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Early stages and feeding ecology of loopers (Lepidoptera: Geometridae) in
a south Ecuadorian montane rainforest.

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Early stages and feeding ecology of loopers (Lepidoptera: Geometridae) in a south Ecuadorian montane rainforest

Abstract

During four months of field surveys at the Reserva Biológica San Francisco in the south Ecuadorian Andes, caterpillars of 64 Geometridae species were collected in a montane rainforest between 1800 and 2800m altitude and reared to adulthood. The resulting data on host plant affiliations of these species is listed and compared with published literature records on species and genus level. Data on larval and pupal morphology is presented, together with data on rearing success and on the proportion of parasitoid infestation. Characteristic features of larval morphology and behaviour are described. For 56 species these are the first records ever to be assembled of their early stages, and for another 5 species the data significantly extend known host plant ranges. Most larvae were collected on woody plants (64% of species). The most important host plant families were Melastomataceae (12 species recorded) followed by Asteraceae and Piperaceae (eight species each), and Dennstaedtiaceae (seven species). Unusual host plant affiliations recorded during this study were a quite high number of seven (11%) fern feeding species (mainly on Dennstaedtiaceae) and 3 (5%) lichen feeding species. The genus *Eois* was confirmed as being bound to larval host plants in the genus *Piper*. Overall, 17% of all larvae (and 34% if only considering those that were reared until the emergence of an adult moth or a parasitoid) died as a consequence of parasitoid infestation, mostly by braconid wasps (41%) and tachinid flies (20%), but also by representatives of the hymenopterous families Ichneumonidae, Chalcididae and Eulophidae. Solitary parasitoids were far more prevalent than gregarious ones. Four geometrid species (6%) were proven to be polyphagous as larvae, for another five (8%) circumstantial evidence suggests that these are also polyphagous, and only six species (9%) are good candidates for true (local) monophagy. As many as 35 species (55%) were only recorded in single individuals. Host plant data from this study in combination with records from literature and internet databases cover now 9.1% of the 1266 geometrid species known from the study area, and even 10.9% of the 972 species

recorded from the elevational belt of 1800-2200m a.s.l. around the Estación Científica San Francisco. Thus, four months of survey allowed to double the available knowledge on host plant relationships in this particular insect group, relative to the study site. Colour plates depict both the preimaginal stages of 63 and adult stages of 64 species to allow for further comparison and assist with identifications.

Keywords

Andes, Geometridae, host plant affiliations, insect herbivores, larval morphology, pupal morphology, Neotropical caterpillars.

Zusammenfassung

Während eines viermonatigen Geländeaufenthaltes im Gebiet der Reserva Biológica San Francisco in den Anden Südost Ecuadors, wurden die Raupen von 64 Spannernarten (Lepidoptera, Geometridae) im Bergregenwald zwischen 1800 und 2800 m Höhe aufgesammelt und im Labor vor Ort aufgezogen. Die so erhaltenen Daten über Wirtspflanzenbeziehungen werden hier aufgelistet und mit bereits bekannten und publizierten Daten auf Art- und Familienniveau verglichen. Daten zur Larval- und Puppenmorphologie sowie zu Zuchterfolg und Parasitierungsraten werden vorgestellt. Charakteristika von Larvalmorphologie und -verhalten der einzelnen Arten werden beschrieben. Für 56 Arten handelt es sich dabei um die erstmalige Erfassung von Informationen zu den Präimaginalstadien, für fünf weitere Arten erweitern diese Daten das bekannte Futterpflanzenspektrum deutlich. Der Großteil der Raupen (64 % der Arten) wurde auf Gehölzpflanzen gefunden. Die wichtigsten Futterpflanzenfamilien waren Melastomataceae (12 Geometridenarten erfasst), gefolgt von Asteraceae und Piperaceae (jeweils acht Arten) und Dennstaedtiaceae (sieben Arten). Besonders ungewöhnlich waren dabei vor allem der hohe Anteil (11 %) an Farnfressern (sieben Arten), und drei Flechtenfressende Arten (5 % der Gesamtarten). Die starke Wirtspflanzenbindung der Gattung *Eois* an Pflanzen aus der

Gattung *Piper* konnte bestätigt werden. Insgesamt lag die beobachtete Parasitierungsrate bei 17 % aller Raupen (bzw. 34 % der Raupen, welche bis zum Schlupf eines Falters oder eines Parasitoiden überlebten). Bei den Parasitoiden handelte es sich zumeist um Wespen aus der Familie Braconidae (41 %) und Fliegen der Familie Tachinidae, außerdem auch um Wespen der Familien Ichneumonidae, Chalcididae und Eulophidae. Es handelte sich dabei fast ausschließlich solitäre Parasitoiden. Für vier Geometridenarten (6 %) konnte der Nachweis der Polyphagie erbracht werden, bei fünf weiteren (8 %) kann Polyphagie als sehr wahrscheinlich angenommen werden, wohingegen nur sechs Arten (9%) als gute Kandidaten für echte (lokale) Monophagie festgestellt werden konnten. 35 Arten (55 %) wurden nur in je einem einzigen Individuum gefunden. Insgesamt decken die Wirtspflanzendaten aus dieser Studie zusammen mit verfügbaren Literaturdaten gegenwärtig 9,1 % der 1266 aus dem Untersuchungsgebiet bekannten Geometridenarten, und sogar 10,9 % der 972 Arten der unteren Höhenstufe von 1800 bis 2100 m um die Estación Científica San Francisco ab. Folglich konnte innerhalb einer viermonatigen Untersuchung das verfügbare Wissen über die Wirtspflanzenbeziehungen der hier behandelten Nachtfalterfamilie für das Untersuchungsgebiet verdoppelt werden. Farbtafeln im Anhang zeigen sowohl die Präimaginalstadien von 63, als auch die Imaginalstadien von 64 Arten um die langfristige Vergleichbarkeit der Daten zu gewährleisten und als Hilfsmittel für Artbestimmungen zu dienen.

Introduction

Herbivorous insects play an important role as primary consumers of plant biomass in terrestrial ecosystems, while also comprising a major fraction of animal biodiversity on earth (FIEDLER 1998, MEYHEW 2001, NOVOTNY et al. 2004). The diversity of herbivorous arthropods has been in the centre of the debate about the magnitude of global animal species richness. While all available estimates agree that true species richness is far higher than are described species numbers, there is substantial controversy about the extent to which estimates diverge from each other. Host plant specificity of herbivorous insects is a particularly critical element of all these estimates (ERWIN 1982, ØDEGAARD 2000, NOVOTNY et al. 2002). While traditionally scientists agreed that host specificity were far higher in tropical rather than temperate zone ecosystems (e.g. BASSET 1994), studies from the last

decade suggest that this is not generally valid (FIEDLER 1998, NOVOTNY & BASSET 2005, NOVOTNY et al. 2006). Thus, basic information on host plant relationships of tropical herbivorous arthropods are crucial for a better understanding of fundamental processes and parameters of ecosystems and community ecology, including the topic of plant-insect co-evolution (SCRIBER 2002, NOVOTNY & BASSET 2005). Moreover, the importance of herbivorous insects for ecosystem function increases where only few, if any, of the large mammalian herbivores occur that visibly dominate most parts of the Holarctic and Palaeotropical regions. Such is the case in Neotropical rain forests (CRISTOFFER & PERES 2003) where larger vertebrate herbivores are virtually absent and insects such as leaf-cutter ants at lower elevations, or beetles and caterpillars at higher altitudes, become the most prevalent consumers of living leaf biomass.

