The altitudinal distribution of Trichoptera species in Mae Klang catchment on Doi Inthanon, northern Thailand : stream zonation and cool- and warm-adapted groups

Studies on caddisflies of Thailand nº 16

Hans MALICKY (1) and Porntip CHANTARAMONGKOL (2)

ABSTRACT

The altitudinal distribution of Trichoptera species in Mae Klang catchment (Northern Thailand) between 400 and 2,300 m is presented. This is probably the first paper of this kind in any tropical region which is based on full faunistic evidence.

Most Trichoptera families are represented by a series of species from the highest to the lowest reaches. It is suggested that cool-adapted groups and warm-adapted groups sensu Ross are hypothetical and probably do not exist, but there are cool- or warm-adapted species. This is particularly striking in Rhyacophila *and* Chimarra *which were considered to be cool- and warm-adapted respectively but are actually not different. Highest diversity was found in the middle reaches of Mae Klang River at 1,200-1,700 m with the lowest temperature variation.*

In tropical regions, Rhithron exists at all elevations and not only in high altitudes as suggested by Illies. The upper temperature limit of Rhithron biotopes may be 25 °C or more instead of 20 °C, and there is a broad overlap in temperature with Potamon biotopes.

KEYWORDS : Tropical river — Stream zonation — Trichoptera — Thailand — Cool-adapted groups — Warm-adapted groups.

RÉSUMÉ

DISTRIBUTION ALTITUDINALE DES ESPÈCES DE TRICHOPTÈRES SUR LE BASSIN DU MAE KLANG, MASSIF DU DOI INTHANON, THAÏLANDE DU NORD : ZONATION DES EAUX COURANTES, NOTION DE GROUPES ADAPTÉS AUX EAUX FROIDES ET AUX EAUX CHAUDES

La distribution altitudinale des Trichoptères du bassin du Mae Klang qui s'étage entre 400 et 2 300 m d'altitude est décrite. C'est probablement la première publication sur ce thème réalisée en zone tropicale et fondée sur une recherche faunistique complète.

(1) *Sonnengasse 13, A — 3293 Lunz am See, Österreich.*
(2) *Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand.*

La plupart des familles de Trichoptères sont représentées par une série d'espèces se succédant des plus hautes aux plus basses stations. Les groupes « adapté au froid » et « adapté au chaud » sensu *Ross sont hypothétiques et n'existent probablement pas. Mais il y a des espèces adaptées au froid ou au chaud. Cela est particulièrement net dans le genre* Rhyacophila *qui était considéré comme « adapté au froid » et dans le genre* Chimarra *qui était considéré comme « adapté au chaud ». Nos résultats n'indiquent aucune différence entre ces deux genres. Nous avons rencontré les richesses spécifiques maximales aux altitudes intermédiaires sur le Mae Klang, entre 1 200 et 1 700 m, où la variation de la température de l'eau est minimale.*

Nous constatons la présence du Rhithron à toutes les altitudes en zone tropicale et pas seulement aux altitudes les plus élevées comme le suggérait Illies. La température maximale de cette zone n'est pas 20 °C mais peut atteindre 25 °C ou plus. Il y a un large recouvrement des températures entre le Rhithron et le Potamon.

MOTS CLÉS : Rivière tropicale — Zonation des eaux — Trichoptères — Thaïlande — Groupes adaptés aux eaux froides — Groupes adaptés aux eaux chaudes.

INTRODUCTION

Altitudinal separation of caddis species, which is part of stream zonation, has long been known in Europe, but information is scarce for tropical countries. The most comprehensive work is by CHANTARAMONGKOL (1985) who reconstructed the altitudinal distribution of caddis species in Sri Lanka, based on museum material. Other work on zonation in tropical river systems include those by MARLIER (1954) in eastern Congo, BISHOP (1973) in Malaysia, STATZNER (1975) in Zaïre, HARRISON and RANKIN (1976) on St. Vincent, DUDGEON (1992) in Hongkong, ANDERSEN and JOHANSON (1993) in Tanzania and GIBON, GUENDA and COULIBALY (1994) in Burkina Faso. There is however no presentation of the distribution of the complete fauna of an individual stream system, and true identification to species is scarce. We are not considering many recent publications from all parts of the world, including the tropics, which are based on inadequate sampling and poor identification (nevertheless most of them are peer-reviewed). In many of them the animals are separated into functional feeding groups although the authors do not know how and on what the species really feed.

Summaries of running water zonation are by ILLIES and BOTOSANEANU (1963) and BOTOSANEANU (1979).

In 1987 we started field studies in northern Thailand, mainly on the mountains Doi Inthanon and Doi Suthep. There is a rich fauna of which about 3/4 of the species were unknown and had first to be described (CHANTARAMONGKOL and MALICKY, 1989, 1995; MALICKY and CHANTARAMONGKOL, 1989, 1989a, 1991, 1991a, 1991b, 1992, 1992a, 1993, 1994; MALICKY, 1987, 1989, 1991, 1994). Some results from Doi Inthanon are presented here. This is probably the first paper on caddis zonation in a tropical river which is based on full faunistic records.

MATERIAL AND METHODS

Biological studies of streams are handicaped by difficulties in identifying to species large numbers of specimens. Identification of all groups exceeds the working capacity not only of an individual but also of a whole institute. Therefore we are restricting our study to Trichoptera which is an ecologically diverse insect group rich in species which allows significant conclusions. Our methods are qualitative only. We made no attempt at quantitative sampling because no suitable methods are known. Surber samplers and the like are not quantitative and cannot be used in all parts of complicated stream beds.

Water temperatures were recorded only when collecting specimens. Correct measuring of water temperatures would need permanent records to determine the limits. This is important in temperate and cold regions where short-term variation of water temperature may be high. In tropical mountain regions, short-term temperature variation is low, so that the values given here are reasonably correct for comparison in this paper.

Collections have included sweeping and light-trapping of adults in all months of the year. Larval records were not normally used because it is impossible to identify them with present taxonomic knowledge. The families Hydroptilidae, Hydropsychidae and Leptoceridae are not completely listed in tables I and III because of unsolved taxonomic problems, but it is evident from our results that the conclusions of this paper are also supported by the distribution of species of these three families. The list of species does not mean that it is absolutely complete. It contains the species which we have found in five years of research, and many of them were found in large numbers, but it is possible that more species may be found.

