pattern has been discussed by HOLDHAUS (1927, 1928) and FRANZ (1970) and, more recently, by GROOTAERT (2009).

Further zoogeographical breakdowns of the Indomalayan region or parts thereof have been proposed by Liang (1998), Kryzhanovsky (2002) and Beuk (2002) and the data on the insects of Laos currently being compiled and analysed will certainly contribute to a better understanding of distribution patterns. The application of Mackinnon's (1997) classification of the biogeographical units to Laos results in the following divisions: "central Indochina" makes up most of the country and includes the tropical Mekong drainage. Most of the Northern Highlands are classified as "north Indochina" with the northernmost part as "Indochina transition zone". The border area

with Vietnam forms part of the "coastal Indochina" bio-unit, in particular the northern part of the eastern coast section, while the "Annamese Mountain" bio-unit is restricted within Laos to the very south. The arrangement and borders of these "bio-units" certainly require refinement based on the more recently gathered knowledge of the actual distribution of mammals and birds, including the new species revealed more recently.

A large proportion of the species occurring in Laos, especially insects, are endemic to the Indochinese subregion within the Indomalayan faunal region. Many species are shared with neighbouring countries, especially Vietnam and Thailand, although the Annamites and the Khammouan karst area contain a number of small-range endemics restricted to Laos (e.g. the Laotian rock-rat Laonastes aenigmamus and the bare-faced bulbul Pycnonotus hualon), or to both Laos and Vietnam. A number of montane species are shared with the southern provinces of China, especially Yunnan and Guangxi. Among the insects, several predominantly Palaearctic genera are found at higher altitudes in the northern Annamites (e.g. Carabus and Spondylis). The southern part of the Mekong valley, on the other hand, contains a number of species typical of the Sunda archipelago (MACKINNON 1997). Among the fish and insects, there are species endemic to the Mekong valley shared with Thailand, Cambodia and South Vietnam, but not found elsewhere (e.g. the carabid Calochroa carissima (Fleutiaux), see NAVIAUX & PINRATANA 2004). Pleistocene rain-forest refuges very probably made important contributions to the relatively high species richness and endemism in mammals (certainly to the insects) of the Annamite range, especially when compared to the situation west of the Mekong (MEIJAARD & GROVES 2002). Faunal differences between northern and southern parts of the Annamite range have been poorly investigated, but appear to exist, at least in some insect genera with small distribution ranges (e.g. Therates, Lacconectus). The fauna in the Laotian part of the Luangprabang range has not been sufficiently sampled to draw any biogeographical conclusions.

A brief history of coleopterological exploration in Laos

The 19th century

Early naturalist exploration of Laos started relatively late, due to the country's remote position in the interior of Indochina, and unrest arising out of occupation by neighbouring Siam (today's Thailand) and subsequent colonial interference on the part of the French. The first insect material to be collected in Laos came from the travels of Henri Mouhot (1826–1861), a French explorer more famous for the first detailed accounts of the Angkor ruins in Cambodia to reach the western world. His tomb can still be found in Laos, near Luangprabang. Mouhot travelled today's Thailand, Laos and Cambodia between 1858 and 1861 and, as a general naturalist, also collected a number of beetles, many of them later named after him (e.g. the carabid genus *Mouhotia* Laporte de Castelnau, 1862). At least part of the material is deposited with MNHP.

A further early French expedition along the course of the Mekong was undertaken by Jules Harmand (1845–1921) between 1875 and 1878, who also collected beetles in some places that lie in Laos today, including the "Montagnes de Lakhon" (vicinity of

Tha Khaek, Khammuane Province, see HARMAND 1880). His material is now deposited with MNHP (HORN *et al.* 1990).

Auguste Pavie (1847–1925), an important figure in the colonial history of Laos and the first French consul in Luangprabang, was also a naturalist. In the course of his travels in Cambodia, Laos and Tonkin (1886-1894), he collected Coleoptera material, which eventually found a home in MNHP. By 1890, he had deposited 3517 specimens of 915 species of insect from Siam, Laos occidental, Laos oriental, Tonkin, Annam, Cambodge and Cochinchine (now Thailand, Laos, Cambodia and Vietnam, see Fig.7) with MNHP (BLANCHARD 1890). Entomological articles appear (partly re-assembled from Nouvelles Archives du Muséum d'Histoire naturelle 1890, 1891) in Etudes Diverses Vol. III (PAVIE 1904) of the 11-volume work on his "Mission" in Indochina (published 1898–1919). The region of Laos in which Pavie collected beetles was "dans la région montagneuse du Laos septentrional, entre Luang-Prabang et Muong-Theng [Dien Bien Phu in Tonkin]" (see also the record of Collyris gigas in Lesne 1904), or "Luang-Prabang à Theng" (see several records listed by TERTRIN 1904) (see also the map of "Haut-Laos" in Pavie's "Atlas", planche VI, and the map in PAVIE 1911). ALLARD (1891) gives the sampling period 30 March to 30 May 1887. However, the year 1888 seems to be more reliable for most or even all records. It was mentioned by Brongniart (1891), based on MNHNP catalogue entries, and FLEUTIAUX (1904) as the sampling date of Pavie in this area (which corresponds to 28 Jan. to 14 Feb. 1888, return journey via Son-La and Lai-Chau in Tonkin 15 Feb. to 26 March 1888, see PAVIE 1911). Sometimes, only "Luang Prabang" (domicile of Pavie in Laos, six times between 1887 and 1895) or "Laos" is reported as locality of material collected by Pavie in this Vol.III, 1904.