Despite the scientific importance and manifold applicability of basic host plant information, actual data on these interactions from tropical regions is still very limited (BREHM 2002, NOVOTNY et al. 2004). Even though, during the last two decades, research projects in some tropical countries, notably JANZEN & HALLWACHS (2007) in Costa Rica and NOVOTNY et al. (2007) in Papua New Guinea, started to accumulate large amounts of such data, these still remain 'few and far between' and are largely geographically limited to the specific countries or regions of the project sites. The paucity and sporadic nature of comprehensive host plant lists also constrains comparisons across sites or regions, and is a major obstacle for generalizations and validations of observed patterns.

For Lepidoptera, the second most species rich group of herbivores after the Coleoptera Phytophaga, the availability of host plant data is usually strongly biased towards taxa that were of special interest to naturalists and collectors in historical times, such as most butterfly families and the larger and often more conspicuously coloured moth families Sphingidae and Saturniidae (FIEDLER 1998, BREHM 2003a). Also quite a number of records exist for economically relevant pest species (e.g. ROBINSON et al. 2007). For other, far more diverse but often less conspicuous moth taxa, like Noctuidae, Pyraloidea and Geometridae, that make up for the majority of Lepidoptera species, host plant records are generally very incomplete, and almost non-existent for most tropical localities (e.g. CORDO et al. 2004, ROBINSON et al. 2007, JANZEN & HALLWACHS 2007).

The present study concentrates on the family Geometridae, one of the three largest families of Lepidoptera worldwide, with a global total of more than 21000 described species (BREHM et al. 2005b), 6450 of whom occur in South America (SCOBLE 1999). The montane forests in the

Ecuadorian Andes were recently identified as one of the global hotspots of geometrid species diversity (BREHM et al. 2005b). In one small region alone, more than 1200 species were recorded during just six sampling campaigns in the years 1999 to 2003. The host plant relationships of these organisms, however, remain largely unknown. BREHM (2002) collated host plant records for 226 species from this family from the Neotropical region from several, mainly web-based sources, notably the large databases by JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007). Still, these records represented a mere 3.8% of the described Neotropical geometrid species. Furthermore, he added novel records for another 19 species from a single south Ecuadorian montane rain forest (BREHM 2003a), meaning that information on larval host plant affiliations was at that time available for 48 (3.8%) of the 1266 species recorded in the area. Since then, host plant records for 11 more species occurring in that specific area have been reported by DYER & GENTRY (2007) and DYER et al. (2007), improving the data set to 59 species or a proportion of 4.7%.

BREHM (2003a) also emphasized the need to further increase the breadth and quality of data to foster our understanding of the trophic interactions between moths and the vegetation they are living in. Building on his study I here set out to shed more light on the host plant affiliations of 64 species of Geometridae from the very same locality in Ecuador. As it turned out, for 56 of these species no information on the early stages had been available before.

Material and Methods

Study organisms

Focal group for this study was the species rich moth family Geometridae, that was reported by BREHM (2005b) to occur with 1266 recorded species (and an estimated total of >1450 species) in the study area. Caterpillars of this family can be easily recognized morphologically, since almost all of them lack three of the four pairs of abdominal prolegs that usually characterize Lepidopteran larvae. This causes the typical looping locomotion eponymous for the family. Only the caterpillars of very few geometrid species, e.g. the subfamily Archiearinae, are known to have all four of these proleg pairs partly developed, but with reduced functionality (e.g. MCQUILLAN 1985, SCOBLE & EDWARDS 1989, ABRAHAM et al. 2001). Misidentification therefore is only likely for caterpillars of some Noctuidae clades, which is the only other

Macrolepidoptera family known to have caterpillars with reduced number of legs in some species, often referred to as semi-loopers. Since however – at least in later stages – more than one pair of mid-abdominal prolegs become fully developed in all Noctuidae species, distinguishing between these two families at later larval stages is unproblematic. Nevertheless all doubtful cases encountered in the field were reared to adulthood to avoid the risk of overlooking representatives of the target group, resulting also in some data on early stages of Andean Noctuidae moths (F. Bodner, unpublished data).

Study area and field work

Data were collected in the Reserva Biológica San Francisco, a privately owned nature reserve adjacent to the Podocarpus National Park in southern Ecuador (province Zamorra-Chinchi). The study area is located on the eastern cordillera of the Andes and has been the target of intensive ecological research since 1997 (BECK et al. in press a). Caterpillar samples were taken in an elevational range from 1800-2800m above sea level, although most of the data was collected below 2100m altitude in the close surroundings of the Estación Científica San Francisco (3°58' S, 79°05' W), in the period from 1st February until 28th May 2006.

The Reserva Biológica San Francisco is mainly covered by near-natural montane rain forest (BECK et al. in press b, HOMEIER et al. in press). Its moth fauna has been studied intensively in the years 1999 to 2006 by light-trapping, yielding large amounts of data on moth diversity and community structure (e.g.: BREHM & FIEDLER 2003b, BREHM et al. 2003c,d, BREHM & FIEDLER 2005a, HILT et al. 2006).

Caterpillar collecting was performed by visually scanning the vegetation during day and searching with torch-lights during night. Alternatively I used the method of beating plants or branches with a stick, so that caterpillars would drop off and be caught in a turned-around umbrella placed below the plant or branch (e.g. SCHAUFF 1986, LEATHER et al. 2005). The latter method is especially useful for collecting smaller caterpillars that would easily be overlooked by the visual searching approach, but has also some disadvantages. For example, by beating one usually misses caterpillars that cling very strongly to the plant. Moreover, a rather high fraction of caterpillars becomes injured. Also the damage to the host plants may be a disadvantage, since it affects later plant identification, resampling, or food collecting.

All caterpillars sampled in the field were transferred to the laboratory and then kept in plastic boxes. These were laid out with damp paper towel to maintain high air moisture. Caterpillars were fed with the plant they had been found on until pupation. Old food plant material was replaced every 2-3 days, or earlier if necessary due to the degree of withering or consumption and to prevent fungal infections of the larvae. Pupae were kept in similar plastic boxes, which had wooden sticks or paper towel along the walls added to offer hold to the emerging moths.

Additionally, one species (*Pantherodes conglomerata*) was reared from eggs obtained from a female moth caught at light. In this case several plants were experimentally offered to find a suitable host plant. With this exception, these larvae were treated like the caterpillars obtained from natural host plants.