The study area is River Mae Klang in Doi Inthanon Mountain (Assessment of National Parks, 1987;

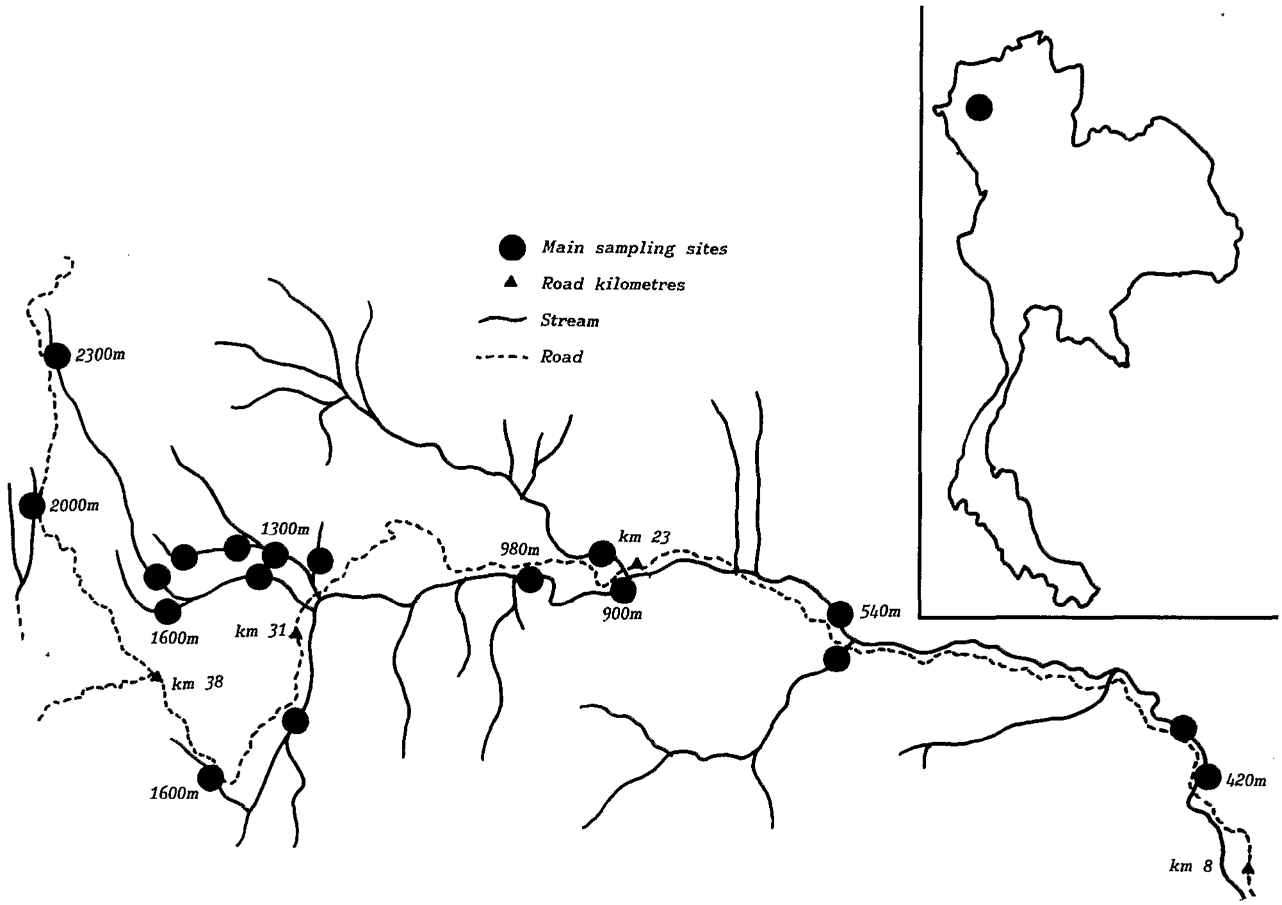

FIG. 1. — Sketch of Mae Klang catchment at Doi Inthanon, with road kilometres (= distances from Chom Tong) and elevations, and situation of the area in Thailand.
Esquisse du bassin du Mae Klang dans la montagne Doi Inthanon avec les distances routières de Chom Tong et les élévations, et situation de la région en Thaïlande.

GRAHAM, 1991; ROBBINS and SMITINAND, 1966), ca. 18°30′ N,98°30′ E, which is the highest mountain in Thailand, with an elevation of 2,564 m. Sampling stations are shown in figure 1. The highest station is in a stream at 2,300 m in dense mountain fog forest with many epiphytic orchids and Rhododendron. Most stations between 1,700 and 1,200 m (photo 1) are small brooklets in dense forest, but also in open agricultural areas. There are mixed forests with many tree species of many families, but lower down, at around 1,000 m, pines and oaks dominate. The lower stations are along the main course of Mae Klang and in tributaries of similar size (photo 2). The lowest reaches of Mae Klang are surrounded by dry dipterocarp forests which are leafless in the dry season. Most of the small forest brooks dry up in the dry season at lower elevations.

Doi Suthep Mountain, whose caddis fauna is compared here with Doi Inthanon, is about 40 km east of this and has a maximum elevation of 1,685 m. It has many small forest streams between 400 and 1,200 m (photo 3), mainly on its eastern slope. There are fine forests rich in tree species, evergreen but not damp at the higher elevations, and dry dipterocarp forest on the foothills. Some of the small streams in the lowest parts may dry up in the dry season, but there is always at least some water running in some of them.

FAUNISTICS

The list of species is given in table I. Apart from the descriptions of species in our papers (see above)

TABLE I

Vertical distribution of caddisfly species in the Mae Klang catchment on Doi Inthanon, and other places in Thailand*
Distribution verticale des espèces de trichoptères du bassin du Mae Klang dans la montagne Doi Inthanon et dans d'autres localités en Thaïlande du Nord