All of these early naturalists were primarily explorers and/or diplomats, not especially engaged with entomology. They collected few insects, but nevertheless provided a number of specimens used as type material by taxonomists.

The early 20th century

Once Laos had become a French protectorate in 1893, it was incorporated into French Indochina (Fig. 7) and became relatively safe for naturalists to explore, although still hard of access. The most active insect collector during this era was René Vitalis de Salvaza (died 1935), a French amateur lepidopterist who spent most of his life in Indochina (CAMBEFORT 2006). He was the keeper of the entomological collections at the Institut Scientifique de l'Indochine in Saigon from 1921 to 1925. Although the majority of his material came from today's Vietnam, he was also the first to make extensive overland journeys in Laos, collecting along the upper Mekong valley from Vientiane to Bokeo (Houay Xai) and in many inland localities, such as Vieng Phoukha (Louangnamtha), Muang Sing (Louangnamtha) and Sen Kham (Phongsaly). Vitalis' material was sold, mainly to private collectors, in France (Maurice Pic among them) whose collections – or at least the majority of them – are now held by MNHP. Some of his specimens were also acquired by the British Museum (BMNH) in 1918 and 1920, and some made their way to MCGD, via R. Gestro. Vitalis de Salvaza was editor of a series of publications on the insects of French Indochina that appeared between 1921 and 1923 in the Opuscules de l'Institut Scientifique de l'Indochine.

Apart from Vitalis, only two French naturalists are known to have collected beetles during this period in Laos: R. Miéville, primarily a botanist, who collected some material between 1916 and 1921 around Xieng Khouang (deposited with MNHP), and Léon Dussault, a geologist, geographer and French military commander. Dussault's Indochinese beetle collection was acquired by NHMB in 1923. It is not very large, but contains material from a number of poorly-known areas, such as Borikhamxay (Kham Kheut), Xiengkhuang and Savannakhet (Xepon).

The mid-20th century

Following the Japanese occupation during World War II, Laos experienced a long period of unrest and civil war, first against the French colonial regime, then between Vietnamese-backed communist forces and the American-backed royalist army. During these times, only a single European insect collector was able to obtain a larger body of Coleoptera material from Laos: Jacques A. Rondon (died 1969), a French citizen based in Vientiane, actively collecting between 1961 and 1969. Specialising in the Cerambycidae, he was able to perform a large-scale survey of the Laotian fauna of this family, at least for the central provinces to which the had access. He also employed a number of local Laotian collectors. Rondon's impressive Cerambycidae collection, including type material, as well as material of other beetle families, is deposited with BIMH, with some specimens (duplicates) sold to BMNH. A small amount of Laotian beetle material from the same time period was collected by S. Quate & L. Quate (1960) and 1965), J.M. Sedlacek (1966) and R.E. Leech (1966), also deposited at BIMH. Furthermore, a still smaller quantity of Laotian beetles, taken in 1963 and 1964, but without a collector's name, is to be found in ZSM and NHMB (via coll. Frey). This material takes in only four localities: Vientiane, "Vanky" (Vientiane prov.), Paklay (Xayabury) and Pakse (Champasack).

The end of the 20th century

After the Second Indochina War, Lao PDR remained closed and inaccessible to nearly all foreigners, until it gradually opened up in the 1990s. The only beetle collector active at this time was the Russian geologist Oleg N. Kabakov, who was able to make a short trip to Khammuane province in 1984, where he also collected some beetle specimens, now deposited with ZISP. The end of the 1990s saw increased activity on the part of entomologists, with some surveys concentrating on the Coleoptera:

- H. Schillhammer & C. Holzschuh (1996), material mostly at NHMW and CCH.
- V. Kubáň & C. Holzschuh (1997), material mostly at NHMB, NMPC and CCH.
- O. Merkl & G. Csorba (1998), material at MTMB.
- V. Kubáň, C. Holzschuh and K-W. Anton (1999), material at NHMB, CCH and CKA.
- E. Jendek & O. Šauša (1998 and 1999), material partly at NMPC and some in private collections.