To each sample a unique identification code was assigned, and all observations and materials were entered into a spread-sheet database under this code for further documentation and data processing.

Documentation

For documentation of the larval stages digital photographs were taken of all larvae from different aspects on a regular basis and whenever developmental changes in appearance were observed. For means of size measurements, scaled paper was used as background for all caterpillar photographs whenever possible. Host plants were also documented with pictures and marked and labelled with yellow tape for ease and reliability of later identification. Pictures were taken at 3072 x 2048 pixel resolution with a Canon EOS 300D digital single lens reflex camera, equipped with a Sigma 105mm F2.8 EX DG macro lens and a Sigma EM-140 DG macro ring flash.

Data processing and identification

Reared moths were killed using standard cyanide jars, stored in pergamine paper insect envelopes, and later on spread according to usual practice (e.g. McMULLEN 1965). All moths were identified to species, or at least morphospecies, level by comparison with digital photographs of previously identified specimens provided by Gunnar Brehm (University of

Jena, Germany) and partly by use of literature (PIÑAS RUBIO 2005a,b,c,d). Caterpillars that failed to develop into adults were conserved in ethanol, as were pupal exuviae and any parasitoids that emerged in captivity. Moth nomenclature follows PITKIN (2002) for species of the subfamily Ennominae and SCOBLE (1999) for all remaining species. Morphospecies codes are those of BREHM (2005b: electronic supplement), except in cases where reared specimens could not be confidently assigned to the morphospecies as delimited there. For the latter species, I assigned new identification codes to assure proper reference to the material.

Hymenopteran parasitoids were identified to family level according to the keys to the Hymenoptera of Costa Rica by HANSON & GAULD (1995). One specimen was identified to family level by Martin Schwarz (Biologiezentrum Linz-Dornach, Austria).

Host plants were identified from pictures taken in the field to the best possible taxonomic level, for the most part by Jürgen Homeier (University of Göttingen, Germany) or, in some cases, with the help of the online data base Visual Plants (HOMEIER & DALITZ 2007). Plant family delimitations follow APG II (2003). Herbarium samples were not taken (with very few exceptions) for several reasons. Especially most host plant individuals in question were unsuitable because of their small size, which was barely sufficient for feeding the collected caterpillars until metamorphosis. Moreover, all but very few of the plants lacked essential identification characters like flowers or fruits, questioning their value as herbarium vouchers. Moth vouchers will be deposited at the Phyletic Museum of the Zoological Institute, University of Jena, after completion of this study.

Results and Discussion

Overview and rearing success

During the field surveys 239 samples of caterpillars of Geometridae species, making up for a total of 325 individuals, were collected. One sample thereby consisted of all caterpillars from the same location and host plant that apparently belonged to the same species.

Of these caterpillars, 105 individuals from 97 samples were successfully reared to the adult stage. Two more species from the genus *Eois* (Larentiinae), that failed to develop into adult

moths, were assigned to morphospecies known from previous light trapping campaigns by means of DNA barcoding (www.barcoding.si.edu) using the usual sequence fraction of the mitochondrial COI gene (Patrick Strutzenberger, personal communication). One additional species (*Pantherodes conglomerata*, Ennominae) was reared from eggs laid by a female moth caught at light. Since plant species accepted as food in captivity are not necessarily part of the natural host plant range, data on this species is not fully comparable. Altogether my surveys resulted in information on host plant affiliations and basic characters of caterpillar morphology for 64 species. These species comprised 45 representatives of the subfamily Ennominae, two from the subfamily Sterrhinae, and 17 species from the subfamily Larentiinae. For 56 of these total 64 species, no reports regarding previous rearings could be found in the literature or web-based data bases.

220 caterpillars (68%) died in captivity due to the emergence of parasitoids (54 individuals, 17%) or from other reasons, like infections, moulting difficulties, handling mistakes, or food refusal (166 individuals, 51%). The overall rearing success was 32% and thus surprisingly close to the 33% success rate reported by BREHM (2003a). Of the 220 caterpillars that failed to develop into adults, 81 (37%) could be reliably assigned to successfully reared species through caterpillar morphology, and five other individuals were identified through DNA barcoding.

The moth species, of which caterpillars could be obtained from the forest, were, as would be expected with such an approach, biased towards the more common species of previous studies (Fig. 1). Nevertheless, some species previously only found in very small numbers as an adult in light trap samples were also observed as larvae.

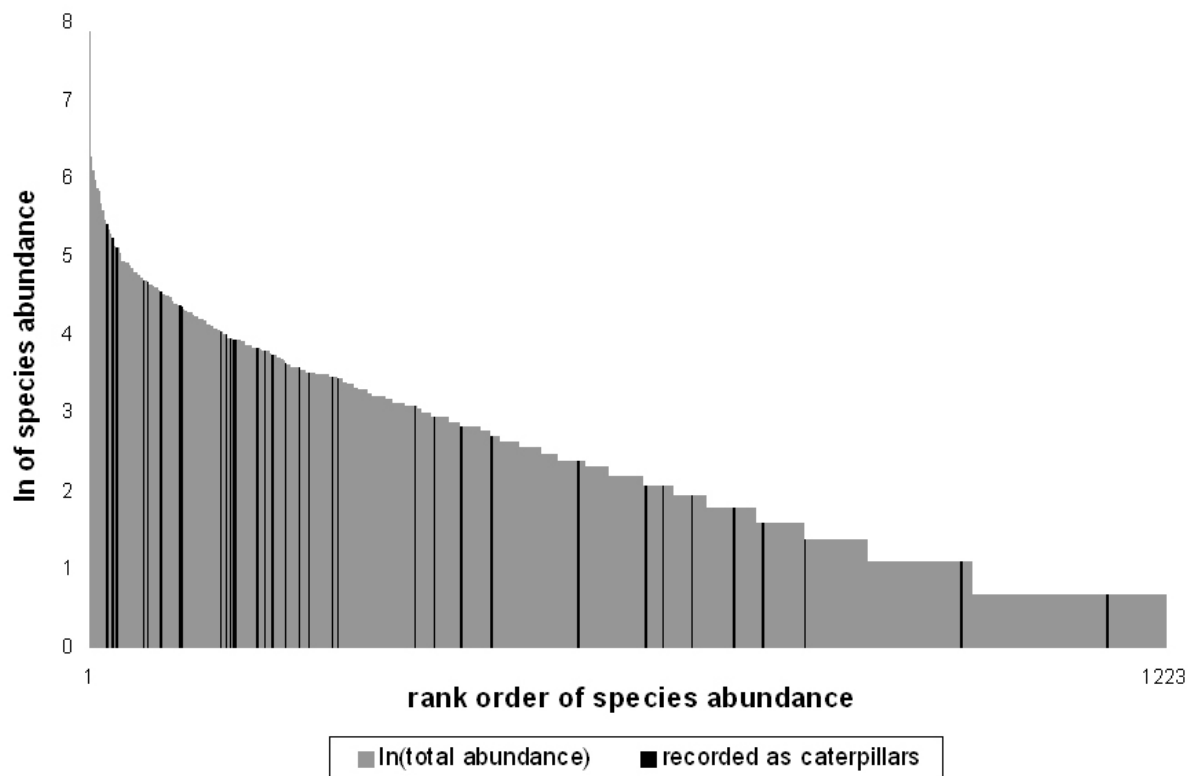


Fig. 1: Logarithmic abundance of 1223 quantitatively sampled Geometridae species from previous light-trap studies by BREHM (2002) and HILT et al. (2006). 35 identified species that were found as caterpillars in this study are marked black. Note: larvae of *Pantherodes conglomerata* (the most abundant species) were obtained by different means and thus not marked here. Neither are two diurnally active species of *Erateina*, which were only qualitatively sampled in previous studies. All reared species which have thus far not been identified precisely had to be excluded as well, since they are not comparable.