Heights (meters)	2 000-2 300	1 600-1 700	1 200-1 300	900-1 000	500-600	400 m
Rhyacophilidae						
Himalopsyche acharai M&C 1989	0	0	0	0 +	0 +	+
Rhyacophila murhu M&C 1989	0					
R.verugia M&C 1993	0					
R. gyamo Schmid 1970	0	0	0 +	+		
R. xayide M&C 1989	0	0	0			
R. scissa Morton 1900	0	0	0			
R. quana M&C 1989	0	0	0 +	+		+
R. voccia M&C 1993	0	0	0			+
R. blenda M&C 1993	0		0			
R. petersorum						
Schmid & Denning 1971	0	0	0 +	0 +	0 +	0 +
R. kyimdongpa Schmid 1970		0				
R. muktepa Schmid 1970		0				
R. pomtipae Malicky 1987		0	0 +	+		
R. drokpa Schmid 1970		0	0			
R. cornuta Kimmins 1953			0	0		+
R. scissoides Kimmins 1953		0	0 +	0 +	+	+
R. mayestril Malicky 1991			0			
R. drosampa Schmid 1970			0	+		
R. inaequalis Denning & Schmid 1971			0	+	+	+
R. ramingwongi Malicky 1987			0	+	+	+
R. suthepensis Malicky 1987			0 +	+	+	+
Glossosomatidae						
Glossosoma atitto M&C 1992	0	0 +	0			+
G. jentumar M&C 1992		0	0 +		+	+
G. malayanum Banks 1934		+	0 +	0 +	+	+
G. elvisso M&C 1992			+	0	0 +	0 +
Agapetus voccus M&C 1992		0	+			+
A. chinensis Mosely 1942			0	0		
A. halong Oláh 1988			+		0 +	+
Nepaloptila ruangjod M&C 1992	0					
N. jisunted M&C 1992				0		
N. kanikar M&C 1992					0 +	
Padunia karaked M&C 1992				0	+	
Poeciloptila briatec M&C 1992				0	+	0
Hydroptilidae*						
Ugandatrichia sanana Oláh 1989		0				
U. maliwan M&C 1991			0	0	0	+
U. kerdmuang M&C 1991				0 +	0 +	+
Philopotamidae						
Chimarra inthanonensis C&M 1989	0	0				
C. exapia M&C 1993		0				
C. matura M&C 1993		0				
C. scopulifera Kimmins 1957		0				
C. karenorum C&M 1989		0				
C. lahuorum C&M 1989		0	0			
C. devva M&C 1993		0	0			
C. schwendingeri C&M 1989		0 +	0 +			
C. nahesson M&C 1993		0 +	0 +	+	+	
C. lannaensis C&M 1989		0 +	0 +	0 +	+	+
C. yaorum C&M 1989			0 +			
C. momma M&C 1993			0			
C. cumata M&C 1993			0			
C. litussa M&C 1993			0 +	+		
C. litugena C&M 1989			0			
C. htinorum C&M 1989			0 +	+		+
C. mlabriorum C&M 1989		+	0			
C. spinifera Kimmins 1957			0 +	+	+	+
C. suthepensis C&M 1989			0 +	+	+	+
C. joliveti Jacquemart 1979		+	0 +		0 +	0 +
C. aneca M&C 1993			0 +	0	0	0
C. monorum C&M 1989			+	0	0 +	0 +
C. bimbltona Malicky 1979				+	0 +	0 +
C. chiangmaiensis C&M 1989		+			+	0 +
C. akkaorum C&M 1989						0 +
Doloclanes serrata Kimmins 1955	0					
D. gressitti Ross 1956		0 +	0	+	+	
Dolophilodes bullu M&C 1993	0					
D. torrentis Kimmins 1955	0					
D. bicolor Kimmins 1955		0				
D. adnamat M&C 1993		0 +	0 +	+	+	
Kisaura longispina Kimmins 1955	0		0			

Heights (meters)	2 000-2 300	1 600-1 700	1 200-1 300	900-1 000	500-600	400 m
K. intermedia Kimmins 1955	0	0	0	+		
K. cina M&C 1993		0	0 +	+		+
K. sura M&C 1993		0 +	0 +	+	+	+
Wormaldia inthanonensis M&C 1993	0	0				
W. relicta Martynov 1935	0	0	+			
Stenopsychidae						
Stenopsyche himalayana						
Martynov 1926		0	0		+	
S. haimavatika Schmid 1969			0	0	0	
S. siamensis Martynov 1931			+		0 +	+
S. hamata Navàs 1930					0	0
Polycentropodidae						
Kambaitipsyche hykrion M&C 1991	0					
Pseudoneureclipsis sukrip M&C 1993			0			
P. josia M&C 1993			0 +	+		
Plectrocnemia eber M&C 1993	0	0				
P. arphachad M&C 1993	0		0			
P. eccingoma M&C 1993		0	0			
Polyplectropus nahor M&C 1993		0 +				
P. arni M&C 1993			0	0	0	
Psychomyidae						
Eoneureclipsis querquobad M&C 1989		0	+	+		
Paduniella dendrobia M&C 1993		0	0			
P. semarangensis Ulmer 1913			0	+	0 +	0 +
P. maeklangensis M&C 1993				0		
P. suwannamali M&C 1993				+	0 +	+
P. wangtakraiensis M&C 1993					+	0 +
Psychomyia chompu M&C 1993		+	0 +	0	0 +	+
P. benyagai M&C 1993			0			
P. kaiya M&C 1993					0	+
P. arthit M&C 1993					0	0
P. lak M&C 1993					0 +	0 +
Lype atnia M&C 1993			+	0 +	+	+
Tinodes mogetius M&C 1993		0	0			
T. cincibilus M&C 1993			0			
Xiphocentronidae						
Melanotrichia attia M&C 1992		0	0	0		
Abaria ateduna M&C 1992			0			
Melanotrichia samaconius M&C 1992					0 +	
Arctopsychidae						
Parapsyche intawitschajanon						
M&C 1992	0					
Arctopsyche variabilis Schmid 1968	0	0				
A.hynreck M&C 1991		0	0 +			+
Hydropsychidae*						
Macrostemum superior C&M 1994		0	0 +			
M. bellum Banks 1916			0			+
M. fastosum Walker 1852			0 +	+	0 +	0 +
M. quinquefasciatum Martynov 1935					+	0
Trichomacronema paniae M&C 1991		0	0 +	0 +	0	
Hydromanicus eliakim M&C 1993		0	0			+
H. truncatus Betten 1909		0	0 +	+	+	+
H. sealthiel M&C 1993		+	0 +	+	+	
H. inferior C&M 1995				0	0 +	0 +
Phryganeidae						
Eubasilissa maclachlani White 1862	0	0	0			
Limnocentropodidae						
Limnocentropus inthanonensis						
M&C 1989	0	0	0			
L. hysbald M&C 1991			0			
L. siribhumensis M&C 1989			0			
Goeridae						
Goera atiugo M&C 1992		0				
G. ilo M&C 1992		0	0			
G. redsat M&C 1992			0	0	0	0
G. redsomar M&C 1992			+		0	0
G. solicur M&C 1992						0

TABLE I

(suite et fin)

