

HIGH SPECIES RICHNESS OF ICHNEUMONIDAE (HYMENOPTERA) FROM THE CANOPY OF A MALAYSIAN RAIN FOREST

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Abstract. We collected arthropods from the canopies of a primary lowland rain forest in the Kinabalu National Park (Sabah, Northern Borneo, Malaysia) and of an oak plantation in Steigerwald (northern Bavaria, Germany) by selective canopy fogging. Comparatively few specimens, but many species, of Ichneumonidae (Insecta, Hymenoptera) were found in the rain forest, and the indicators of diversity (relative number of species, percentage of singletons, evenness, Williams' alpha) of the rain forest samples are much higher than those of the oak forest samples or of other samples from restricted areas analyzed so far. The subfamilies Tryphoninae, Ichneumoninae, Banchinae, Ctenopelmatinae, Ophioninae, Anomaloniinae and Diplazontinae are poorly represented or lacking in the rain forest samples, whereas the Orthocentrinae (parasitoids of Diptera Nematocera) are species-rich. The percentages of idiobionts (parasitoids which kill their host at or shortly after oviposition) in the rain forest samples are not principally different from those in samples from temperate regions. The nocturnal activity of Ichneumonidae in the rain forest canopy is higher than the diurnal activity. In particular, large specimens belonging to the subfamily Cryptinae are active at night. Re-fogging experiments demonstrate that the recolonization of fogged trees by small Hymenoptera is still incomplete after periods of 7-19 months. *Accepted 07 September 1998.*

Key words: Canopy, diversity, Hymenoptera, Ichneumonidae, idiobionts, nocturnal activity, rain forest, re-colonization, species richness.

INTRODUCTION

Wasps of the family Ichneumonidae (Hymenoptera) are considered to be one of the few larger taxa of arthropods which are not more diverse and species-rich in the tropics than in temperate regions (Owen & Owen 1974, Janzen & Pond 1975, Gauld 1986, Noyes 1989, Stork 1991). However, the material on which this assumption is based was mostly collected in disturbed habitats, in suburban gardens or in secondary vegetation ("old fields"). Samples from undisturbed primary vegetation are scarce, and the ichneumonids from these samples were not analyzed in detail. This is especially true for samples from the canopy of tropical rain forests, which is thought to

be the most species-rich habitat (Erwin 1982, 1988; Stork 1988, 1991, 1993; Linsenmair 1990; Floren & Linsenmair 1997). Furthermore, the ecological differences in the tropics between humid and less seasonal habitats on the one hand, and semi-arid and/or highly seasonal habitats on the other, were not adequately taken into account in previous discussions. Therefore the Ichneumonidae from a fairly rich collection of arthropods from the canopy of a primary lowland rain forest in the Kinabalu National Park in Sabah (northern Borneo, Malaysia) (Floren & Linsenmair 1997; including material recently collected) are analyzed here. This region is regarded as being one of the centers of floristic diversity in southeast Asia (Myers 1988, Ashton 1989). For com-

parison, the ichneumonid fauna from the canopy of a German managed oak forest is also analyzed. Oaks (and willows) have been proved to harbor the most species-rich arboreal arthropod fauna in western Europe (Southwood 1961; Southwood *et al.* 1982a, b; Kennedy & Southwood 1984).

MATERIAL AND METHODS

The material from Malaysia was collected near Poring Hot Spring (6°5'N, 116°33'E; at 500–700 m a.s.l.) in the Kinabalu National Park in Sabah, Borneo, in a "Dipterocarp Hill Forest" (Kitayama 1992), a mature primary lowland rain forest with few epiphytes in the canopy. Three tree species with relatively small trees in the lower canopy layer (maximum height 30 m) were selected for canopy fogging: two species of Euphorbiaceae (*Aporosa lagenocarpa* and *A. subcaudata*) and one Polygalaceae (*Xanthophyllum affine*). The material was collected in the years 1992–1993 and again in 1996. The forest in Germany is a 166-year-old plantation of oaks (*Quercus robur*; Fagaceae) in the Steigerwald (49°58'N, 10°36'E; at about 300 m) in northern Bavaria, with some young beeches (*Fagus sylvatica*; Fagaceae) and hornbeams (*Carpinus betulus*; Corylaceae) in a partly developed second canopy layer. The material was collected in August 1995 and in the growing season of 1996.

The method of selective canopy fogging, which allows tree-specific sampling of arthropod communities in the multi-layered rain forest, is described in detail by Floren & Linsenmair (1997, in press; see also Stork & Hammond 1997). The fogging method is efficient only in dry weather with little wind drift. The fogging experiments in Malaysia were therefore conducted early in the morning (06:00–07:00 h) and sometimes at night (at about 23:00 h). Eighteen trees were fogged in daytime for the first time (the Hymenoptera from one additional sample mentioned by Floren & Linsenmair 1997 got lost), and seven of these were fogged again after intervals of 3–4 years. Because the latter samples do not differ from those of the primary fogs (see below), they are included in the series of primary day samples. Three samples were taken at night. Twenty-four primary day samples and all night samples were collected in the period January–May, one primary day sample in October. For some analyses the material from all fogging experiments (including 23 samples from trees re-fogged after shorter intervals; Floren & Linsenmair 1997) is used. In Germany, fogging is efficient only during

high-pressure weather periods, and in 1996, after a very cold and rainy spring, the first period suitable for canopy fogging was at the end of May. To get samples representative of the growing season, 16 trees were fogged in daytime in four periods (30 May–1 June, 16–19 July, 6–10 August, 31 August 1996; four trees in each period). The samples were taken at various times of day (06:45–14:00 h). During the period at the end of May, three additional fogging experiments were conducted in daytime and two at night. Because of the high seasonal variation in the oak forest the night fogs taken in this period can only be compared with day fogs taken at the same time (e.g., in Table 2). Ten additional day samples were collected in the period 2–4 August 1995.

Since the mean body size of Ichneumonidae possibly varies according to habitat (Townes 1958, Horstmann 1992), the thorax length of Ichneumonidae and Braconidae (sister taxon of Ichneumonidae) was measured. Because the frontal edge of the prothorax is often concealed inside the occiput and can be seen only if the head is removed, the distance between the frontal edge of the mesoscutum and the caudal edge of the propodeum was taken as a measure.