Parasitoids

From 54 (17%) of the 325 caterpillars collected, larvae or imagines of a total of 58 parasitoid wasps and flies emerged (Fig. 2). Most of these parasitoids were hymenopterans (34 specimens from 32 caterpillars), and among them the major groups were the families Braconidae (22 specimens from 22 caterpillars) and Ichneumonidae (eight specimens from eight caterpillars). From one further caterpillar hatched three individuals of a species belonging to the family Eulophidae, and from another caterpillar one specimen of the family Chalcididae. Seven hymenopteran individuals from five caterpillars failed to develop to adulthood and could not yet be assigned to any family.

In addition twelve fly larvae emerged, each from a different caterpillar. Eleven representatives of the family Tachinidae successfully developed until adult stage, the remaining one failed to develop. Another five parasitoid specimens from five caterpillars, that did not develop successfully, could not yet be reliably assigned to either Hymenoptera or Diptera.

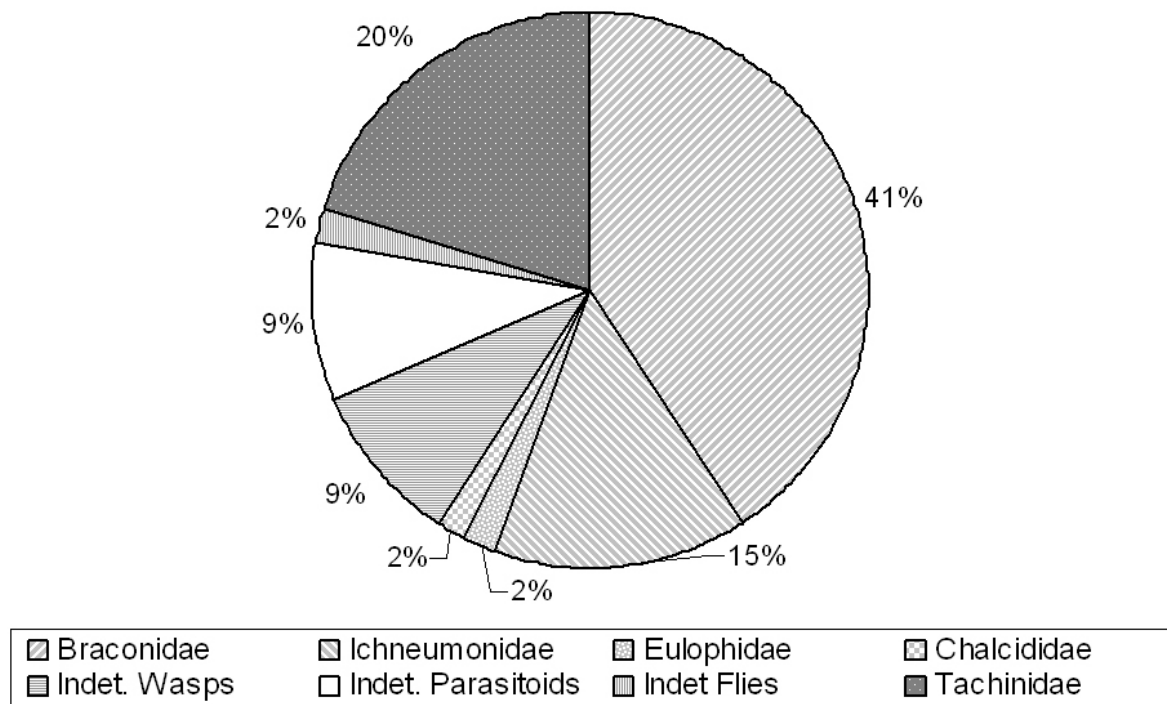


Fig. 2: Taxonomic distribution of the parasitoids that emerged from Geometridae caterpillars of this study. Parasitoids that failed to develop into adults were sorted to either ‘indet. wasps’ or ‘indet. flies’, based on general preimaginal morphology. All remaining parasitoids were listed as ‘indet. parasitoids’.

Overall, solitary parasitoids were far more prevalent than gregarious ones (52 vs. 2 attacked hosts). No incidence of multiparasitism or superparasitism was observed (see Godfray 1994 for definitions).

When only the 54 caterpillars that were verifiably parasitized and the 105 caterpillars that survived until adulthood are considered, the overall rate of parasitism among those caterpillars, where the question of parasitism can be definitely answered, rises to 34% (from 17% relative to the entire sample). Beyond those 159 caterpillars, the incidence of parasitoids remains uncertain. Some fraction of the 166 specimens that died of various, often uncertain reasons before adulthood, may well have been parasitized, but their premature death killed the parasitoids within them. Taking into account the considerable physiological stress that a parasitoid larva eating the caterpillar from within its own body presents to that caterpillar, the rate of parasitism may have been about the same or even greater as the aforementioned 34%.

These results are in some contrast to those of Brehm (2003a), who reported only six of his 101 specimen as lost to parasitism, resulting in a total parasitism degree of 6% and a degree of

15% if only these 6 and the successfully reared 33 specimen are considered. Combination of both data sets yields 14% total parasitism degree for all 426 caterpillars and 30% for 198 caterpillars that were reared to the emergence of either an adult moth or a parasitoid.

Host plants

In general, all accessible plants (i.e. the lower 2-3 m stratum of the vegetation) were searched for caterpillars, but some plant taxa received particular attention. These were mainly the genus *Piper* from the family Piperaceae, the bracken fern (genus *Pteridium*), and the family Asteraceae. The genus *Piper* was chosen to investigate the close trophic association between this plant genus and the geometrid genus *Eois* (DYER & PALMER 2004). Asteraceae and even far more so the fern genus *Pteridium* are dominant taxa in many disturbed habitats of the study area. Especially *Pteridium* presents an increasing problem for natural succession (HARTIG & BECK 2003). Therefore, both these plant groups are of high ecological interest for understanding forest regeneration in the Andes. Most caterpillar collections (197 samples, 82%) were made in succession habitats such as those covered by light-trapping campaigns for community-wide analyses of Geometridae and Arctiidae moths (HILT & FIEDLER 2005a, HILT et al. 2006). Some samples (35, 15%) also came from trails inside near-natural forest, i.e. habitats covered by the studies of BREHM et al. (2003c, d) and BREHM & FIEDLER (2003b).