The 21st century

As Laos became easily accessible and widely known among the entomology community, and the country's infrastructure improved, the number of beetle collectors visiting the country reached unprecedented levels. Several natural history museums contributed to the exploration of the still poorly-known beetle fauna. By far the most comprehensive beetle surveys, covering nearly all the provinces in Laos, were carried out by NHMB, between 2003 and 2012, under the leadership of Michel Brancucci (see following section). Smaller-scale beetle surveys of Laos were carried out by:

- EHUM, J. Yamasako, 2005
- NMPC, V. Kubáň and J. Hájek, 2008, 2009 and 2011
- NRMS, N. Jönsson, T. Malm & B. Viklund, 2005
- ZMUC, A. Solodovnikov & J. Pedersen, 2008

Apart from these museum expeditions, a number of entomologists, both amateur and professional, visited Laos and collected valuable beetle material. While a part of this material is now in private collections, a large amount was also deposited with public institutions (or purchased by them), including material collected by J. Bezděk in 2001 and 2004 (NMPC), V. Kubáň in 2001 and 2002 (NHMB), J. Kolibáč in 2001 (MMB, NHMB), P. Pacholátko in 2001 (NHMB), S. Kawabe in 2001 (KMNH), N. Ohbayashi in 2002, 2003, 2004 and 2007 (EHUM), F. and L. Kantner in 2004 (NMPC), M. Satô in 2004 (EHUM), E. Jendek and O. Šauša in 2004 (NMPC), P. Kresl in 2005 (NMPC), H. Wakahara in 2005 and 2006 (EHUM), S. Tarasov in 2008 (ZMUC) and C. Holzschuh from 2010 to 2012 (BMNH). More collectors could almost certainly be added to this list.

Several private insect collectors provided additional material, not deposited with public institutions, but kept either in private collections, given away to entomologist colleagues or sold individually.

The NHMB expeditions to Laos

This list includes all localities surveyed during the NHMB entomological expeditions to Laos, between 2003 and 2012. Province, district (not mentioned on the labels), altitude and coordinates are given for each locality, as well as the dates and collectors.

The expeditions between 2009 and 2012 were part of the formal "Beetles of Laos" project, initiated by Michel Brancucci. The 2010, 2011 and 2012 expeditions were conducted in collaboration with the Faculty of Agriculture of the National University of Laos (Khosada Vongsana and Souphaphone Rattanalasy), that of 2009 in collaboration with the NMPC (Vítězslav Kubáň) and the one in 2010 also with the University of Basel, Environmental Sciences, Biogeography (Peter Nagel, Jan Beck).

"Major" localities are those visited for an extended amount of time, using several different collecting techniques. "Minor" localities were surveyed more superficially, on only a few collecting days, mostly by individual collecting, beating and collecting in small water bodies. For "major" localities, a brief description of the habitats sampled is provided (see Fig. 8).

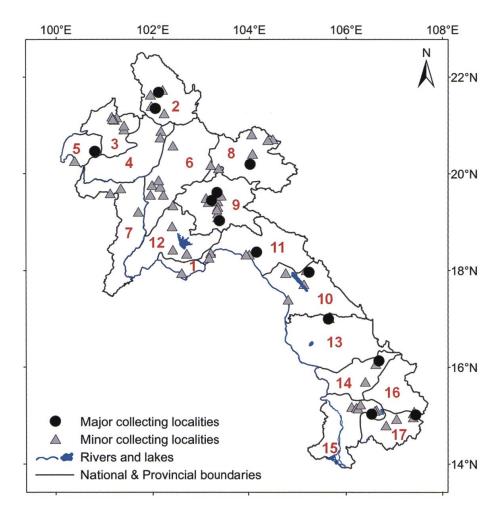


Fig. 8. Collecting localities in Laos (see text) and the provinces (1 to 17, spelling after LSB 2013b; capital cities of provinces in brackets, spelling after Messerli *et al.* 2008, map A.2). 1. Vientiane prefecture (Vientiane City), 2. Phongsaly (Phongsaly), 3. Luangnamtha (Luang Namtha), 4. Oudomxay (Muang Xay), 5. Bokeo (Houay Xay), 6. Luangprabang (Luangprabang), 7. Xayabury (Xayabury), 8. Huaphanh (Xamneua), 9. Xiengkhuang (Phonsavan), 10. Khammuane (Thakhek), 11. Borikhamxay (Pakxanh), 12. Vientiane (Phonhong), 13. Savannakhet (Savannaketh), 14. Saravane (Salavan), 15. Champasack (Pakse), 16. Sekong (Sekong), 17. Attapeu (Attapeu).

Major locality

Phongsaly prov., Phongsaly district, Phongsaly env., 21°41–2′ N / 102°06–8′ E, ~1500m, 28. V. –20.VI.2003. MB, VK, PP. Secondary tropical montane deciduous forest and cultivated area around town.