RESULTS

Abundance of some major taxa of Arthropoda and Hymenoptera. In Table 1, the numbers of individuals belonging to some major taxa of arthropods from primary day fogs in Malaysia (full data listed by Floren & Linsenmair 1997), which may act as hosts or as predators of Ichneumonidae, are compared with data from the German oak forest. If the numbers of individuals are standardized (calculated for a crown projection of 1 m² and a leaf cover of 100%; Floren & Linsenmair, in press), the average numbers of arthropods in day fog samples from both habitats are similar. The Formicidae are much more abundant, and the Coleoptera and Araneida slightly more abundant in the Malaysian rain forest than in the German oak forest. On the other hand, the Lepidoptera (mostly larvae) are much less abundant, and the Hymenoptera (in this paper always excluding ants) slightly less abundant in the rain forest. Because Hymenoptera nocturnal activity is high in the Malaysian rain forest, but low in central Europe (Table 2; see below), the standardized numbers of Hymenoptera calculated for the whole day probably do not differ much between both habitats. Because

TABLE 1. Mean numbers of individuals of some major taxa of Arthropoda from canopy fogging samples from a rain forest in Kinabalu, Malaysia (primary day fogs) and an oak forest in Steigerwald, Germany (day fogs from 1996), calculated for one fog and for a crown projection of 1 m² and a leaf cover of 100 % (n: number of fogs) (data from Floren & Linsenmair 1997 and unpublished results by Floren and by Kessler).

Taxa	Kinabalu		Steigerwald			Mean for 1996 (n=16)
	(n=25)	30-31.5. (n=4)	16-19.7. (n=4)	6-10.8. (n=4)	31.8. (n=4)	
All Arthropoda	350.8	1278.7	157.5	56.4	79.8	393.1
Araneida	19.7	9.6	3.6	2.6	5.1	5.2
Formicidae	180.1	7.3	0.7	0.4	0.6	2.2
Other Hymenoptera	8.6	22.2	15.8	5.2	9.7	13.2
Coleoptera	17.6	33.4	6.1	2.0	5.2	11.7
Lepidoptera, adults	0.6	3.8	4.9	0.7	0.2	2.4
Lepidoptera, larvae	3.8	496.5	1.9	1.0	1.7	125.3
Diptera	21.7	33.8	48.0	9.0	7.6	24.6

only one primary day fog sample is available from the Malaysian rain forest for a time of year outside the period January–May, four re-fog samples (fogged again after intervals of 7–19 months) are included in an analysis. The data from these five samples (standardized numbers of individuals per fog: 373.0 Arthropoda, 6.0 Hymenoptera, 0.31 Ichneumonidae), all collected in the period October–November, do not differ greatly from those presented in Table 2. The material is insufficient, however, to rule out a low seasonal variation. On the other hand, there is a very strong seasonal variation in numbers of individuals in the German oak forest, not only for Lepidoptera larvae, as already noted by Moeller & Lotz (1968), but also for other major taxa (Table 1). The extremely high numbers of Lepidoptera in the May samples from the oak forest originate to a large extent from larvae of the green oak tortricid (*Tortrix viridana* Linnaeus; Tortricidae), the population of which was in the final stage of an outbreak in 1996. But other Lepidoptera (Geometridae, other Tortricidae) are also more abundant in spring than in summer and autumn. The samples taken in August 1995 do not differ much from those of August 1996. The numbers of arthropods and Hymenoptera collected by canopy fogging in the oak forest are not noticeably affected by time of day (between 06:45 and 14:00 h) or by temperature (between 12 and 20° C).

About 95 % of the Hymenoptera collected in both habitats are Parasitica (Table 2). The abundance

of adult Symphyta is very low in all samples. By contrast, 63 larvae of Symphyta were collected in the oak forest in May 1996 (four samples), but none was found in all rain forest samples. The percentages of Microhymenoptera (Chalcidoidea + Cynipoidea + Proctotrupeoidea + Ceraphronoidea) are similar in both habitats, as are the percentages of Ichneumonoidea (Braconidae + Ichneumonidae). Within the Microhymenoptera, Cynipoidea are rare in Malaysia, but much more abundant in the German oak forest (for discussion see Noyes 1989). Within the Ichneumonoidea, Braconidae are more abundant and Ichneumonidae are much less abundant in Malaysia than in Germany (2 x 2 table Chi²-test, *P* < 0.001). In Malaysia, Braconidae are by a factor of 6 more abundant than Ichneumonidae, while in Germany they are by a factor of 2 less abundant. Aculeata are more abundant in Malaysia than in Germany. As was already noted for the major taxa of arthropods from Borneo (Stork 1991, Floren & Linsenmair 1997), the standardized numbers of Hymenoptera per fogging sample (see above) from the rain forest vary strongly (by a factor of 37), whereas the percentages of the major groups of Hymenoptera vary much less (Microhymenoptera 32–87 %, Braconidae 8–50 %, Ichneumonidae 0–13 %) if the five samples with the lowest numbers of individuals are excluded from the calculation. Altogether 4953 specimens of Hymenoptera (without ants) were collected by canopy fogging in the rain forest, 260 of which were Ichneumonidae.

TABLE 2. Mean numbers of individuals of Arthropoda and of some major taxa of Hymenoptera (without ants) from canopy fogging samples (day fogs and night fogs) from a rain forest in Kinabalu, Malaysia and an oak forest in Steigerwald, Germany, calculated for one fog and for a crown projection of 1 m² and a leaf cover of 100 % (n: number of fogs). For Braconidae and Ichneumonidae the mean thorax length is also indicated. The values marked with a are significantly different, so are those marked with b (Mann-Whitney U-test, $P_a < 0.02$, $P_b < 0.01$). The values marked with c or d are not significantly different.