The resulting data on host plant affiliations is presented in Table 1, together with information on the approximate body length of the last instar caterpillar and references to additional literature records on the preimaginal stages of the species (if such are available).

Table 1: Successfully reared Geometridae species, sorted by subfamily and genus. For every species the number of emerged adults and the number of assigned dead caterpillars (in brackets) are shown. Also information on host plants and approximate body length of the last instar larvae before entering the prepupal phase is listed. ID numbers follow BREHM et al. (2005b, electronic supplement) or are newly assigned ones (starting with ‘B’) for species not yet fully identified. References to available literature on the caterpillars or host plant affiliations are coded: GB: BREHM (2003a), J&H: JANZEN & HALLWACHS (2007), D: DYER et al. (2007), I: INBIO (2007) and R: ROBINSON et al. (2007). Species that could not yet be formally identified and therefore could not be compared with literature are marked with *. Host plant family delimitations follow APG II (2003).

Fam. / Subfam. / Genus/ Species	Host plant family	Host plant species	Length (mm)	N	ID	Lit.
Ennominae						
Azelinini						
<i>Pero maculicosta</i> WARREN, 1897	Myricaceae	<i>Myrica pubescens</i>	45	1	251	
Boarmiini						
<i>Bryoptera</i> sp. B33	Lamiaceae	<i>Hyptis</i> sp.	55	1	B33	*
<i>Glena</i> sp. B13	Tiliaceae	<i>Heliocharis americanus</i>	40	1 (1)	B13	*
	Begoniaceae	<i>Begonia parviflora</i>		1		
<i>Glena</i> sp. B24	Solanaceae	sp. indet.	30	1	B24	*
<i>Glena</i> sp. B28	Melastomataceae	sp. indet.	--	1	B28	*
<i>Iridopsis scolancala</i> PROUT, 1932	Asteraceae	<i>Agarata dendroides</i>	35	1	259	
<i>Iridopsis</i> sp. nr. <i>subnigrata</i> WARREN, 1905	Viburnaceae	<i>Viburnum obtectum</i>	40	1	256	
	Ericaceae	<i>Cavendishia</i> sp.		1		
<i>Melanolopia atigrada</i> DOGNIN, 1893	Myricaceae	<i>Myrica pubescens</i>	40	1	199	
<i>Melanolopia</i> sp. B34	Asteraceae	<i>Baccharis latifolia</i>	40	1	B34	*
<i>Melanolopia</i> sp. B35	Asteraceae	<i>Baccharis latifolia</i>	40	1	B35	*
<i>Melanolopia</i> sp. B36	Tiliaceae	<i>Heliocharis americanus</i>	40	1	B36	*
Cratoptera Group						
<i>Apiciopsis</i> sp. nr. <i>maciza</i> DOGNIN, 1896	Solanaceae	<i>Cestrum</i> sp.	35	1	B41	*
<i>Callipseustes</i> sp. B08	Urticaceae	<i>Boehmeria</i> sp.	20	2	B8	*
<i>Mychonia violacea</i> WARREN, 1907	Melastomataceae	<i>Monochaetum lineatum</i>	25	1	921	
<i>Mychonia</i> sp. B43	Asteraceae	<i>Munnozia hastifolia</i>	25	1	B43	*
Nacophorini						
<i>Cargolia arana</i> DOGNIN, 1895	Melastomataceae	<i>Tibouchina lepidota</i>	25	1	75	R
<i>Ischnopteris brehmi</i> PITKIN, 2005	Melastomataceae	<i>Tibouchina laxa</i>	45	1	308	GB
	Clethraceae	<i>Clethra revoluta</i>		2		
‘ <i>Ischnopteris</i> ’ sp. nr. <i>fasta</i> DOGNIN, 1904 ⁶	Rubiaceae	<i>Faramea</i> sp.	40	1	B27	
<i>Rucana bisecta</i> DOGNIN, 1914	Viburnaceae	<i>Viburnum obtectum</i>	35	1	660	

Nephodiini							
<i>Bonatea duciata</i> MAASSEN, 1890	Ericaceae	sp. indet	60	1	80	J&H ⁷	
<i>Bonatea viridilinea</i> WARREN, 1904	Asteraceae	<i>Erato polymnioides</i>	60	2	76	GB	
	Malvaceae	<i>Sida cf. rhombifolia</i>		1		J&H ⁷	
	Melastomataceae	<i>Monochaetum lineatum</i>		1			
	Myricaceae	<i>Myrica pubescens</i>		(1)			
<i>Nephodia admirationis</i> PROUT, 1911	Anacardiaceae	<i>Tapirira cf. guianensis</i>	40	1	1092	*	
<i>Nephodia</i> sp. nr. <i>astyochiodes</i> WARREN 1904 ⁵	Ericaceae ¹	sp. indet. ¹	35	1	299	*	
Ourapterygini							
<i>Isochromodes duplicata</i> Warren, 1904	Urticaceae	sp. indet	45	1	842		
<i>Isochromodes</i> sp. nr. <i>polvoreata</i> DOGNIN, 1893	Begoniaceae	<i>Begonia parviflora</i>	45	1	B26	*	
<i>Isochromodes</i> sp. B06	Lichen	sp. indet	25	1 (1)	B6	*	
<i>Isochromodes</i> sp. B12	Gleicheniaceae	<i>Sticherus</i> sp.	40	1	B12	*	
	Melastomataceae	sp. indet		1			
	Dennstaedtiaceae	<i>Pteridium arachnoideum</i>		1			
<i>Isochromodes</i> sp. B39	Bignoniaceae	<i>Tabebuia chrysantha</i>	40	1	B39	*	
	Clethraceae	<i>Clethra revoluta</i>		1			
	Melastomataceae	<i>Tibouchina lepidota</i>		1			
		sp. indet.		1			
	Dennstaedtiaceae	<i>Pteridium arachnoideum</i>		1			
<i>Isochromodes</i> sp. B40	Actinidiaceae	<i>Saurauia</i> sp.	40	1	B40	*	
	Piperaceae	<i>Piper</i> sp.		1			
	Onagraceae	<i>Fuchsia lehmanii</i>		1			
<i>Mesedra</i> sp. nr. <i>confinis</i> WARREN, 1904	Melastomataceae	<i>Tibouchina laxa</i>	30	1	178	*	
<i>Mesedra</i> sp. B16	Dennstaedtiaceae	<i>Pteridium arachnoideum</i>	40	1	B16	*	
<i>Perusia praecisaria</i> HERRICH-SCHÄFFER, 1855	indet., probably Verbenaceae	sp. indet.	20	1	812		
<i>Perusia</i> sp. 135	Lichen	sp. indet	25	1 (2)	135	*	
Unplaced Genera							
<i>Certima</i> sp. 97	Asteraceae	<i>Munnozia hastifolia</i>	40	1	97	*	
<i>Eustenophasma fuscata</i> WARREN, 1907	Urticaceae	<i>Boehmeria</i> sp.	--	1	2075		