Heights (meters)	2 000- 2 300	1 600- 1 700	1 200- 1 300	900- 1 000	500- 600	400 m
Limnephilidae						
Nothopsyche muqua M&C 1989			0			
Moropsyche gerolan M&C 1991	0		+			
M. suteminn M&C 1991		0				
M. huaysaillianga M&C 1989		0	0			+
Uenoidae						
Uenoa lobata Hwang 1957	0					
U. hiberna Kimmins 1964			0			
Lepidostomatidae						
Anacrunoecia digitata Mosely 1949	0					
Adinarthrella brunnea Mosely 1941	0					
A. parva Mosely 1941	0					
Zephyropsyche weaveri M&C 1994	0					
Lepidostoma ratanapruksi M&C 1994	0					
Paraphlegopteryx malickyi Weaver 1994	0 +					
Dinarthrum aprilius M&C 1994	0					
D. octobrius M&C 1994	0					
D. inthanon M&C 1994	0	0	0			
Adinarthrum moulmina Mosely 1949	0	0 +	0 +	+	+	+
Paraphlegopteryx angkangensis Weaver 1994	+	0 +				
Lepidostoma varithi M&C 1994		0				
Dinarthrum siribhum M&C 1994		0				
D. lannaensis M&C 1994		0				
D. augustus M&C 1994		0	0			
D. fischeri M&C 1994		0	0			+
D. februarius M&C 1994		0	0 +	+		+
D. brueckmanni M&C 1994		0	0 +	0	0 +	
D. septembrius M&C 1994			0			
D. baenzigeri M&C 1994			0			
D. pratetaiensis M&C 1994			0 +	+	+	+
Crunoeciella hirta Navás 1932			0			+
Goerodes abruptus Banks 1931			0			+
Brachycentridae						
Micrasema turbo M&C 1992		0	0			
M. fortiso M&C 1992			0 +			+
Helicopsychidae						
Cochliophylax admata M&C 1992		0				
Helicopsyche rodschana M&C 1992		[illegible]			0	+
Odontoceridae						
Inthanopsyche trimeresuri Malicky 89	0	0 +	0	0		
Lannapsyche chantaramongkolae Malicky 1989		0	0	0 +	+	+
Psilotreta baureo Malicky 1989		0	+	+	+	+
Marilia mogtiana Malicky 1989			0 +	0 +	0 +	
Psilotreta quin M&C 1991				0		
Marilia sumatrana Ulmer 1951				+	+	0 +
Leptoceridae*						
Leptocerus inthanonensis M&C 1991						0
Calamoceratidae						
Anisocentropus pandora M&C 1994		0				
Ganonema dracula M&C 1994		0 +				
Anisocentropus diana M&C 1994		0	+	+	+	+
A. salsus Betten 1909			0			
Ganonema extensum Martynov 1935			0 +			+
Anisocentropus janus M&C 1994				0 +	0 +	+
Molannidae						
Molanna n. sp.	0					
M. oglamar M&C 1989		0	0	+		+

*The species of this family are not completely listed for taxonomic problems. *La liste des espèces de cette famille n'est pas complète parce qu'il y a encore des problèmes taxonomiques.*
Abbreviations: C&M = Chantaramongkol & Malicky, M&C = Malicky & Chantaramongkol.
O: record from Mae Klang catchment. *Trouvé dans le bassin du Mae Klang.*
+: records from other places outside Doi Inthanon. *Trouvé ailleurs hors du Doi Inthanon.*

PHOTO 1. — Small forest brook at 1,600 m on Doi Inthanon.
Petit ruisseau dans la forêt à 1600 m au Doi Inthanon.

there are apparently no records of Trichoptera from Doi Inthanon in the literature.

Most families were recorded from the highest to the lowest sampling points with a series of species. In some groups one might have the impression that they are concentrated at the highest or the lowest altitudes, but, as this list gives only the records from Doi Inthanon, many species known in Thailand are missing here. For instance, the arctopsychids were found on Doi Inthanon at higher elevations only, but there is another species in northern Thailand, *Maesaipsyche prichapanyai* which was found at an elevation of 400 m. *Rhyacophila* species are lacking from lower elevations here, but we know *R. noebia* and *R. tantichodoki* only from low elevations which do apparently not occur in Doi Inthanon. It was a surprise that we have not yet found any Ecnomidae or Dipseudopsidae on Doi Inthanon despite knowing 20 species of *Ecnomus* and 6 species of *Dipseudopsis* from Thailand. It appears that these two families are more or less concentrated at low altitudes, but some species may nevertheless live at higher altitudes, e.g. *Dipseudopsis diehli* in Sumatra. The same may be true for many *Polyplectropus* and *Psychomyia* species.

ZOOGEOGRAPHY

It has been known for a long time (SCHMID, 1966) that the South East Asian caddis fauna is exclusively oriental, without any traces of palaearctic

PHOTO 2. — Small forest brook at 900 m on Doi Suthep.
Petit ruisseau dans la forêt à 900 m au Doi Suthep.

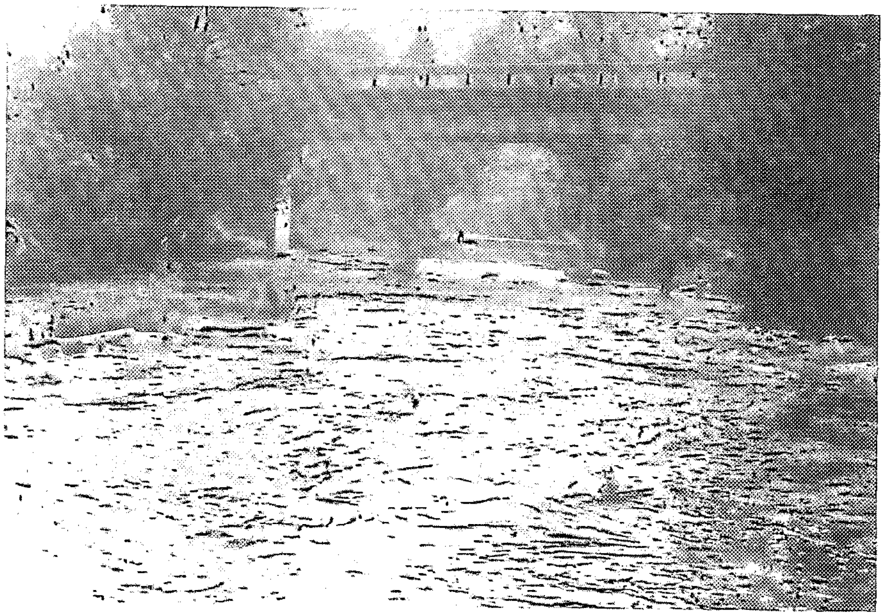

PHOTO 3. — Lowermost sampling site of Mae Klang at 420 m.
La localité étudiée la plus basse du Mae Klang à 420 m.

influence. This is also true for northern Thailand. There are some groups which are more or less concentrated at higher elevations, e.g. *Himalopsyche* or *Eubasilissa*, but they are also Oriental. Generally spoken, the so-called palaearctic groups are scarce in Trichoptera. Limnephilini is one of them which may better be called holarctic. Most Trichoptera living in running waters in Europe are purely European and not palaearctic (MALICKY, 1983).

STREAM ZONATION

The zonation of running waters has been well investigated in Europe. The system proposed by ILLIES and BOTOSANEANU (1963) is generally accepted; this divides streams into Krenon, Rhithron and Potamon, mainly according to the distribution of animal species, but also according to temperature, discharge, water velocity and particle size of the sediment.

The Stream Order System which is widely used in limnological papers is useless for biological studies because it counts only the bifurcations upstream, but says nothing about temperature, discharge, nutrition, insolation, chemistry, animal communities, riparian vegetation, water velocity, etc.