Taxa	Kinabalu		Steigerwald		
	Day fogs (n=25)	Night fogs (n=3)	Day fogs 1996 (n=16)	Day fogs May 1996 (n=7)	Night fogs May 1996 (n=2)
All Arthropoda	350.8	426.3	393.1	1216.7	1162.5
Hymenoptera	8.6	9.3	13.2	21.5	4.1
Symphyla, adults	0.01	0.03	0.01	0.02	0
Symphyla, larvae	0	0	0.32	0.81	0.05
Microhymenoptera	(5.66)	(4.99)	(8.44)	(12.07)	(2.07)
Chalcidoidea	4.11	3.14	5.73	7.56	1.30
Cynipoidea	0.06	0.19	1.71	2.56	0.67
Proctotrupoidea	1.30	1.48	0.76	1.44	0.05
Ceraphronoidea	0.19	0.18	0.24	0.51	0.05
Ichneumonoidea	(2.51)	(3.56)	(4.34)	(8.18)	(2.02)
Braconidae	2.15	2.36	1.55	2.66	0.34
Thorax length (mm)	0.95 ^a	1.14 ^a	1.20	1.00 ^c	1.08 ^c
Ichneumonidae	0.36	1.20	2.79	5.52	1.68
Thorax length (mm)	1.38 ^b	1.92 ^b	1.67	2.10 ^d	2.23 ^d
Aculcata	0.43	0.74	0.13	0.39	0

TABLE 3. Numbers of individuals (I), numbers of species (S), and diversity (H_S after Shannon-Weaver, Williams' alpha after Fisher *et al.* 1943) of several samples of Ichneumonidae from Europe, Africa and Southeast Asia (Leicester, England, Skåne, Sweden, Kampala, Uganda, and Freetown, Sierra Leone: Owen & Owen 1974, Noyes 1989; Mellum-Memmert, Germany, and Moraira, Spain: Horstmann 1992; Steigerwald, Germany, and Kinabalu, Malaysia: this study).

Locations	Individuals (I)	Species (S)	Singletons (% of S)	Diversity (H_S)	Evenness ($H_S/\ln S$)	Diversity (alpha)
Leicester	6445	455	31	4.98	0.81	112
Skåne	10994	758	27	5.48	0.83	185
Mellum-Memmert	12198	469	27	4.30	0.70	97
Steigerwald	826	109	40	3.21	0.68	34
Moraira	3355	187	28	4.13	0.79	43
Kampala	2268	293	40	4.52	0.80	90
Freetown	1979	319	37	4.93	0.86	108
Kinabalu						
primary day fogs	127	106	90	4.53	0.97	302
all fogs	260	189	82	5.01	0.96	311

Abundance and species composition of Ichneumonidae. The Ichneumonidae from Malaysia were determined to genera and separated into morphospecies (see Appendix). The Ichneumonidae from Germany were determined to species (Horstmann *et al.*, in prep.). With a similar sampling effort about the same numbers of species were collected in Malaysia and in Germany, in spite of the very different sample size (Table 3). The relative numbers of species, the evenness and Williams' alpha (index of diversity after Fisher *et al.* 1943) are much higher in the samples from the Malaysian rain forest than in other samples of Ichneumonidae from restricted areas analyzed so far. In the canopy of the rain forest, 80-90 % of the species were taken once only, as opposed to 30-40 % in other samples. Consequently, a doubling of the sample size results in an increase of the number of species by a factor of 1.8. As is also demonstrated by the Shinozaki curves (Fig. 1; for calculation and interpretation see Floren & Linsenmair 1997), the sampling effort for Ichneumonidae in the rain forest was by no means sufficient to collect even a moderate proportion of the species present in that habitat, and the size of the local species pool cannot be estimated. Certainly it is much larger than the species pool in the German oak forest.

The subfamily Cryptinae is the most abundant subfamily both in the Malaysian rain forest and in the German oak forest (Table 4). In the rain forest, it is even more abundant at night than in daytime. Ichneumoninae and Banchinae are less, Mesochorinae and Orthocentrinae more abundant in the rain forest than in the oak forest. The subfamily compositions of samples from the canopy fogging experiments in Malaysia and Germany do not differ much in other aspects.

Many Ichneumonidae in the canopy of the Malaysian rain forest parasitize Lepidoptera (Table 5), but this host group is less important than in the German oak forest. On the other hand, parasitoids of Nematocera (all belonging to the subfamily Orthocentrinae) are much more, and parasitoids of sub-adult spiders, of Parasitica and of Coleoptera are slightly more important in the rain forest. Parasitoids of Symphyta and Brachycera (including Cyclorhapha) are lacking in the rain forest samples. The specific host group is unknown for about one third of the individuals and species from Malaysia. Most of these species belong to the subfamily Cryptinae, tribe Phygadeuontini (in particular the species-rich genus *Paraphylax* Förster), which, according to the few published host records (Gupta 1987), should

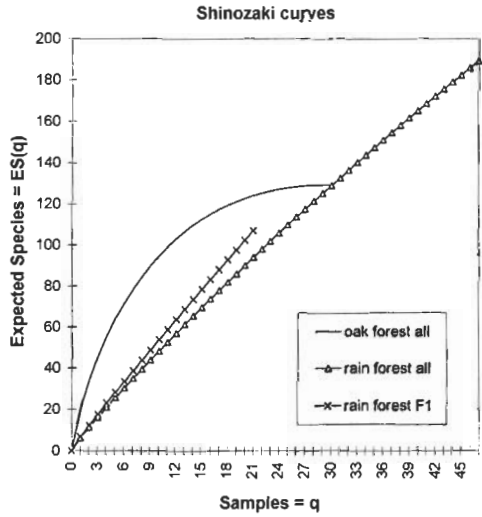


FIG. 1. Shinozaki-curves of the communities of Ichneumonidae of a German oak forest and a Malaysian lowland rain forest. The rain forest curves were calculated for all fogs, and only for the primary fogs (for details see text). ES(q) = Expected numbers of species in q discrete samples.

parasitize cocoons of other parasitoids (Braconidae and Ichneumonidae), small larval cases and cocoons of Lepidoptera, spider egg cocoons, and perhaps cocoons of Planipennia, thus enlarging the numbers of parasitoids of these hosts. A few parasitoids of Aculeata may also be hidden among those species of Cryptini for which the host group is unknown. Samples from day fogs and night fogs do not differ much (see below). In the samples from the German oak forest the most frequent species [*Gelis areator* (Panzer)] parasitizes hosts from several orders: Hymenoptera (Symphyta and Parasitica), Planipennia and Lepidoptera (Horstmann 1986), and for three rarer species the situation is similar. At the species level, the percentages of idiobionts (parasitoids which kill their hosts at or shortly after oviposition, contrary to koinobionts, which allow their hosts to grow after oviposition; Haeselbarth 1979, Askew & Shaw 1986) in the samples from the Malaysian rain forest are not substantially different from those of the German oak forest. In the oak forest samples however, the three most frequent species are idiobionts [*Gelis areator* (Panzer), *Dirophanes invisor* (Thunberg), *Itoplectis maculata* (Fabricius)], and the percentage of idiobiont individuals is higher.