<i>Microxydia colorata</i> WARREN, 1904 ⁴	Rubiaceae	<i>Faramea</i> sp.	15	1	159	
<i>Microxydia orsitaria</i> GUENÉE, 1858	Asteraceae	<i>Baccharis latifolia</i>	15	3 (2)	2045	I, R
		<i>Agaratina dendroides</i>		1		
<i>Microxydia</i> sp. B37	unknown	unknown		1	B37	*
<i>Nematocampa</i> sp. nr. <i>falsa</i> WARREN, 1906	Lichen	sp. indet	15	1	130	*
<i>Pantherodes conglomerata</i> WARREN, 1894 ²	Urticaceae	<i>Boehmeria</i> sp.	30	--	298	
<i>Phyllodonta flabellaria</i> THIERRY-MIEG, 1894	Myricaceae	<i>Myrica pubescens</i>	40	1	45	
<i>Phyllodonta semicava</i> WARREN, 1904	Melastomataceae	sp. indet.	40	1	47	
<i>Prochoerodes pilosa</i> WARREN, 1897	Ericaceae ¹	sp. indet. ¹	50	1	89	J&H ₈
<i>Sabulodes caberata oberthuri</i> RINDGE, 1978	Bignoniaceae	<i>Tabebuia chrysantha</i>	40	1	93	R ⁹
	Sapindaceae	sp. indet		1		
<i>Sabulodes</i> sp. B38	Asteraceae	<i>Baccharis genistelloides</i>	35	1 (1)	B38	*
Sterrhinae						
Cosymbiini						
<i>Cyclophora costinotata</i> WARREN, 1900	Siparunaceae	<i>Siparuna aspera</i>	20	1	1	
<i>Cyclophora viator</i> PROUT, 1920	Myricaceae	<i>Myrica pubescens</i>	25	1	845	
Larentiinae						
Erateinini						
<i>Erateina radiaria</i> HERRICH-SCHÄFFER, 1853	Melastomataceae	<i>Monochaetum lineatum</i>	20	6 (8)	1057	
<i>Erateina siliquata</i> GUENÉE, 1858	Melastomataceae	<i>Tibouchina laxa</i>	20	2	1055	
Euphyiini						
<i>Euphyia</i> sp. B07	Melastomataceae	<i>Tibouchina laxa</i>	30	1 (1)	B7	*
Eupitheciini						
<i>Eois encina</i> DOGNIN, 1899	Piperaceae	<i>Piper</i> sp.	20	4 (3)	378	
<i>Eois muscosa</i> DOGNIN, 1910 ³	Piperaceae	<i>Piper</i> sp.	--	(3)	803	
<i>Eois olivacea</i> FELDER & ROGENHOFER, 1875	Piperaceae	<i>Piper</i> sp.	15	1	416	D
<i>Eois</i> sp. nr. <i>encina</i> DOGNIN, 1899	Piperaceae	<i>Piper</i> sp.	20	8 (6)	412	*
<i>Eois</i> sp. B04	Piperaceae	<i>Piper</i> sp.	15	1 (1)	B4	*
<i>Eois</i> sp. B05	Piperaceae	<i>Piper</i> sp.	15	1 (6)	B5	*
<i>Eois</i> sp. B42 ³	Piperaceae	<i>Piper</i> sp.	--	(1)	B42	*
<i>Eupithecia sobria</i> PROUT, 1910	Ericaceae	<i>Gaultheria erecta</i>	15	4 (2)	674	
<i>Eupithecia yangana</i> DOGNIN,	Myricaceae	<i>Myrica pubescens</i>	20	1 (3)	667	GB

1899						
<i>Eupithecia</i> sp. B15	Dennstaedtiaceae	<i>Pteridium arachnoideum</i>	20	2 (14)	B15	*
<i>Eupithecia</i> sp. B17	Dennstaedtiaceae	<i>Pteridium arachnoideum</i>	15	1	B17	*
<i>Eupithecia</i> sp. B30	Dennstaedtiaceae	<i>Pteridium arachnoideum</i>	15	1 (1)	B30	*
Hydriomenini						
<i>Psaliodes inundulata</i> GUENÉE, 1858	Dennstaedtiaceae	<i>Pteridium arachnoideum</i>	10	4 (28)	488	
Larentiini						
<i>Spargania naranquilla</i> DOGNIN, 1893	indet. Clethraceae or Actinidiaceae	indet. <i>Clethra</i> sp. or <i>Saurauia</i> sp.	25	2	451	

- 1: original host plant unknown, since specimen was not found on a plant, but later accepted alternative food
- 2: species was not reared from collected caterpillars, but from eggs obtained from caught female
- 3: caterpillars failed to develop into adults and were identified through DNA barcodes by Patrick Strutzenberger
- 4: leg. Friedrich Angermüller & Alexander Hähnel
- 5: leg. Jutta Kapfer
- 6: leg. Florian Werner
- 7: reported as *Bonatea duciata*, but probably conspecific with this study's *Bonatea viridilinea*
- 8: probably not conspecific with specimen from this study
- 9: records refer to a different subspecies

Diet breadth and feeding strategies

Diet breadth must always be discussed with care, particularly in highly undersampled tropical communities (e.g. FIEDLER 1998). With consideration of undersampling and sampling biases, it is especially problematic to assign a species as monophagous, since less preferred or rare host plants might easily have been overlooked. Moreover, regional bias in available host plant data often does not allow to distinguish between local and strict monophagy (FIEDLER 1998). Pronounced polyphagy, to the contrary, is obviously rather easy to prove.

Of the 64 species addressed in this study, 35 were only found as singletons and therefore can not be subject to analysis of local diet breadth. Comparison with literature revealed host plant records for four of these species from additional locations: *Cargolia arana* has been reported from Colombia to feed on Cupressaceae and Pinaceae (both not native to the Andes) by Dognin (ROBINSON et al. 2007). *Bonatea duciata* has been reported from two different plant families by JANZEN & HALLWACHS (2007), but the voucher provided in this source strongly resembles what has been identified as *Bonatea viridilinea* in this study (Fig. 101). Also

Prochoerodes pilosa has been reported from three different plant families by JANZEN & HALLWACHS (2007) from Costa Rica, and therefore would be considered to be polyphagous. However, comparison of the adult specimen from the present study (Fig. 124) with the vouchers depicted by JANZEN & HALLWACHS lets conspecificity appear doubtful. *Eois olivacea* has been reported by DYER et al. (2007) from Ecuador from two different hostplants: *Piper baezanum*, which is probably a sister species to the host plant recorded in this study, and *Piper longifolium*. However, different caterpillar morphs constantly feeding on the same host suggest that this species might rather actually comprise of a species group (Genoveva Rodríguez & Lee Dyer, personal communication), what is also indicated by preliminary DNA barcoding results (Patrick Strutzenberger, personal communication).