ILLIES (1961 a, 1964) made an attempt to transpose his system to tropical rivers. He investigated 6 sites along the River Huallaga in Peru over a length of about 300 km between 4,100 m and 600 m elevation. From the study of 22 insect taxa (of which only 5 were identified to species) he concluded : "The andine and Brasilian tributaries above an elevation of about 2,000 m offer typical Rhithrons... These Rhithrons are followed or replaced by Epipotamons in elevations down to about 500 m ... All the rest of running-water biotopes within the Amazon area may be considered as to consist of a faunistically rather uniform Hypopotamon". However, his six sampling sites were only in the main course of River Huallaga which is about 50 cm broad in the uppermost site and 2-3 m broad in the second site but 100 m broad in the lowest site. Obviously he made no attempt to take samples from small tributaries near the lower parts. Therefore it is evident that Potamon in South America may be found up to about 2,000 m elevation which is much higher than in Europe, but from these data it cannot be concluded that no Rhithron exists at low elevations in the tropics.

HARRISON and RANKIN (1976) in their study of streams on St. Vincent found conditions in small brooks as in typical Rhithron, the insects belonging to "cool adapted groups", but are "warm adapted species"; the temperature was always between 20 and 25 °C. The authors conclude (p. 298) that "the existence of upper zones of tropical and subtropical rivers in mountains arising below his (i.e. Illies') rhithric boundary but which exhibit true montane conditions and support a true montane but warm-adapted fauna must be recognised. We suggest the term 'pseudorhithron' to distinguish these mountain zones characterised by a warm-adapted 'pseudorhithric' fauna, from true Rhithron, with its cold-adapted rhithric fauna". We think that a new term is not necessary.

Another proposed solution of the problem is simply to call everything in warm water at lower elevations in the tropics "Potamal" (see the footnote on p. 127 in BOTOSANEANU, 1979), regardless of other circumstances. This cannot be accepted because it makes every definition useless.

Our results from Thailand may contribute to a better understanding of tropical river zonation. We cannot yet give detailed outlines of the zonation in Thailand, because our results are not sufficient. It is beyond doubt that Rhithron and Potamon may be easily distinguished at the first glance, see photos 1, 2 and 4, but it is not fully clear how to define the boundary between them in the Tropics.

According to the definition by ILLIES (1961) and ILLIES and BOTOSANEANU (1963), translated by HAWKES (1975 : 366), "Rhithron is defined as part of the stream from its source down to the lowermost point where the annual range of monthly mean temperature does not exceed 20 °C. The current velocity is high and the flow volume is small. The substratum may be composed of fixed rock, stones or gravel and fine sand. Only in pools and sheltered areas is mud deposited. Potamon is the remaining downstream stretch of river where the annual range of monthly mean temperatures exceeds 20 °C, or, in tropical latitudes, with a summer maximum of the monthly mean exceeding 25 °C. The current velocity over the river bed is low and tends to be laminar. The river bed is mainly of sand or mud, although gravel may also be present. In the deeper pools oxygen may be depleted, light penetration limited and mud deposited."

It must be noted that in the definition of Potamon, ILLIES (1961) said that the monthly mean in tropical latitudes exceeds 20 °C *(sic!)*, but this was changed to 25 °C by ILLIES and BOTOSANEANU (1963) and HAWKES (1975).

In Mae Klang River, all of our sampling sites between 1,200 and 2,300 m are Rhithron according to this definition. The variation of monthly means is clearly below 20 °C. But this is also true in the sites below 1,000 m whose temperature amplitudes are about 12 °C over the year, their maxima however exceeding 25 °C. According to the above definition, our sites in Mae Klang between 1,000 and 400 m

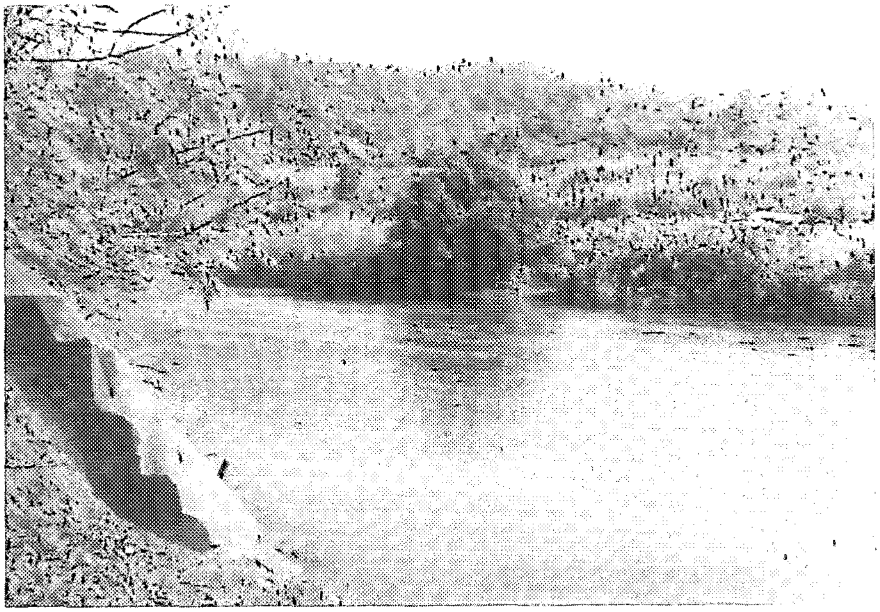

PHOTO 4. — River Mae Ping south of Chiang Dao.
Rivière Mae Ping au sud de Chiang Dao.

would be Potamon according to the version of 1961, but the sites at 900-1,000 m were not Potamon according to the version of 1963 as they do not exceed 25 °C.

These definitions do not help. We must remember that they were made 30 years ago according to the knowledge of that time, but we know more now and must try to adapt accordingly.

We note that before ILLIES there were other proposals, mainly based on fish distribution, and ILLIES' definition is based on the distribution of animal species. Although the Rhithron in Europe and in Thailand must be considered homologous and are Isocoenoses (sensu BALOGH, 1958), a direct comparison of animal species is not possible because there are no species in common, neither can we use geographical transitions because they are unknown and probably do not exist. The dominance of species groups instead of species may be erroneous, e.g. dominance of *Rhyacophila* species could be used as an indicator of Rhithron, but this is not enough. Limnephilids which dominate in Europe are almost absent in Thailand, and the dominating genus *Chimarra* in Thailand has only one species in Europe. It is similar in many other groups.

We are therefore proposing another method.

Any worker with some field experience will be able to decide at the first glance whether a stream is rhithral or potamal from its appearance. If the brooklet in photo 1 was in Europe, everyone would recognize it as Rhithron. Ping River in photo 4 would likewise be recognized as Potamon (whose caddis fauna, by the way, is very different from any site of Mae Klang). The brooklet in Mae Klang catchment in figure 1 is in 1,600 m elevation, its temperature is always under 20 °C, so it is Rhithron not only from its appearance but also from definition; its caddis fauna is well known.