TABLE 4. Subfamily composition of Ichneumonidae (%) in canopy fogging samples from a rain forest in Kinabalu, Malaysia (primary fogs only) and an oak forest in Steigerwald, Germany (16 day fogs from 1996).

Taxa	Kinabalu				Steigerwald	
	Day fogs		Night fogs		Day fogs	
	Individuals (n=127)	Species (n=106)	Individuals (n=39)	Species (n=35)	Individuals (n=826)	Species (n=109)
Pimplinae	12.6	14.2	5.1	5.7	24.0	17.4
Poemeniinae	0	0	2.6	2.9	0.5	3.7
Rhyssinae	1.6	1.9	2.6	2.9	0	0
Xoridinae	1.6	1.9	0	0	0.6	2.8
Tryphoninae	0	0	0	0	0.7	3.7
Adelognathinae	0	0	0	0	0.1	0.9
Cryptinae	29.9	27.4	51.3	51.4	45.0	29.4
Ichneumoninae	0.8	0.9	2.6	2.9	13.2	7.3
Stilbopinae	0	0	0	0	0.6	0.9
Banchinae	0	0	0	0	5.4	6.4
Ctenopelmatinae	0	0	0	0	0.1	0.9
Campopleginae	6.3	6.6	2.6	2.9	4.6	13.8
Cremastrinae	2.4	2.8	0	0	0.5	0.9
Ophioninae	0	0	2.6	2.9	0	0
Tersilochinae	3.9	4.7	0	0	0.2	1.8
Phrudinae	0.8	0.9	0	0	0	0
Mesochorinae	7.1	8.5	2.6	2.9	0	0
Anomaloninae	0	0	0	0	0.4	0.9
Orthocentrinae	27.6	25.5	25.6	22.9	1.7	8.3
Metopiinae	5.5	4.7	2.6	2.9	2.3	0.9

TABLE 5. Host groups of Ichneumonidae (%) in canopy fogging samples from a rain forest in Kinabalu, Malaysia (primary fogs only) and an oak forest in Steigerwald, Germany (16 day fogs from 1996). The percentage of idiobionts in the samples is also given.

Taxa	Kinabalu				Steigerwald	
	Day fogs		Night fogs		Day fogs	
	Individuals (n=127)	Species (n=106)	Individuals (n=39)	Species (n=35)	Individuals (n=826)	Species (n=109)
Araneida, eggs	0.8	0.9	0	0	0.4	1.8
Araneida, subadults	4.7	5.7	0	0	1.2	2.8
Hymenoptera						
Symphyta	0	0	0	0	0.7	5.5
Parasitica	7.7	8.5	2.6	2.9	0.1	0.9
Aculeata	0	0	0	0	0.2	0.9
Coleoptera	6.3	7.5	2.6	2.9	1.5	7.3
Planipennia	0	0	0	0	1.8	3.7
Raphidioptera	0	0	0	0	2.5	2.8
Lepidoptera	26.8	28.3	30.8	34.3	51.2	48.6
Diptera						
Nematocera	27.6	25.5	25.6	22.9	1.7	8.3
Brachycera	0	0	0	0	0.6	1.8
Several orders	0	0	0	0	34.7	3.7
Host group unknown	26.8	23.6	38.5	37.1	3.3	11.9
Idiobionts	42	41	64	66	81	58

Fogging experiments at night. In both areas, some fogging experiments were conducted at night. Although the material is limited, some trends can be seen. In Malaysia, the standardized numbers of individuals of Arthropoda, of Hymenoptera and of Parasitica from primary night fogs do not differ much from those of primary day fogs (Table 2). Aculeata are more abundant at night. Within the Parasitica, the numbers of Microhymenoptera are somewhat reduced at night, the numbers of Braconidae do not differ much, and the numbers of Ichneumonidae are increased (2 x 3 table Chi²-test, $P < 0.001$). Apparently three times as many individuals of Ichneumonidae are active at night as in daytime, but still the Braconidae remain more abundant than the Ichneumonidae. Large specimens of Ichneumonidae are particularly active at night, therefore the mean body size is larger than in daytime (Table 2). For Braconidae, a similar but less pronounced trend was found. The species of Ichneumonidae collected at night mostly belong to the subfamily Cryptinae (Table 5), tribes Cryptini (several genera) and Phygadeuontini (*Paraphylax* Förster), and do not differ in morphology or color from other species of these taxa collected in daytime. Only one specimen of a nocturnally active ichneumonid with an "ophionoid facies" (rather large, pale yellowish brown, with long antennae and large ocelli; Gauld & Huddleston 1976) was found in the night fogs (*Leptophion* sp.1). By contrast, several large yellow nocturnal Vespidae were collected. Similarly in Germany, the standardized numbers of Arthropoda in the night fogs do not differ from those of the day fogs, due to the high nocturnal activity of Lepidoptera larvae. But ap-

parently the numbers of all Hymenoptera and of the larger subgroups are much reduced in the night fogs (not statistically significant because of small sample numbers). Within the Parasitica, the Microhymenoptera and Braconidae are more reduced at night than the Ichneumonidae (2 x 3 table Chi²-test, $P < 0.05$). Aculeata were not collected at night. Two specimens of nocturnally active ichneumonids with an ophionoid facies were found in the night fog samples [*Perilissus albitarsis* Thomson, *Cidaphus alarius* (Gravenhorst)], but none in daytime.

Re-fogging experiments. In the Malaysian rain forest, ten trees were re-fogged after intervals of 7–19 months (Floren & Linsenmair 1997). The average numbers of arthropods in the re-fog samples are reduced, and this trend also holds true for the Hymenoptera (Table 6). However, neither difference is significant owing to the high variation in numbers of individuals. But in all cases the percentages of Microhymenoptera, which include the smallest Hymenoptera, are lower in the second than in the first sample (Wilcoxon's matched pairs signed rank test, $P < 0.01$), whereas the percentages of other Hymenoptera groups are higher in the second sample (though not significant for any of these taxa). The samples from re-fogging experiments after intervals of 3–4 years do not differ materially from those of the primary fogs (Table 6).