Pantherodes conglomerata was not reared from collected caterpillars but from eggs laid in captivity and fed with a *Boehmeria* species, which may or may not be part of its natural host plant range. The data can therefore not be used for analysis of host plant breadth. However, *Boehmeria* species and other Urticaceae have been recorded as natural host plant for *Pantherodes* species elsewhere (DYER et al. 2007, ROBINSON et al. 2007).

Further 13 species were recorded in two to six individuals from only one plant species each, but the small numbers do not yet allow for any valid conclusions on diet breadth. *Eupithecia yangana* has been found in four individuals on *Myrica pubescens* and was reported by BREHM (2003a) from the same host plant in two more individuals, indicating at least some kind of local preference for this particular host plant. One further species (*Microxydia orsitaria*) was found in six individuals on two plant species from the same Family (Asteraceae). ROBINSON et al. (2007) list one record from Costa Rica on Leguminosae.

On the other hand, eight of the sampled Geometridae species were found to be either polyphagous or at least oligophagous on plant family level. Six species (*Glena* sp. B13, *Iridopsis* sp. nr. *subnigrata*, *Ischnopteris brehmi*, *Sabulodes caberata oberthuri*) were observed on two plant species from different families. *Ischnopteris brehmi* was recorded by BREHM (2003a) as *Ischnopteris* sp. near *chryses* in two individuals from Bignoniaceae and Grossulariaceae. *Sabulodes caberata* also occurs, with a different subspecies, in northern America and is listed by ROBINSON et al. (2007) to feed on more than two dozen plant families in the Nearctic region. No literature data could however be found for the subspecies

oberthuri addressed in this study and only one published record originates from the northernmost edge of the Neotropical realm, viz. Cuba.

Bonatea viridilinea was found on four different plant families in this study and additionally on Urticaceae by BREHM (2003a). If the specimens listed as *Bonatea duciata* by JANZEN & HALLWACHS (2007) were found to be conspecific, this would add two more plant families to the host range. In any case, *Bonatea viridilinea* appears to be very polyphagous.

Three of the *Isochromodes* species addressed here were also found to be good candidates for pronounced polyphagy. *Isochromodes* sp. B12 and sp. B40 were both recorded on three plant species from different families, and *Isochromodes* sp. B39 on five species from four families. Since none of these moths could be securely identified to species level thus far, comparison with the literature was not yet possible, however both BREHM (2003a) and JANZEN & HALLWACHS (2007) list several species from this same moth genus which collectively use a quite wide range of host plant families.

Erateina radiaria was found in 14 individuals always on *Monochaetum lineatum*, a herbaceous Melastomataceae very common in disturbed habitats of the study area. It was not found on the other common herbaceous Melastomataceae *Tibouchina laxa*, utilized by the more rarely found *Erateina siliquata*, or any other woody Melastomataceae that were searched rather intensely. Hence, this species can be considered a candidate for monophagy.

Two further species that were recorded in reasonable numbers, but only found on one host plant, were *Eupithecia* sp. B15 (16 specimens) and *Psaliodes inundulata* (32 specimens). In both cases the host plant was a bracken fern, *Pteridium arachnoideum*. The present data therefore indicate both species as candidates for (at least local) monophagy. However, the data on these species is also among the most biased in this study, since the bracken fern was sampled extensively, but other ferns – the most likely alternative host plants – were mostly omitted. Overall, fern feeding in the Geometridae is usually confined to a few specialist species or entire small clades (e.g. Ennominae: Lithinini: HOLLOWAY 1987), but occasionally polyphagous feeders of spermatophytes also accept ferns as minor hosts (HENDRIX 1980, ROBINSON et al. 2007).

One species group of particular interest for questions of monophagy and host plant specialization is the genus *Eois*. This species rich geometrid genus is reported to be strongly affiliated with plants of the Piperaceae genus *Piper* from other sites in the Neotropics (e.g. DYER & PALMER 2004). During the present study, caterpillars of probably five species of *Eois* were reared to adulthood and unsuccessfully reared caterpillars of two more species were identified with DNA barcodes. All of them were exclusively found on *Piper* plants, matching the supposed association.

For *Eois encina*, *Eois muscosa* and *Eois* sp. nr. *encina*, an exclusive one-to-one relationship between different *Eois* and *Piper* species was observed. Basically, this applied also to *Eois olivacea* and its host species, but the data on this species was yet too scarce for further consideration (see above). *Eois* sp. B04, *Eois* sp. B05 and *Eois* sp. B42 appear to feed on the same – or very similar – species of *Piper*. However, the identification of these *Piper* plants as belonging to the same species is not entirely certain, and *Eois* sp. B04 was only found in two and *Eois* sp. B42 only in one individuals and their host plant range can therefore not be addressed further. Also these three *Eois* species were partly rather similar in the appearance of the adult moths and caterpillars (see observations on morphology) and might be just variations of the same species. Altogether, the available data is still by far too scarce to allow any conclusions on real exclusiveness on either side of these affiliations. In any case the reported numbers of 102 species of *Eois* (Brehm 2005b, electronic supplement) and about 35 species of *Piper* (Benjamin Hell, unpublished data) in the study area do not speak in favour of a strict, reciprocal one-to-one affiliation between the species of these two genera.

FIEDLER (1998) defined species as monophagous on family level if they were only recorded on one plant family, oligophagous if reported from two to three plant families, and polyphagous if reported to use four or more plant families. According to these criteria, three of the 64 species addressed in this study are probably polyphagous on local and at least one further species on global level (together 6%). Four more species are at least oligophagous on local level, one further on global level (together 8%) with all of them being good candidates for true polyphagy, when considering the low numbers of records. Six species (9%) occurred in more than six individuals on only a single plant species and were therefore considered candidates for monophagous host plant specialists. The remaining 49 species (77%) either occurred in singletons or were found in too few (i.e. less than six) individuals on a single host plant family and can therefore not be subject to a meaningful analysis.

An additional noteworthy feature was the rather high number of species that use host plants or food sources that are considered unusual for Geometridae (and for macromoths in general), like ferns (e.g. HENDRIX 1980, but see LAWTON 1982) or lichens (e.g. SIGAL 1984, see also HESBACHER et al. 1995). Of the 64 species addressed in this study, for seven (11%) bracken fern was either the only (*Mesedra* sp. B16, *Eupithecia* sp. B15, *Eupithecia* sp. B17, *Eupithecia* sp. B30, *Psaliodes inundulata*) or at least one of the identified host plants (*Isochromodes* sp. B12, *Isochromodes* sp. B39). Also, *Isochromodes* sp. B12 fed additionally on an umbrella fern (genus *Sticherus*).