Minor localities

Borikhamxay prov., Pakkading district, Pakkading, c. 300m, 18°20′ N / 104°00′ E, 26.–27. V. 2003. MB, VK, PP.

Phongsaly prov., Boon Neua district, 4 km E Ban Boun Neua, c. 1100m, 21°38′ N / 101°57′ E, 20. VI. 2003. MB, VK, PP.

Phongsaly prov., Phongsaly district, Ban Hatsa (Hat Xa), c. 550m, 21°44′ N / 102°12′ E, 17. VI. 2003. PP.

Major localities

Phongsaly prov., Boon Tai district, Ban Sano Mai env., c. 1150 m, 21°21′ N / 102°03′ E, 19.–26. V. 2004. MB, VK, PP. Secondary tropical montane deciduous forest and cultivated area around village.

Phongsaly prov., Phongsaly district, Phongsaly env., c. 1500 m, 21°41–2′ N / 102°06–8′ E, 6.–17. V. 2004. MB, VK, PP. Secondary tropical montane deciduous forest and cultivated area around town.

Minor localities

Luangprabang prov., Nambak district, 5 km SW Pak Mong, c. 450 m, 20°35′ N / 102°25′ E, 3. V. 2004. MB, VK, PP.

Oudomxay prov., Xay district, 17 km NEE Oudom Xai, c. 1100m, 20°45′ N / 102°09′ E, 3. V. 2004. MB, VK, PP.

Oudomxay prov., La district, 4 km NE Muang La, *c*. 500 m, 20°53′ N / 102°10′ E, 4. V. 2004, MB, VK, PP. Phongsaly prov., Samphanh district, 5 km NW Ban Nam Li, *c*. 900 m, 21°15′ N / 102°14′ E, 4. V. 2004, MB, VK, PP.

Phongsaly prov., Boon Neua district, 4 km E Boun Neua, *c.* 1100 m, 21°38′ N / 101°57′ E, 26. V. 2004. MB, VK, PP.

Phongsaly prov., Boon Tai district, Boun Tai, 580 m, 21°24′ N / 101°58′ E, 4. + 18. V. 2004, MB, VK, PP. Phongsaly prov., Phongsaly district, Ban Hatsa, c. 550 m, 21°44′ N / 102°12′ E, 9. + 17. V. 2004. MB, PP.

2007 expedition

Major localities

Houaphanh prov., Xamneua district, Phou Pane (Phu Phan) mt., 1500–1900 m, 20°12′ N / 104°01′ E, 17. V.–3. VI. 2007. MB, VK. Degraded primary and secondary tropical montane deciduous forest, bamboo thickets and patches of recently-burnt forest.

Minor localities

Houaphanh prov., Viengthong district, Muanghiam: thermal springs, 680 m, 20°07′ N / 103°22′ E, 15.–16. V. 2007. MB, VK.

Houaphanh prov., Viengthong district, Ban Sako (N env.), 750–900 m, 20°11′ N / 103°12′ E, 16. V. 2007. MB, VK.

Houaphanh prov., Xamneua district, Ban Saluei village, 1350 m, 20°13′ N / 103°59′ E, 3. VI. 2007. MB, VK. Xiengkhuang prov., Pek district, Phonsavan env., 1150 m, 19°27′ N / 103°13′ E, 5.–6. VI. 2007. VK, MB.

2009 expedition

Major localities

Houaphanh prov., Xamneua district, Ban Saluei to Phou Pane, 1300–1900 m, 20°11–13′ N / 103°59′–104°01′ E, 1.–16. VI. 2009. MB, MG, DH, ZH, VK. Degraded primary and secondary tropical montane deciduous forest, bamboo thickets, patches of recently-burnt forest, pastures and rice fields around village.

Xiengkhuang prov., Pek district, Ban Na Lam to Phou Sane, 1300–1700 m, 19°37–38′ N / 103°20–21′ E, 10.–31. V. 2009. MB, MG, DH, ZH, VK. Degraded primary and secondary tropical montane deciduous forest, bamboo thickets and pastures.

Xiengkhuang prov., Pek district, Phonsavan town to Phu Padaeng, 1100–1200 m, 19°26′ N / 103°13′ E, 8.–9. + 20.–31. V. + 18.–24. VI. 2009. MB, MG, DH, ZK, VK. Pine forest, small pastures and rice fields around town.

Minor localities

Borikhamxay prov., Pakkading district, Pakkading, c. 200 m, 18°20′ N /103°59′ E, 5. V. 2009. MG, DH. Borikhamxay prov., Thaphabath district, Wat Phonsa, c. 180 m, 18°16′09″ N / 103°10′48″ E, 5. V. 2009. MG, ZK.