DISCUSSION

In this study, the numbers of individuals were calculated for standardized parts of trees, both for the Malaysian rain forest and the German oak forest.

TABLE 6. Comparison between primary fogs and re-fogs after different intervals in canopy fogging samples from a rain forest in Kinabalu, Malaysia (day fogs only).

	Primary fogs	Re-fogs after 7–19 months	Primary fogs	Re-fogs after 3–4 years
Fogged trees (n)	10	10	7	7
Arthropoda (n/fog)	4744	3034	4817	4391
Hymenoptera (n/fog)	117	53	109	112
Microhymenoptera (%)	66.8	54.5	61.8	63.8
Braconidae (%)	23.5	31.6	27.3	26.7
Ichneumonidae (%)	4.5	6.4	5.6	4.7
Aculeata (%)	5.0	6.4	4.9	4.7
Other Hymenoptera (%)	0.3	1.1	0.4	0

It has to be taken into account, however, that the canopy of the rain forest is multi-layered, whereas that of the oak forest studied here is for the greater part single-layered, and that arthropods are active throughout the year in Malaysia but only during the growing season in Germany. It is beyond the aims of the present paper to deal with these problems. It has also to be taken into account that an undisturbed natural forest is compared here with a managed forest (Floren & Linsenmair 1998). The consequences of this difference cannot be assessed, because Ichneumonidae from undisturbed deciduous forests in temperate regions are virtually unknown. In contrast to the Malaysian nights, with a darkness period of 11–12 hours and high Hymenoptera activity, darkness in central Europe is restricted to 6–8 hours in late spring and summer, and Hymenoptera nocturnal activity is low, probably as a result of lower nighttime temperatures (Gauld 1987). Apparently many specimens stay in hiding-places at night, where they are not reached by the fog cloud or from where they cannot fall down. Therefore the nocturnal activity of Hymenoptera in central Europe is of little importance, and the Ichneumonidae from the day fogs in the German oak forest have to be compared with those from both the day and night fogs in the Malaysian rain forest.

For a circular area around Bremen (northern Germany) with a radius of 40–50 km, the regional species pool of Ichneumonidae has been estimated at 1500–2000 species (Horstmann 1988). In the area around the Steigerwald, it should be of the same magnitude. The number of species in the canopy of the oaks studied may be approximately 200. On the other hand, Hilpert (1989) estimated the number of species of Ichneumonidae in the soil and leaf litter of a deciduous forest in southern Germany at about 350. Therefore the number of species in the total oak forest (including soil, leaf litter, low vegetation, bushes and trees of other deciduous species, gaps and clearings, edges of tracks and roads) may range somewhere between 500 and 1000. The regional species pool of Ichneumonidae in the Kinabalu National Park should be much larger. For the canopy fauna of Oriental lowland rain forests at least, the discussion about the supposed low species richness of Ichneumonidae in the tropics and its causes and consequences must be re-opened (Owen & Owen 1974; Janzen & Pond 1975; Rathcke & Price 1976; Hespeneide 1978; Janzen 1981; Askew & Shaw 1986; Gauld 1986, 1987; Noyes 1989; Askew 1990;

Gauld *et al.* 1992; Hawkins *et al.* 1992; Sime & Brower 1998). Probably the high species numbers in the rain forest canopy have escaped attention because disturbed habitats have been studied, mostly on the ground, and/or because the numbers of individuals in the samples were too small (Morrison *et al.* 1979).

So far, the ichneumonid fauna of no other habitat in the tropics has been analyzed in detail. The Ichneumonidae subfamily composition and host group composition from the canopy of the German oak forest do not differ much from those of other European habitats (Horstmann 1970, 1988, 1992; Owen *et al.* 1981), except that, as in the samples from the rain forest canopy, the parasitoids of Brachycera are sparse. Also the percentages of idiobiont individuals in samples from other European habitats are of the same magnitude as those of the rain forest, and lower than those of the oak forest: in Leicester, England 42%, on Mellum-Memmert, Germany 34%, and in Moraira, Spain 54% of the individuals are idiobionts (calculated from Owen *et al.* 1981; Horstmann 1988, 1992).

The composition of the ichneumonid fauna in the Malaysian rain forest differs somewhat from the predictions and conclusions presented by Janzen (1981), Gauld (1986, 1987, 1991, 1997) and Gaston & Gauld (1993). Indeed the mostly idiobiont Ichneumoninae, and the koinobiont Tryphoninae, Banchinae, Ctenopelmatinae, and Anomaloniinae are poorly represented or lacking, whereas the idiobiont Cryptinae are species-rich. But the mostly idiobiont Pimplinae and the koinobiont and nocturnal Ophiioninae are not exceptionally species-rich, while the koinobiont Campopleginae are rather well represented. The species richness of Orthocentrinae (parasitoids of Nematocera) and the absence of Diplazontinae (parasitoids of Syrphidae, almost entirely Syrphinae) have not been discussed before. Diplazontinae may be lacking because Aphididae, the prey species of many Syrphinae, are rare in the tropics (Price 1991). Townes (1958) and Gauld (1986, 1987) have predicted a high Ichneumonidae nocturnal activity in the tropics, and this is confirmed by the data presented here. But it is not characteristicly nocturnal ichneumonids with an ophiionid facies that are common at night, but rather species of Cryptinae, which do not differ in appearance from diurnally active species. Because most species have been collected only once it cannot be proven whether the species collected at night are also diurnally active.

It is unlikely that ichneumonids searching in daytime for hosts in the soil or leaf litter are fogged at night from roosting positions in the canopy because the number of characteristic soil ichneumonids with stout antennae and legs is not higher in the night fog samples, and because obviously resting ichneumonids stay in hiding-places, from where they are not easily collected by canopy fogging (e.g., ichneumonids with an ophioid facies in daytime, or European canopy ichneumonids at night; see above). Perhaps the relative numbers of ichneumonids with an ophioid facies in the tropics have been overestimated because they are attracted by light and can readily be collected in light traps, whereas no equally effective collecting method is known for other Ichneumonidae species groups. In general, the predictions of Gauld (1987) that diurnal koinobionts are less abundant and that nocturnal koinobionts and diurnal idiobionts are more abundant in the tropics than in temperate regions are not supported by the present study. Koinobionts (particularly Campopleginae, Cremastinae, Tersilochinae, Mesochorinae, Orthocentrinae, and Metopiinae) are rather common in the Malaysian rain forest canopy, characteristically nocturnal koinobionts are rare, and idiobionts (most Pimplinae, all Cryptinae) are not more common (in relative numbers) than in temperate regions, and are active in daytime and at night.