If we find a similar brooklet (photo 3) at a lower elevation, e.g. on Doi Suthep in 400 to 900 m elevation with a very similar caddis fauna with many species in common (most of the records marked with + in table I are from these brooklets on Doi Suthep), we see no reason why this brooklet should not be Rhithron, despite its temperature being normally around 24 °C! Many species were found in Mae Klang only at higher elevations, but also at lower elevations in other streams, many of them on Doi Suthep, which means that they prefer their specific biotopes regardless of temperature. River Klang has a high discharge and high temperatures downstream at about 400-600 m (tab. II), but the small forest brooks at the same elevations of Doi Suthep have roughly the same conditions as those higher up in Doi Inthanon, with the exception of temperature. The wide temperature tolerance range of some species may also go along with a change of preferred biotopes. The larvae of *Himalopsyche acharai* live in

TABLE II

Water temperature (°C) of streams and rivers in northern Thailand in the coolest (Dec.-Feb.) and hottest (Apr.) seasons of the year, and number of species found in these zones
Température de l'eau en °C des ruisseaux et rivières en Thaïlande du Nord dans la saison la plus froide (décembre-février) et la plus chaude (avril), avec le nombre des espèces trouvées dans les zones respectives

	Dec.-Feb.	April	Nb. species found
River Klang (Doi Inthanon)			
2,000 - 2,300 m	8 - 9	12 - 13	41
1,600 - 1,700 m	13 - 15	13 - 16	74
1,200 - 1,300 m	12 - 17	16 - 17	95
900 - 1,000 m	15 - 18	22 - 23	29
500 - 600 m	16 - 21	21 - 27	31
400 m	17 - 20	25 - 29	22
Forest brooks on Doi Suthep			
400 - 900 m	14 - 18	20 - 24	
River Ping near Chiangmai			
300 m	19 - 21	25 - 30	

cool forest brooks in the highest parts of Doi Inthanon, but they live also in warm water of over 25 °C at 400 m on Doi Suthep where they inhabit waterfalls, probably because these provide a better oxygen supply for the larvae.

If this idea is accepted, we can stepwise compare the species composition in other streams in SE Asia, and we can use the same procedure also in other tropical regions. Finally we shall find out that true Rhithron occurs in all tropical continents at low elevations.

Why, then, should Rhithron be acceptable under 20 °C, but not over 20 °C? Even in Europe, mainly in its Mediterranean part, we know streams of this kind (MALICKY, unpublished data). Earlier authors have called the species of *Neurorthus*, an aquatic lacewing, cold stenothermous, but MALICKY (1984) has found that they may live in streams up to temperatures of 27 °C in Sardinia and Sicily. It appears therefore that the 20 °C limit for Rhithron is too low. According to our present knowledge, the mean maximum of water temperature of Rhithron may be 25 °C or more, but there is a broad overlap with Potamon temperatures, and temperature is only one of the distinguishing features. Basically, the difference is in the specific composition of the fauna, but this depends on a multitude of factors of which temperature is important but not the only deciding one. The decision must be made on the knowledge of animal species and not functional feeding groups or other dubious aggregates. Rhithral species are not necessarily cold stenotherms; on the contrary, real cold stenothermous species are extremely rare even in Europe (MALICKY, 1990), and every species has its specific preferences and tolerance ranges (MALICKY, 1978).

THE CONCEPT OF COOL-ADAPTED AND WARM-ADAPTED GROUPS

Cool-adapted groups has become part of the standard terminology in papers on running water, but this term remained hypothetical, and is not confirmed by facts.

Ross (1956) has used Rhyacophilidae, Glossosomatidae and Philopotamidae as examples to reconstruct past dispersal patterns of cool adapted animal groups because "the evolutionary history of that part of the biota adapted to cool or cold conditions has remained an enigma" (p. 1). For this analysis, the author presents a careful morphological study of caddisfly families to find out which families are primitive or derived. For the temperature conditions however, it is not quite clear from where he took his knowledge. "The scale of temperature adaptation is acknowledgedly arbitrary. Cool-adapted groups typically include living in areas with regular periods of freezing weather and in streams which are cool for the entire year. On the basis of unfortunately few records, there seems to be a significant change in caddisfly fauna in the neighborhood of a maximum water temperature of 65° to 68 °F (= 18-20 °C)... For the present, therefore, those streams are considered cool that have temperatures not exceeding 68 °F (= 20 °C) except perhaps for rare periods of only few hours." (p. 19). In a combination of morphological and temperature data he shows that "primitiveness coincides to a remarkable extent with cool-adaptation. Of the 18 primitive lines, 17 are cool-adapted and one has primitive genera which are cool-adapted. Not one is warm-adapted" (p. 19). "Adaptation to warmer, slower waters was a later specialization dependent on the development of physiological characteristics facilitating more efficient utilization of oxygen" (p. 19).

If we compare our data from Thailand (tab. I) with these statements we find that almost all families are represented from the highest to the lowest sampling sites by a series of alternating species, irrespective of whether Ross has characterized the family as cool- or warm-adapted (tab. II). Ross was one of the most prominent workers of his time, but we have the impression that he has separated the groups into cold or warm adapted more or less according to his personal feeling. This is particularly striking in *Rhyacophila* (which is cool-adapted according to him) and *Chimarra* (which is said to be warm-adapted). The proportions of species living in the

TABLE III

Distribution of "cool-adapted" and "warm-adapted" groups (sensu Ross) in three regions of Thailand : number of species
Distribution des groupes « adaptés au frais » et « adaptés au chaud » selon Ross dans trois régions de la Thaïlande : nombre des espèces

			Mae Klang		Doi Suthep	Hat Yai
Groups after Ross	Category of Ross	only under 20 °C	under and over 20 °C	only over 20 °C	all over 20 °C	all over 20 °C
Heights (meters)		1,200-2,300	400-2,300	400-1,000	400-900	100-600
Rhyacophilidae	cold	9	12	0	12	2
Glossosomatidae	cold	0	7	0	8	0
Protoptilinae	both	1	0	4	0	0
Phylopotaminae	cold	7	5	0	8	2
Chimarra	warm	13	10	2	19	11
Stenopsychidae	cold	0	3	1	1	1
Polycentropodidae	both	6	2	0	11	10
Psychomyidae	warm	4	4	6	9	9
Xiphocentronidae	warm	1	1	1	4	4
Arctopsychidae	cold	2	1	0	1	0
Goeridae	cold	2	2	1	4	2
Limnephilidae	cold	3	1	0	2	0
Phryganeidae	cold	1	0	0	0	0
Lepidostomatidae	*both*	*16*	7	0	10	1
Brachycentridae	cold	1	1	0	2	0
Helicopsychidae	warm	1	0	1	3	1
Odontoceridae	cold	0	3	1	2	0
Marilia	warm	0	1	1	2	1
Calamoceratidae	cold	1	1	0	0	1
Anisocentropus	warm	2	1	1	4	1
Molannidae	cold	1	1	0	3	0

cooler and in the warmer parts of Mae Klang and Doi Suthep are practically the same in *Rhyacophila* and *Chimarra*. The same is evident for the sum of all groups in table III. From the list one may also have the impression that no *Rhyacophila* or lepidostomatids exist which are living only at low altitudes, but we know several species which live only low down at high water temperatures. This is remarkable from the point of view of cold stenothermous groups.