Houaphanh prov., Add district, Ban Muang Van, 300–800 m, 20°49–50′ N / 104°01–2′ E, 2.–5. VI. 2009. MG, DH.

- Houaphanh prov., Sopbao district, Ban Pahang env., 1000–1370 m, 20°42–43′ N / 104°28–29′ E, 7. VI. 2009. MG, DH.
- Houaphanh prov., Sopbao district, Muang Sop Bao, 300 m, 20°42.40′ N / 104°23.70′ E, 6.–8. VI. 2009. MG, DH.
- Houaphanh prov., Xamneua district, Sam Neua town, 900–1035 m, 20°25′ N / 104°03–05′ E, 1.–9. VI. 2009. MG, DH.
- Luangprabang prov., Phoukhoune district, Muang Phou Khoun, 1370 m, 19°26.38′ N / 102°25.61′ E, 20. VI. 2009. MG.
- Luangprabang prov., Xieng Ngeun district, Ban Kiukacham env., 1400–1450 m, 19°34′ N / 102°13′ E, 19. VI. 2009. MG, DH.
- Vientiane city, Chanthabuly district, shore of Mekong, 160 m, 17°57′ N / 102°36′ E, 4.+ 7. V. + 25. VI. 2009. MB, DH, ZK.
- Vientiane prov., Thoulakhom district, Phou Khao Khouay NBCA, c. 250 m, 18°21′ N / 102°42′ E, 6. V. 2009. MB, MG, DH, ZK, VK.
- Xiengkhuang prov., Khoune district, Muang Khoun, 1070 m, 19°19.91' N / 103°21.99' E, 22. VI. 2009. MG, DH
- Xiengkhuang prov., Pek district, Phonsavan airport, 1110 m, 19°26.90'N / 103°10.11' E. MG
- Xiengkhuang prov., Phathom district, Ban Thaviang, 400 m, 19°02′ N / 103°23′ E, 21. VI. 2009. MG, DH.
- Xiengkhuang prov., Phathom district, road Muang Khoun to Ban Thaviang, c. 20 km from Ban Thaviang, 700 m, 19°11.80′ N / 103°21.20′ E, 22. VI. 2009. MG, DH.

Major localities

- Borikhamxay prov., Pakkading district, Nam Kading NBCA, Tad Paloy camp-site, 280–400 m, 18°21–23′ N / 104°09′ E, 7.–12. VII. 2010. MB, MG. Primary lowland semi-evergreen dipterocarp forest.
- Champasack prov., Paksong district, Ban Nong Panouan env., 770–800 m, 15°02′ N / 106°31–34′ E, 10.–17. VI. 2010. DH, MG. Degraded primary semi-evergreen forest, coffee plantations and patches of recently-burnt forest.
- Xiengkhuang prov., Phathom district, Ban Thaviang env., 400–600 m, 18°59′–19°03′ N / 103°22–25′ E, 17.–21. V. 2010. MG, DH. Degraded primary lowland semi-evergreen dipterocarp forest, secondary forest and shrublands, bamboo thickets and rice fields around village.

Minor localities

- Attapeu prov., Samakkhixay district, Attapeu town, 105 m, 14°48.35′ N / 106°50.14′ E, 30. V. 2010. DH.
- Attapeu prov., Xaysetha district, Ban Pa-am env., 150 m, 14°56′ N / 107°03′ E, 31. V. 2010. MG, DH.
- Attapeu prov., Xaysetha district, near Tad Katamtok (road Ban Lak 52 to Paksong), 435 m, 15°07.94′ N / 106°38.84′ E, 7. VI. 2010. MG.
- Borikhamxay prov., Pakkading district, Nam Kading NBCA research training centre, c. 200 m, 18°20.45′ N / 104°08.66′ E, 6. + 11.–12. VII. + 2010. MB, MG.
- Borikhamxay prov., Pakkading district, Pakkading, c. 200 m, 18°20′ N / 103°59′ E, 6. VII. 2010. MB.
- Borikhamxay prov., Pakxane district, Paksan town, c. 200 m. 18°20' N / 103°56' E, 6. VII. 2010. MB
- Champasack prov., Paksong district, 13 km NE Paksong (Tha Teng road), 1250 m, 15°14.36′ N / 106°18.62′ E, 1. VI. 2010. MG, DH.
- Champasack prov., Paksong district, Ban Nam Touad env. (near Xe Katamtok), 500–800 m, 15°06′ N / 106°35–38′ E, 8.–10. VI. 2010. MG, DH.
- Champasack prov., Paksong district, c. 5 km SE Paksong, 1300–1330 m, 15°09′ N / 106°15′ E, 5. VI. 2010. MG, DH.
- Champasack prov., Paksong district, Dong Hua Xao NBCA, Tad Fane env., (10–14 km W Paksong), 900–1000 m, 15°10–12′ N / 106°07–08′ E, 2.–4. VI. 2010. MG, DH.
- Champasack prov., Paksong district, Paksong town, 1280 m, $15^{\circ}10.72'$ N / $106^{\circ}13.64'$ E, 5.-7.+18.-19. VI. 2010. MG, DH.
- Luangprabang prov. Xieng Ngeun district, Houay Khot agricultural research station (near Xieng Ngeun), 380 m, 19°44.15′ N / 102°09.29′ E, 30. VI. 2010. MG.
- Luangprabang prov., Luangprabang district, Ban Tha Pen, Tad Kouangsi, 430 m, 19°45.99′ N / 101°59.74′ E, 29. VI. 2010. MG.