Rathcke & Price (1976) argued that a high predation pressure might be responsible for the low abundance of Ichneumonidae in the tropics. Ants especially are much more abundant and species-rich in the rain forest studied here than in any forest in temperate zones (Floren & Linsenmair 1997), and spiders are also common. But the influence of ants and other predators (spiders, tree frogs, lizards, birds, bats) on parasitoids is not well understood. There is some evidence that these predators reduce the abundance of exophytic larvae of important host groups, such as Coleoptera and Lepidoptera (Stork 1991; Floren & Linsenmair 1997, 1998). Predation does not reduce the species richness of these groups, however, and obviously does not reduce the species richness of their parasitoids either [as Stork (1988) and Askew (1990) have also demonstrated for Chalcidoidea]. The relatively low abundance of parasitoids of Lepidoptera may be partly caused by this indirect influence. Whereas adult Symphyta are very rare in the canopy of both the rain forest and the oak forest, Symphyta larvae are rather common in the latter, but

lacking in the former, and parasitoids of Symphyta are also lacking in the rain forest. Usually the low abundance of parasitoids of Symphyta in the tropics is explained by the rarity of their hosts (Gauld 1986, 1987; Noyes 1989). Predation may further reduce accessible hosts because many Ichneumonidae parasitizing Symphyta (most Tryphoninae, most Ctenopelmatinae) depend on oviposition on or into exophytic larvae. Many of the above-mentioned potential predators are optically orientated and nocturnal activity should reduce predation. Indeed the Ichneumonidae are more active at night than in daytime. However, predominantly large specimens of Hymenoptera increase their nocturnal activity. This can be demonstrated for taxa with a comparatively high mean body size, Ichneumonidae and Aculeata as a whole, and also for larger specimens within the Ichneumonidae and Braconidae. Diurnal predation should therefore be directed mainly towards large prey specimens, which would exclude ants and spiders as efficient predators because both are very variable in size and will prey on all size classes of Hymenoptera, whereas predatory Vertebrata will endanger mainly large specimens. Apparently, nocturnal predators (e.g., bats) are of minor importance for large Hymenoptera. Townes (1958) argued that the danger of desiccation may be the reason for nocturnal activity in ichneumonids. This hypothesis might be correct for dry habitats but not for the situation studied here, because desiccation should endanger small specimens more (see below). Finally, every hypothesis explaining the low abundance of Ichneumonidae in the canopy of tropical rain forests must take into consideration the high abundance of Braconidae.

Competition between Braconidae and Ichneumonidae may therefore be an additional factor. Braconidae and Ichneumonidae are rather similar ecologically, and between them there is a considerable host-group overlap. As far as is known, Braconidae are less abundant in the canopy of temperate forests (Martin 1966, Wolf *et al.* 1968), but more abundant in the canopy of subtropical and tropical rain forests (Noyes 1989, Basset 1991, Stork 1991, Guilbert 1997). Possibly Braconidae species are better competitors in the tropics, but poorer competitors in temperate regions. One factor explaining this pattern might be the smaller mean body size of Braconidae (see Table 2), for the following reasons: (1) If the high predation pressure in the tropics is directed mainly towards large specimens, Braconidae should be fa-

vored. (2) In the climatically rather uniform rain forest studied here, species with short generation times might have an advantage, and among the smaller Braconidae there might be a higher percentage of polyvoltine species than among the larger Ichneumonidae (Gaston 1988). High predation pressure against parasitized host stages might reinforce this tendency (Rathcke & Price 1976, Morrison *et al.* 1979). (3) Gregarious parasitism, which occurs frequently in the Braconidae but is rare in the Ichneumonidae (Gauld & Bolton 1988), might enable species with small specimens to utilize large but rare hosts more efficiently. (4) Because the ratio of evaporation surface to water reserve is higher, small specimens should suffer more from desiccation in dry habitats than large ones (Townes 1958, Horstmann 1992). This factor might favor the Ichneumonidae in highly seasonal and/or semi-arid regions, but not in humid habitats with low seasonal variation. More material, in particular from semi-arid tropical regions, is necessary to test these hypotheses.

As the re-fogging experiments have shown, the re-colonization of fogged trees by some predominantly small Hymenoptera remains incomplete after periods of 7–19 months. These results would agree with studies from central Europe demonstrating that Chalcidoidea colonize slowly (Kruess & Tscharrtker 1994), whereas Ichneumonidae are good colonizers (Horstmann 1970, 1988). But the possibility cannot be ruled out that the re-colonization of the trees by some hosts is still not complete after one year. In any case, the recovery time of a part of the arthropod fauna is longer than was previously assumed (Stork & Hammond 1997).

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REFERENCES

- Askew, R.R. 1990. Species diversity of hymenopteran taxa in Sulawesi. Pp. 255–260 in Knight, W.J., & J.D. Holloway (eds.). *Insects and the rain forest of South East Asia* (Wallacea). London.
- Askew, A.A., & M.R. Shaw. 1986. Parasitoid communities: their size, structure and development. Pp. 225–264 in Waage, J., & D. Greathead (eds.). *Insect parasitoids*. London.
- Ashton, P.S. 1989. Species richness in tropical forests. Pp. 239–251 in Holm-Nielsen, L.B., & B. Lauritz (eds.). *Tropical forests*. London.
- Basset, Y. 1991. The taxonomic composition of the arthropod fauna associated with an Australian rainforest tree. *Austr. J. Zool.* 39: 171–190.
- Erwin, T.L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* 36: 74–75.
- Erwin, T.L. 1988. The tropical forest canopy: the heart of biotic diversity. Pp. 123–129 in Wilson, E.O., & F.M. Peter (eds.). *Biodiversity*. Washington, D.C.
- Fisher, R.A., Steven Corbet, A., & C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12: 42–58.
- Floren, A., & K.E. Linsenmair. 1997. Diversity and recolonisation dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, Malaysia with special reference to Formicidae. Pp. 344–381 in Stork, N.E., Adis, J., & R.K. Didham (eds.). *Canopy arthropods*. London.
- Floren, A., & K.E. Linsenmair. 1998. Non-equilibrium communities of Coleoptera on trees in a lowland rain forest of Borneo. *Ecotropica* 4: 55–67.
- Floren, A., & K.E. Linsenmair. In press. Diversity and recolonisation of arboreal Formicidae and Coleoptera in a lowland rain forest in Sabah, Malaysia. *Selbyana*.
- Gaston, K.J. 1988. The intrinsic rates of increase of insects of different sizes. *Ecol. Entomol.* 14: 399–409.
- Gaston, K.J., & I.D. Gauld. 1993. How many species of pimplines (Hymenoptera: Ichneumonidae) are there in Costa Rica? *J. Trop. Ecol.* 9: 491–499.
- Gauld, I.D. 1986. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecol. Entomol.* 11: 155–161.
- Gauld, I.D. 1987. Some factors affecting the composition of tropical ichneumonid faunas. *Biol. J. Linn. Soc.* 30: 299–312.
- Gauld, I.D. 1991. The Ichneumonidae of Costa Rica, 1. *Mem. Am. Entomol. Inst.* 47: 1–589.
- Gauld, I.D. 1997. The Ichneumonidae of Costa Rica, 2. *Mem. Am. Entomol. Inst.* 57: 1–485.
- Gauld, I.D., & B. Bolton. 1988. *The Hymenoptera*. Oxford.