The differences in the figures for Hat Yai in table III are explained by the different faunal composition in this region 1,200 km south of Doi Inthanon.

The present study shows clearly that almost all Trichoptera families include warm- and cool-adapted species.

Ross (1956) repeats in his book several times that *Chimarra* is warm adapted and "not a montane group" (p. 50). In an apparent combination of the statements of Ross and ILLIES, HAWKES (1975) has listed some caddis families to be associated with rhithron and potamon zones of rivers; for the Rhithron, among others, "Philopotamidae except *Chimarra*" There are however the following facts:

— as far as we know, nobody has ever found in any *Chimarra*-rich region of the world that *Chimarra* do not live in the Rhithron;

— in our own records, we have 21 *Chimarra* species from those parts of Mae Klang which are clearly Rhithron, i.e. under 20 °C, but only one from nearby Mae Ping (photo 4) which is clearly Potamon.

ILLIES (1961) repeats many of Ross' statements but says, in contrast, that Phryganeidae are warm adapted.

We do not think that these statements about warm- and cool-adaptation were based on careful research. Once more it appears that easy and beautiful hypotheses are in danger of becoming floppy (although not short-lived: in the last 40 years nobody had made objections).

The existence of cool-adapted (or even cold stenothermous) families or similar groups remains hypothetical and they probably do not exist. There are cool-adapted species in almost all caddis families. There was certainly an adaptation to temperature conditions early in the evolution of groups, which was expressed at genus or family level (which is the hypothetical background of Ross's warm- or cool-adapted groups), but such adaptations continued until now, therefore we find now closely related species with very different temperature preferences and tolerances. Of course there is no evidence that temperature is immediately deciding for the presence or absence of a species. Instead, there is a complicated combination of factors which cannot be measured as easily as temperature.

TABLE IV

Sum of all groups from table III : number of species
Somme de tous les groupes du tableau III : nombre des espèces

Categories of Ross		Mae Klang			Doi Suthep	Hat Yai
	total	under 20 °C	both	over 20 °C	over 20 °C	over 20 °C
Cold	67	27	37	3	43	8
Both	36	23	9	4	21	11
Warm	50	21	17	12	41	27

DIVERSITY

From tables I and IV it is evident that the number of recorded species, which is an indicator of diversity, is highest in the elevations between 1,200 and 1,700 m. Collecting intensity has of course its influence on the results, and indeed the most intensively studied zone is between 1,200 and 1,300 m with the highest number of 95 species in the list. But on the other hand, our collecting intensity was about the same in the zones 1,600-1,700 and 2,000-2,300 m, with a clear difference in results, with 74 and 41 species. Compared with the temperatures in table II, it is noteworthy that this highest diversity coincides with the lowest temperature variation. We do not speculate that the species presently found have evolved here in these streams, but if the present conditions are favourable for the existence of many species, it was probably so at all times, and constant ecological conditions were probably always favourable both for the existence and for the evolution of more species.

In a study of quantitative emergence of caddisflies from a cold stream with a constant temperature in Europe, MALICKY (1976) has shown that, in comparison with a stream with large temperature variations, the proportions in the composition of the fauna are more constant. More species were present with approximately equal dominance rates, and also the year-to-year variation was lower than in the stream with large temperature variations. Some caddis species may migrate in their streams seasonally to find the more constant conditions (MALICKY, 1980). Life conditions in mountain streams in temperate regions are not very different from those in similar streams in tropical mountain regions, so that, in some respects, mountain stream insects may anywhere be considered to be tropical animals in a physiological respect, and the mountain streams of temperate regions may be considered, for the same reason, to be extrazonal tropical biotopes (MALICKY, 1980). To modify the hypothesis by Ross (1956 : 19), from this point of view, it seems more likely that the evolution of the primitive lineages among caddisflies took place in the intermediate elevations of tropical mountains, with the most constant conditions, rather than in the cold regions of these mountains "where streams are cooled throughout the year by snow melt water" (Ross : l.c.).

ACKNOWLEDGEMENTS

We wish to thank the Director of Doi Inthanon National Park, Mr. Phuchong Insompune and the Head of Bang Khun Klang Royal Project, Mr. Bunyong Uttayasaivisuit, for the permission to work there, and Mr. Sakorn Promkutkaew and Mr. Montri Yanon for technical assistance. Our sincere thanks are due to Dr. M.I. Crichton for correction of the English text and Dr. F.-M. Gibon for translation of the French summary.

Manuscrit accepté par le Comité de rédaction le 3 novembre 1994.

REFERENCES

ANDERSEN (T.), JOHANSON (K.A.), 1993. — "Caddis flies (Trichoptera) from a mountain rain forest in NE Tanzania". *In : Proc. 7th Int. Symp. Trichoptera*, Leiden, Backhuys Publishers : 59-64.

Assessment of National Parks, Wildlife Sanctuaries and other preserves in Thailand, 1987. — Draft Report, Fac. Forestry, Kasetsart University, Bangkok, 124 p.

BALOGH (J.), 1958. — *Lebensgemeinschaften der Landtiere*. Budapest and Berlin.

BISHOP (J.E.), 1973. — *Limnology of a small Malayan river Sungai Gombak*. The Hague, Junk, 485 p.

BOTOSANEANU (L.), 1979. — Quinze années de recherches sur la zonation des cours d'eau : 1963-1978. Revue commentée de la bibliographie et observations personelles. *Bijdr. Dierk.* 49 : 109-134.

CHANTARAMONGKOL (P.), 1985. — *Die Köcherfliegen von Sri Lanka : Taxonomische Grundlagen für ihre Verwendung als Gewässer-Indikatoren*. Diss. Univ. Wien, 399 p.

CHANTARAMONGKOL (P.), MALICKY (H.), 1989. — Some Chimarra (Trichoptera : Philopotamidae) from Thailand (Studies on caddisflies from Thailand, nº 2). *Aquatic Insects* 11 : 223-240.

CHANTARAMONGKOL (P.), MALICKY (H.), 1995. — Drei neue asiatische *Hydromanicus* (Trichoptera: Hydropychidae) (Arbeiten über thailändische Köcherfliegen nº 17). *Ent. Z.* (Essen) 105 : 92-99.

DUDGEON (D.), 1992. — Patterns and processes in stream ecology. A synoptic review of Hong Kong running waters. *In :* Schweizerbart, Stuttgart, *Die Binnengewässer*, vol. 29, 147 p.

GIBON (F.-M.), GUENDA (W.), COULIBALY (B.), 1994. — Observations sur la zonation des cours d'eau de la savane ouest-africaine : Trichoptères du Sud-Ouest du Burkina Faso. *Annls Limnol.* 30 : 101-121.