- Luangprabang prov., Luangprabang district, Luangprabang town, 300 m, 19°52.91′ N / 102°07.79′ E, 28. VI. 2010. MG.
- Luangprabang prov., Nan district, Thong Khang env., 670–1160 m, 19°33–34′ N / 101°57′ E, 30. VI. 1. VII. 2010. MB, MG.
- Luangprabang prov., Phoukhoune district, Muang Phou Khoune, 1370 m, 19°26.38′ N / 102°25.61′ E, 28. VI. 2010. MG.
- Vientiane prov., Kasy district, Ban Hin Ngon (road Kasi to Phou Khoune), 960 m, 19°21.75′ N / 102°25.36′ E, 28. VI. 2010. MG.
- Vientiane prov., Phonhong district, Vang Xang (near Phon Home), 250 m, 18°26′ 21" N / 102°25′ 26" E, 26. VI. 2010. MB, MG.
- Vientiane prov., Vangvieng district, Vang Vieng env., 240–300 m, 18°55′ N / 102°23–26′ E, 27. VI. 2010. MB, MG.
- Xiengkhuang prov., Khoune district, c. 7 km SE Muang Khoun, c. 900 m, 19°16.79′ N / 103°20.98′ E, 16. V. 2010. MG, DH.
- Xiengkhuang prov., Nonghed district, Ban Tha Chôk to Ban Na Sala, 930–1175 m, 19°32–35′ N / 103°25–27′ E, 23.–26. V. 2010. MG, DH.
- Xiengkhuang prov., Pek district, c. 10 km W Phonsavan, 1070 m, 19°30′02″ N /103°06′47″ E, 3. VII. 2010. MB, MG.
- Xiengkhuang prov., Pek district, c. 5 km SW Phonsavan (Plain of Jars), 1100 m, 19°25.82′ N / 103°09.32′ E, 4. VII. 2010. MB, MG.
- Xiengkhuang prov., Pek district, Phonsavan town, c. 1130 m, 19°26′ N / 103°13′ E, 15., 22. + 27 V. + 3.-4. VII. 2010. MG, DH.
- Xiengkhuang prov., Pek district, Phonsavan, Phou Padaeng, 1150–1200 m, 19°26′ N / 103°13′ E, 22. V. 2010.
- Xiengkhuang prov., Phathom district, Ban Xiengkhong, c. 600 m, 19°06.00′ N / 103°21.05′ E, 21. V. 2010. DH.

Major localities

- Attapeu prov., Sanxay district, Thong Kai Ohk, Ban Kachung (Mai) env., 1200–1450 m, 15°01–02′ N / 107°26–27′ E, 10.–24. VI. 2011. MB, MG, DH, ZK, AP, EV. Degraded primary tropical montane evergreen forest, pine groves, small cultivated areas and pastures around village.
- Bokeo prov., Houaixai district, c. 5 km W Ban Toup, Bokeo Nature Reserve, 500–700 m, 20°27–28′ N / 100°45′ E, 4.–18. V. 2011. MB, MG, DH, ZK, AP, EV. Primary lowland evergreen dipterocarp forest, patches of secondary forest and small agricultural areas.
- Borikhamxay prov., Pakkading district, Ban Phone Kham env., 200–300 m, 18°20′ N / 104°08′ E, 23.–29. V. 2011. MB, MG, DH, ZK, AP, EV. Edge of primary lowland semi-evergreen forest, secondary forest and shrubland, rocks on river shore.
- Borikhamxay prov., Pakkading district, Nam Kading NPA, Tad Paloy camp-site, 250–400 m, 18°21–23′ N / 104°09′ E, 24.–28. V. 2011. MG, DH. Primary lowland semi-evergreen dipterocarp forest.
- Savannakhet prov., Atsaphone district, Phou Xang He NBCA, c. 5 km SW Ban Pa Phaknau, 250–400 m, 17°00′ N / 105°38′ E, 31. V. 6. VI. 2011. MB, MG, DH, ZK, AP, EV. Primary lowland semi-evergreen forest, rocky slabs with sparse vegetation on hilltops.