- Gauld, I.D., Gaston, K.J., & D.H. Janzen. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* 65: 353–357.
- Gauld, I.D., & T. Huddleston. 1976. The nocturnal Ichneumonidae of the British Isles, including a key to genera. *Entomol. Gaz.* 27: 35–49.
- Guilbert, E. 1997. Arthropod biodiversity in the canopy of New Caledonian forests. Pp. 265–277 in Stork, N.E., Adis, J., & R.K. Didham (eds.). *Canopy arthropods*. London.
- Gupta, V.K. 1987. The Ichneumonidae of the Indo-Australian area (Hymenoptera). *Mem. Am. Entomol. Inst.* 41: 1–1210.
- Haeselbarth, E. 1979. Zur Parasitierung der Puppen von Forleule [*Panolis flammea* (Schiff.)], Kiefernspanner [*Bupalus piniarius* (L.)] und Heidelbeerspanner [*Boarmia bistortata* (Goeze)] in bayerischen Kiefern-wäldern. Teil I und II. *Z. ang. Entomol.* 87: 186–202, 311–322.
- Hawkins, B.A., Shaw, M.R., & R.R. Askew. 1992. Relations among assemblage size, host specialisation, and climatic variability in North American parasitoid communities. *Am. Nat.* 139: 58–79.
- Hespenheide, H.A. 1978. Are there fewer parasitoids in the tropics? *Am. Nat.* 113: 766–769.
- Hilpert, H. 1989. Zur Hautflüglerfauna eines südbadischen Eichen-Hainbuchenmischwaldes. *Spixiana* 12: 57–90.
- Horstmann, K. 1970. Ökologische Untersuchungen über die Ichneumonidae (Hymenoptera) der Nordseeküste Schleswig-Holsteins. *Oecologia* 4: 29–73.
- Horstmann, K. 1986. Die westpaläarktischen Arten der Gattung *Gelis* Thunberg, 1827, mit macropteren oder brachypteren Weibchen (Hymenoptera, Ichneumonidae). *Entomofauna* 7: 389–424.
- Horstmann, K. 1988. Die Schlupfwespenfauna der Nordsee-Inseln Mellum und Memmert (Hymenoptera, Ichneumonidae). *Drosera* 1988: 183–206.
- Horstmann, K. 1992. Zur Zusammensetzung und Phänologie der Ichneumoniden-Zönose eines mediterranen Habitats in Südost-Spanien (Hymenoptera). *Zool. Beitr.* 34: 157–166.
- Janzen, D.H. 1981. The peak in North American ichneumonid species richness lies between 38° and 42°N. *Ecol. Monogr.* 62: 532–537.
- Janzen, D.H., & C.M. Pond. 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England and Costa Rica. *Trans. R. Entomol. Soc. London* 127: 33–50.
- Kennedy, C.E.J., & T.R.E. Southwood. 1984. The number of species of insects associated with British trees: a re-analysis. *J. Anim. Ecol.* 53: 455–478.
- Kitayama, K. 1992. An altitudinal transect of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102: 149–171.
- Kruess, A., & T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. *Science* 264: 1581–1584.
- Linsenmair, K.E. 1990. Tropische Biodiversität: Befunde und offene Probleme. *Verh. Dr. Zool. Ges.* 83: 245–261.
- Martin, J.L. 1966. The insect ecology of red pine plantations in central Ontario. IV. The crown fauna. *Can. Entomol.* 98: 10–27.
- Moeller, J., & G. Lotz. 1968. Vergleichende Untersuchungen an der Kronenfauna der Eichen in Latenz- und Gradationsgebieten des Eichenwicklers (*Tortrix viridana* L.). I. Die Lepidopteren. *Z. ang. Entomol.* 61: 282–297.
- Morrison, G., Auerbach, M., & E.D. McCoy. 1979. Anomalous diversity of tropical parasitoids: a general phenomenon? *Am. Nat.* 114: 303–307.
- Myers, N. 1988. Threatened biotas: "Hot Spots" in tropical forests. *Environmentalist* 8: 187–208.
- Noyes, J.S. 1989. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecol. Entomol.* 14: 197–207.
- Owen, D.F., & J. Owen. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* 249: 583–584.
- Owen, J., Townes, H., & M. Townes. 1981. Species diversity of Ichneumonidae and Serphidae (Hymenoptera) in an English suburban garden. *Biol. J. Linn. Soc.* 16: 315–336.
- Price, P.W. 1991. Patterns in communities along latitudinal gradients. Pp. 51–69 in Price, P.W., Lewinsohn, T.M., Wilson Fernandes, G., & W.W. Benson (eds.). *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. New York.
- Rathcke, B.J., & P.W. Price. 1976. Anomalous diversity of tropical ichneumonid parasitoids: a predation hypothesis. *Am. Nat.* 110: 889–893.
- Sime, K.R., & A.V.Z. Brower. 1998. Explaining the latitudinal anomaly in ichneumonid species richness: evidence from butterflies. *J. Anim. Ecol.* 67: 387–399.
- Southwood, T.R.E. 1961. The number of species of insects associated with various trees. *J. Anim. Ecol.* 30: 1–8.
- Southwood, T.R.E., Moran, V.C., & C.E.J. Kennedy. 1982a. The richness, abundance and biomass of the arthropod communities on trees. *J. Anim. Ecol.* 51: 635–649.
- Southwood, T.R.E., Moran, V.C., & C.E.J. Kennedy. 1982b. The assessment of arboreal insect fauna: comparisons of knockdown sampling and faunal lists. *Ecol. Entomol.* 7: 331–340.
- Stork, N.E. 1988. Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc.* 35: 321–337.
- Stork, N.E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *J. Trop. Ecol.* 7: 161–180.
- Stork, N.E. 1993. How many species are there? *Biodiversity and Conservation* 2: 215–232.