GRAHAM (M.), éd., 1991. — *National Parks of Thailand*. Bangkok, 238 p.

HARRISON (A.D.), RANKIN (J.J.), 1976. — Hydrobiological studies of Eastern Lesser Antillean Islands. II. St. Vincent : Freshwater fauna its distribution, tropical river zonation and biogeography. *Arch. Hydrobiol. Suppl.* 50 : 275-311.

HAWKES (H.A.), 1975. — River zonation and classification. *In* Whitton (B.A.), éd. : *River Ecology*, Oxford, Blackwell : 312-374.

ILLIES (J.), 1961. — Versuch einer allgemeinen biozönotischen Gliederung der Fliessgewässer. *Int. Rev. ges. Hydrobiol.* 46 : 205-213.

ILLIES (J.), 1961 a. — Gebirgsbäche in Europa und in Südamerika, ein limnologischer Vergleich. *Verh. Int. Ver. Limnol.* 14 : 517-523.

ILLIES (J.), 1964. — The invertebrate fauna of the Huallaga, a Peruvian tributary of the Amazon river from the sources down to Tingo Maria. *Verh. Int. Ver. Limnol.* 15 : 1077-1083.

ILLIES (J.), BOTOSANEANU (L.), 1963. — Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes, considérées surtout du point de vue faunistique. *Mitt. SIL* 12 : 1-57.

MALICKY (H.), 1976. — Trichopteren-Emergenz in zwei Lunzer Bächen 1972-74. *Arch. Hydrobiol.* 77 : 51-65.

MALICKY (H.), 1978. — Der Temperaturgang einiger niederösterreichischer Gebirgsbäche. *Wetter und Leben* 30 : 170-183.

MALICKY (H.), 1980. — Evidence for seasonal migrations of larvae of two species of philopotamid caddisflies (Trichoptera) in a mountain stream in Lower Austria. *Aquatic Insects* 2 : 153-160.

MALICKY (H.), 1983. — Chorological patterns and biome types of European Trichoptera and other freshwater insects. *Arch. Hydrobiol.* 96 : 223-244.

MALICKY (H.), 1984. — Ein Beitrag zur Autökologie und Bionomie der aquatischen Netzflüglergattung Neurorthus (Insecta, Neuroptera, Neurorthidae). *Arch. Hydrobiol.* 101 : 231-246.

MALICKY (H.), 1987. — On some Rhyacophila from Doi Suthep Mountain, Northern Thailand. *Trichoptera Newsletter* 14 : 27-29.

MALICKY (H.), 1989. — Odontoceridae aus Thailand (Trichoptera). Studien über thailändische Köcherfliegen nº 4. *Opusc. zool. flumin.* 36 : 1-16.

MALICKY (H.), 1990. — Spuren der Eiszeit in der Trichopterenfauna Europas (Insecta, Trichoptera). *Riv. Idrobiol.* 27 (1988) : 247-297.

MALICKY (H.), 1991. — "Some unusual caddisflies (Trichoptera) from southeastern Asia. Studies on caddisflies of Thailand, nº 5". *In : Proc. 6th Int. Symp. Trich.*, Poznań, Adam Mickiewicz Univ. Press : 381-384.

MALICKY (H.), 1994. — Ein Beitrag zur Kenntnis asiatischer Calamoceratidae (Trichoptera). (Arbeit über thailändische Köcherfliegen nº 13). *Z. Arbgem. Öst. Ent.* 46 : 62-79.

MALICKY (H.), CHANTARAMONGKOL (P.), 1989. — Einige Rhyacophilidae aus Thailand (Trichoptera). Studien über thailändische Köcherfliegen nº 3. *Ent. Z.* (Essen) 99 : 17-24.

MALICKY (H.), CHANTARAMONGKOL (P.), 1989 a. — Beschreibung von neuen Köcherfliegen (Trichoptera) aus Thailand und Burma. Arbeiten über thailändische Köcherfliegen nº 6. *Ent. Ber. Luzern* 22 : 117-126.

MALICKY (H.), CHANTARAMONGKOL (P.), 1991. — Elf neue Köcherfliegen (Trichoptera) aus Thailand und angrenzenden Ländern. Studien über thailändische Köcherfliegen nº 7. *Ent. Z.* (Essen) 101 : 80-89.

MALICKY (H.), CHANTARAMONGKOL (P.), 1991 a. — Einige Leptocerus Leach (Trichoptera, Leptoceridae) aus Thailand. Arbeiten über thailändische Köcherfliegen nº 8. *Braueria* 18 : 9-12.

MALICKY (H.), CHANTARAMONGKOL (P.), 1991 b. — Beschreibung von Trichomacronema paniae n.sp. (Trichoptera, Hydropsychidae) aus Nord-Thailand und Beobachtungen über ihre Lebensweise. Arbeiten über thailändische Köcherfliegen nº 9. *Ent. Ber. Luzern* 25 : 113-122.

MALICKY (H.), CHANTARAMONGKOL (P.), 1992. — Neue Köcherfliegen (Trichoptera) aus Thailand und angrenzenden Ländern. Arbeiten über thailändische Köcherfliegen nº 11. *Braueria* 19 : 13-23.

MALICKY (H.), CHANTARAMONGKOL (P.), 1992 a. — Einige Goera (Trichoptera, Goeridae) aus Südasien. Studien über thailändischer Köcherfliegen nº 10. *Ent. Ber. Luzern* 27 : 141-150.

MALICKY (H.), CHANTARAMONGKOL (P.), 1993. — Neue Trichopteren aus Thailand (Arbeiten über thailändische Köcherfliegen nº 12). *Linzer Biol. Beitr.* 25 : 433-487, 1137-1187.

MALICKY (H.), CHANTARAMONGKOL (P.), 1994. — Neue Lepidostomatidae aus Asien (Trichoptera) (Arbeiten über thailändische Köcherfliegen nº 14). *Ann. Naturhist. Mus. Wien* 96 B : 349-368.

MARLIER (G.), 1954. — Recherches hydrobiologiques dans les rivières du Congo Oriental. II — Étude écologique. *Hydrobiologia* 6 : 225-264.

ROBBINS (R.G.), SMITINAND (T.), 1966. — A botanical ascent of Doi Inthanon. *Nat. Hist. Bull. Siam Soc.* 21 : 205-227.

ROSS (H.H.), 1956. — *Evolution and classification of the mountain caddisflies.* Univ. Illinois Press, Urbana.

SCHMID (F.), 1966. — À propos des limites de la zone paléarctique dans l'Himalaya ou les limnophilines en Inde (Trichoptera). *Acta Zool. Acad. Sci. Hung.* 12 : 363-369.

STATZNER (B.), 1975. — Zur Longitudinalzonierung eines zentralafrikanischen Fliessgewässersystems unter besonderer Berücksichtigung der Köcherfliegen (Trichoptera, Insecta). *Arch. Hydrobiol.* 76 : 153-180.