Minor localities

- Attapeu prov., Samakkhixay district, Attapeu town, 105 m, 14°48′ N / 106°50′ E, 8.–9. VI. 2011. MB, MG, DH, ZK, AP, EV.
- Attapeu prov., Sanxay district, Ban Vang Tat Noi env., 900 m, 15°03–04′ N / 107°24′ E, 10. + 25. VI. 2011. MB, MG, DH, ZK, AP, EV.
- Attapeu prov., Sanxay district, Nong Fa crater lake, 1150–1300 m, 15°05–07′ N / 107°25′ E, 21.–25. VI. 2011. MB, MG, DH, ZK, AP, EV.
- Attapeu prov., Sanxay district, Vang Tat gold mine, 950 m, 14°58′ N / 107°24′ E, 26. VI. 2011. MB, MG, DH, ZK, AP, EV.

- Bokeo prov., Houaixai district, Ban Toup vill., 500 m, 20°28' N / 100°48' E, 4.–13. V. 2011, M. Geiser, Z. Kraus & A. Phantala leg. MB, MG, DH, ZK, AP, EV.
- Bokeo prov., Houaixai district, Houay Xay town, 390 m, 20°16′ N / 100°24′ E, 3. V. 2011. MB, MG, DH, ZK, AP. EV.
- Louangnamtha prov., Namtha district, Louang Namtha bus station, 575 m, 20°55′ N / 101°24′ E, 20. V. 2011. MG, DH.
- Louangnamtha prov., Namtha district, Louang Namtha town, 600 m, 21°00′ N / 101°24′ E, 13. V. 2011. MG, DH.
- Louangnamtha prov., Sing district, c. 10 km E Muang Sing, Ban Oudomsinh / Ban Nam Det / Ban Nam Mai env., 750–1400 m, 21°09–10′ N / 101°13–15′ E, 16.–19. V. 2011. DH, MG.
- Louangnamtha prov., Sing district, *c.* 10–11 km SE Muang Sing, 800 m, 21°07′ N / 101°12′ E, 15. V. 2011. MG, DH.
- Louangnamtha prov., Sing district, c. 5 km SE Muang Sing, Xieng Thung Stupa, 750 m, 21°08′ N / 101°10′ E, 15. V. 2011. MG, DH.
- Louangnamtha prov., Sing district, Muang Sing town, 700 m, 21°11′ N / 101°09′ E, 14.–20. V. 2011. MG, DH. Savannakhet prov., Atsaphone district, Ban Pa Phaknau vill., 180 m, 17°01′ N / 105°39′ E, 30.–31. V. + 6. VI. 2011. MB, MG, DH, ZK, AP, EV.
- Vientiane prefecture, Chanthabuly district, Vientiane City, near Mekong, 21.–22. V. 2011. MB, MG, DH, ZK, AP, EV.

Major localities

- Bokeo prov., Houaixai district, Nam Kan NPA, Ban Toup env., 500–600 m, 20°28′ N / 100°47–48′ E, 3.–7. V. 2012. MB, MG. Edge of primary lowland evergreen dipterocarp forest, patches of secondary forest and small agricultural areas around village.
- Houaphanh prov., Xamneua district, Ban Saluei to Phou Pane mt., 1300–1900 m, 20°12–13′ N / 103°59′–104°00′ E, IV. 2012. KS. Degraded primary and secondary tropical montane deciduous forest, bamboo thickets, patches of recently-burnt forest, pastures and rice fields around village.
- Khammuane prov., Nakai district, Nakai-Nam Theun NPA, Ban Navang env., 600–750 m, 17°57–59′ N / 105°13–16′ E, 18.–21. V. 2012. MB, MG, KP, SX. Secondary evergreen forest, bamboo thickets and cultivated areas around village.
- Saravane prov., Ta-oi district, Xe Xap NPA, c. 15 km NE of Ta-oy, Ban Doub env., 400–1000 m, 16°08′ N / 106°40–43′ E, 25.–31. V. 2012. MB, MG, KP, SX. Primary semi-evergreen montane forest, secondary forest and shrubland, cultivated areas around village.

Minor localities

Borikhamxay prov., Thaphabath district, Tha Bok, 170 m, 18°22′ N / 103°12′ E, 9. V. 2012. KS.

Bokeo prov., Houaixai district, Houay Xay town, 400 m, 20°16′ N / 100°24′ E, 2. + 9. V. 2012. MG.

Khammuane prov., Hinboon district, Ban Konglo (Kong lor) env., 180 m, 17°57′ N / 104°44–48′ E, 12.–15. V. 2012. MG, KP, SX.

Khammuane prov., Nakai district, Ban Oudomsouk near Nakai, 550 m, 17°42′ N / 105°09′ E, 16.–17. V. 2012. MB, MG, KP, SX.