- Stork, N.E., & P.M. Hammond. 1997. Sampling arthropods from tree-crowns by fogging with knockdown insecticides: lessons from studies of oak tree beetle assemblages in Richmond Park (UK). Pp. 3–26 in Stork, N.E., Adis, J., & R.K. Didham (eds.). *Canopy arthropods*. London.
- Townes, H. 1958. Some biological characteristics of the Ichneumonidae (Hymenoptera) in relation to biological control. *J. Econ. Entomol.* 51: 650–652.
- Wolf, F., Gaspar, C., & C. Verstraeten. 1968. Recherches sur l'écosystème forêt. Série C. La chênaie à Galeobdolon et à Oxalis de Mesnil-Église (Féage). Contribution n° 7. Hyménoptères récoltés dans des bacs d'eau. *Bull. Rech. agr. Gembloux* 3: 566–579.

APPENDIX. Ichneumonidae from the Kinabalu National Park in Sabah, Malaysia

The Ichneumonidae from all canopy fogging samples from the Malaysian rain forest are listed here, sorted to subfamilies, tribes, genera and species, with the numbers of specimens per species given in brackets. The figures differ somewhat from those indicated in Table 4, because in the latter only primary fogs are dealt with.

Pimplinae Ephialtini: *Acropimpla* sp.1–2 (1; 1), *Clistopyga* sp.1 (1), *Gregopimpla* sp.1 (1); Polysphinctini: *Zatyptota* sp.1–8 (1; 1; 1; 2; 1; 1; 1; 1), *Zatyptota* sp.9 (1); Pimplini: *Theronia* sp.1 (1), *Xanthopimpla* sp.1–8 (1; 1; 1; 1; 1; 1; 2; 1).

Poemeniinae: *Cnastis* sp.1 (1).

Rhyssinae: *Sychnostigma* sp.1–2 (1; 1), *Sychnostigma* sp.3 (1).

Xoridinae: *Xorides* sp.1–4 (1; 1; 1; 1).

Tryphoninae Phytodietini: *Phytodietus* sp.1 (1).

Brachycyrtinae: *Brachycyrtus* sp.1 (1).

Cryptinae Phygadeuontini: *Benthya* sp.1 (1), *Caenopimpla* sp.1 (1), *Chivotica* sp.1–3 (2; 1; 1), *Chivotica* sp.4 (2), *Gnotus* sp.1 (4), *Handaovia* sp.1 (1), *Liniella* sp.1 (1), *Nipponaetes* sp.1–2 (2; 1), *Orthizema* sp.1 (1), *Palpostilpnus* sp.1–5 (3; 3; 1; 1; 1), *Paraphylax* sp.1–17 (2; 2; 1; 1; 1; 1; 2; 1; 11; 1; 1; 1; 1; 1; 2; 2), *Paraphylax* sp.18 (2), *Stibentes* sp.1 (1), *Xenolytus* sp.1 (1); Cryptini: *Arhytis* sp.1 (1), *Atelete* sp.1–2 (1; 1), *Buodius* sp.1 (1), *Dagathia* sp.1 (1), *Euchalinus* sp.1 (1), *Goryphus* sp.1–6 (1; 1; 1; 1; 1; 1), *Gotra* sp.1–2 (1; 1), *Listrognathus* sp.1 (1), *Torbda* sp.1 (1), *Xoridescopus* sp.1–3 (1; 1; 1).

Ichneumoninae Alomyini: *Diadromus* sp.1 (1), *Oronotus* sp.1 (1); Listrodromini: *Listrodromus* sp.1 (1); Oedicephalini: *Imeria* sp.1 (1); Heresiarchini: *Coelichneumon* sp.1 (1).

Campopleginae: *Campoplex* sp.1–2 (1; 1), *Casinaria* sp.1 (1), *Charops* sp.1–2 (1; 1), *Chriodes* sp.1 (1), *Enytus* sp.1 (1), *Hyposoter* sp.1–2 (2; 1), *Melalophacharops* sp.1 (1), *Phaedroctonus* sp.1 (1), *Xanthocampoplex* sp.1 (1).

Cremastrinae: *Pristomerus* sp.1–3 (1; 1; 1), *Temelucha* sp.1 (1).

Ophioninae: *Leptophion* sp.1 (1).

Tersilochinae: *Allophrys* sp.1 (1), *Diaparsis* sp.1–3 (1; 1; 1), *Phrudis* sp.1–2 (1; 1), *Probles* sp.1 (1).

Phrudinae: *Phrudus* sp.1 (1).

Mesochorinae: *Mesochorus* sp.1–10 (4; 2; 1; 2; 1; 1; 1; 1; 4).

Orthocentrinae: *Aperileptus* sp.1 (1), *Eusterinx* sp.1 (1), *Megastylus* sp.1–3 (1; 1; 1), *Neurateles* sp.1 (1), *Orthocentrus* sp.1–19 (1; 1; 2; 1; 9; 1; 1; 1; 1; 1; 1; 1; 1; 1; 2; 1), *Plectiscus* sp.1–22 (1; 1; 1; 1; 1; 3; 1; 1; 14; 2; 1; 1; 2; 1; 1; 2; 1; 1; 1; 1; 1), *Proclitus* sp.1 (2), *Stenomacrus* sp.1 (1), *Symplecis* sp.1 (1), *Symplecis* sp.2 (1).

Metopiinae: *Drepanoctonus* sp.1 (1), *Exochus* sp.1 (1), *Hysicera* sp.1–6 (2; 2; 2; 1; 1; 2), *Hysicera* sp.7 (1), *Trieces* sp.1 (1).