Khammuane prov., Nakai district, Nakai-Nam Theun NPA, Ban Nahao, 550 m, 17°59′ N / 105°10′ E, 18. V. 2012. MB, MG.

Khammuane prov., Thakhek district, Thakhek town, 150 m, 17°24′ N / 104°48–49′ E, 15. V. 2012. MB.

Saravane prov., Saravane district, Salavan town, 200 m, 15°42′ N / 106°24′ E, 23.–24. V. + 1. VI. 2012. MG. Saravane prov., Ta-oi district, Ta-oy, 390 m, 16°04′ N / 106°37′ E, 1. VI. 2012. MG.

Vientiane prefecture, Chanthabuly district, Vientiane City, 180 m, 17°58′ N / 102°36′ E, 1. V. + 3.–6. VI. 2012. MG, KS.

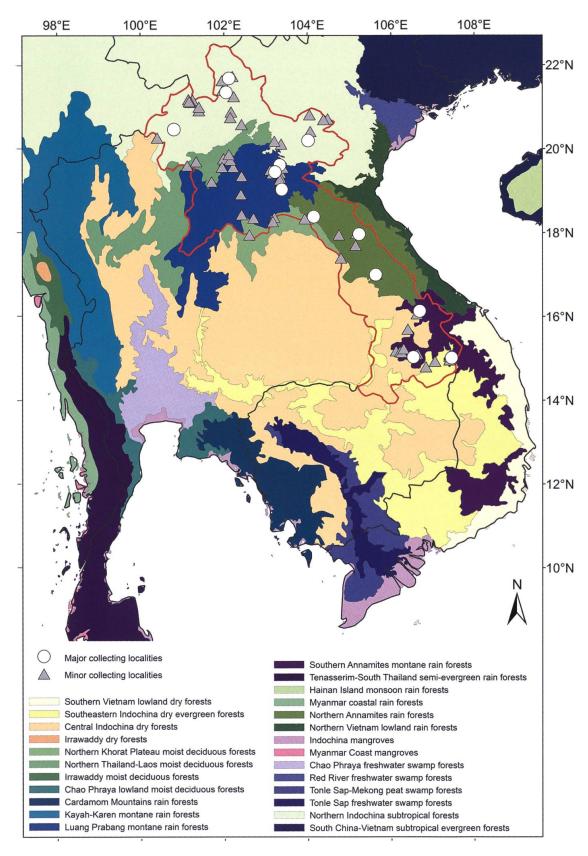


Fig. 9. WWF terrestrial ecoregions as part of the Indochinese subregion (see Olson *et al.* 2001, http://worldwildlife.org/publications/terrestrial-ecoregions-of-the-world), showing country boundaries and collecting localities in Laos (see Fig. 8).

Conclusions

Despite relatively intensive collecting activity in recent years, the increase in surveyed localities has been rather limited. After 2001, only few expeditions, including those of the NHMB, NMPC and ZMUC, provided a substantial number of "new" localities. Nearly all of the activities of private collectors were centred around a few species-rich but well-sampled localities, such as Mt. Phou Pane (Houaphanh prov.) and Mt. Phou Khao Khouay (Vientiane prov.). This leaves a large part of the country, especially the southern half, still poorly explored and in need of additional data.

Further, not all Laotian ecoregions and habitat types have been sampled equally (Fig. 9). Most of the beetle collecting took place in the montane forest of the Northern Highlands and in the valley of the Mekong. The forests of the southern Annamites have only been visited by a small number of entomologists in very few localities, mostly by the NHMB expeditions, and large areas, such as the mountainous parts of Sekong Province remain completely unexplored. The Khammuane karst rocks, home to several recently discovered vertebrates, have hardly ever been sampled for beetles. Additional blank areas in terms of coleopterological knowledge include the Laotian western portion of the Luangprabang mountain range in Xayabury province and the higher altitudinal zones of the highest mountains, Phu Bia, Phu Xamxum and the Phu Xailaileng massif. The remaining natural or less disturbed habitats of the lowland east and west of the southernmost section of the Mekong have also been beyond the focus of entomofaunistic work.

Only a limited number of collecting methods have been used in some areas. A large number of additional species may be expected if, for example, Malaise traps or canopy fogging are employed in some of the otherwise well-explored areas (see BASSET *et al.* 2012).

The disappearance of original habitats, especially forest habitats, places increasing demands on entomological exploration. For example, the faunal surveys undertaken for the environmental impact assessment of the Nam Theun 2 Hydropower Project signally failed to include entomological research (EAMP 2005). The reservoir has now inundated most of the former floodplain of Nam Theun and tributaries at the Nakai Plateau and it must remain unknown whether locally restricted or specialised aquatic and semi-aquatic insects have been lost to the impoundment.

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