While HENDRIX (1980) described ferns as generally underutilized, LAWTON (1982) pointed out that in particular the bracken fern, which was also the predominant fern host plant in this study, does support a notable fauna of herbivores at least in parts of its cosmopolitan distribution. Three species (5%) were recorded and successfully reared on unidentified lichens (*Isochromodes* sp. B06, *Perusia* sp. 135, *Nematocampa* sp. nr. *falsa*). In all three cases these lichens were the only larval resources recorded thus far for the species.

In general feeding behaviour of geometrid larvae in the study region was ectophagous. Only one species (*Eupithecia sobria*) was partly endophagous in flowers and fruits of its host plant. One further species (*Sabulodes caberata oberthuri*) was noted to live inside a leaf-shelter constructed from leaves loosely spun together with silk. One species (*Eois olivacea*) was consuming only small pieces of the host plants leaf, causing a grid like feeding damage pattern (see observations on species).

Host plant spectra of geometrid genera – some general trends

In this section, host plant information on various genera (for individual species see above) covered in this study is synoptically compared with literature records (BREHM 2003a, DYER et al. 2007, DYER & GENTRY 2007, JANZEN & HALLWACHS 2007 and ROBINSON et al. 2007). The main aim of these comparisons is to assess whether characters can be derived for the nutritional ecology of the larvae on this higher taxonomic level, as is often the case in the Lepidoptera. Only sources with data on the specific genus are listed and host plant families not listed there and therefore apparently new to any moth genus are explicitly noted.

Ennominae: Azelinini

Pero: One species found on a Myricaceae, which is among the more than two dozen host plant families listed by DYER & GENTRY (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007) from the New World. Hence, *Pero* species appear to generally feed on a wide range of woody plants.

Ennominae: Boarmiini

Bryoptera: One species recorded on Lamiaceae, which is not among the nine families listed for two *Bryoptera* species by BREHM (2003a), INBIO (2007) and JANZEN & HALLWACHS (2007) from the Neotropics and therefore appears to be a new host plant family for this moderately diverse moth genus.

Glena: This genus was found on four unrelated plant families (Begoniaceae, Melastomataceae, Solanaceae and Tiliaceae). Only the Solanaceae are listed among the more than two dozen host plant families reported for this genus by INBIO (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007) for the New World, the other three are therefore apparently new to the genus. Overall, larvae of *Glena* species feed on a wide variety of (predominantly) woody plants.

Iridopsis: Three unrelated plant families (Asteraceae, Viburnaceae and Ericaceae) were recorded, all but the Viburnaceae were among the approximately three dozen plant families listed by INBIO (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007) for this genus in the New World. The Viburnaceae therefore appear to be a new record for this genus.

Melanolophia: Recorded on three unrelated plant families (Asteraceae, Myricaceae and Tiliaceae). All three were among the more than two dozen plant families listed for this genus by BREHM (2003a), INBIO (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007).

Ennominae: Cratoptera group

Apiciopsis: One species was found on Solanaceae; no literature record on host plants was found for this genus.

Callipseustes: One species was recorded on Urticaceae; no host plant record was found in the literature.

Mychonia: Two species were found on two unrelated plant families (Asteraceae and Melastomataceae); no literature records could be obtained for this genus.

Ennominae: Nacophorini

Cargolia: One species was recorded on Melastomataceae, this plant family was not among the two listed by ROBINSON et al. (2007) and therefore appears to be a new record.

Ischnopteris: Three unrelated host plant families (Clethraceae, Melastomataceae and Rubiaceae) were recorded; for Clethraceae no entry was found among the close to three dozen plant families listed by BREHM (2003a), DYER & GENTRY (2007), INBIO (2007) and JANZEN & HALLWACHS (2007). Therefore this appears to be a new host plant family for this overall rather polyphagous moth group.

Rucana: One species was found on Viburnaceae; no host plant records could be retrieved from literature.

Ennominae: Nephodiini

Bonatea: This genus was found on five unrelated plant families (Asteraceae, Ericaceae, Malvaceae, Melastomataceae and Myricaceae), only Asteraceae was covered by the four host plant families listed by BREHM (2003a), and JANZEN & HALLWACHS (2007), the other four are apparently new.

Nephodia: Two host plant families (Anacardiaceae and Ericaceae) were recognised in this study, that are not listed among the six host plant families stated by BREHM (2003a), INBIO (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007).

Ennominae: Ourapterygini

Isochromodes: Species of this genus were found to feed on nine unrelated families of vascular plants (Actinidiaceae, Begoniaceae, Bignoniaceae, Clethraceae, Dennstaedtiaceae, Gleicheniaceae, Melastomataceae, Onagraceae, Piperaceae) and also on lichens. Only the Melastomataceae are covered by the seventeen plant families listed by BREHM (2003a) and JANZEN & HALLWACHS (2007), the remaining eight vascular plant families can therefore be assumed as new records.

The newly obtained records for Dennstaedtiaceae and Gleicheniaceae appear to be the first proof for the utilization of any fern family by this moth genus, as is the new record for lichens. Both are rather unusual resources for geometrid caterpillars. Overall, *Isochromodes* is widely polyphagous as a genus with host plants records comprising many woody as well as herbaceous angiosperms.

Mesedra: This genus was found on two unrelated plant families (Dennstaedtiaceae and Melastomataceae); no records could be obtained from the literature.

Perusia: Two species were recorded on an undetermined plant family (probably Verbenaceae) and on lichen; no records were found in the literature.

Ennominae: Unplaced genera

Certima: One species was recorded from Asteraceae, which is one of the five plant families reported by BREHM (2003a) and ROBINSON et al. (2007) for this genus from the New World.

Eustenophasma: One species was found on Urticaceae; no entries could be found in the literature.

Microxydia: Two species from this genus were found on two unrelated plant families (Asteraceae and Rubiaceae). Asteraceae are one of the two plant families reported by BREHM (2003a), INBIO (2007) and ROBINSON et al. (2007), Rubiaceae appear to be new.

Nematocampa: One species was found on lichen. Literature analysis yielded about two dozen plant family entries, but none for lichen.

Pantherodes: One species of this genus was reared on Urticaceae, which is one of the three families listed by DYER et al. (2007) and ROBINSON et al. (2007) for the Neotropical region.

Phyllodonta: Two species of this genus were found on two unrelated plant families (Melastomataceae and Myricaceae). Both are not among the four host plant families reported

by INBIO (2007) and JANZEN & HALLWACHS (2007) and are therefore probably new to the genus.

Prochoerodes: One species has been reared on Ericaceae, which are among the more than two dozen plant families reported for this genus by DYER & GENTRY (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007).

Sabulodes: Two species were found on three unrelated plant families (Asteraceae, Bignoniaceae and Sapindaceae), only Sapindaceae was not among the approximately three dozen host plants listed by BREHM (2003a), INBIO (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007).

Sterrhinae: Cosymbiini

Cyclophora: Two species of this cosmopolitan genus were found on two unrelated plant families (Myricaceae and Siparunaceae). Myricaceae are one of the 16 plant families reported by DYER & GENTRY (2007), DYER et al. (2007), JANZEN & HALLWACHS (2007) and ROBINSON et al (2007). Siparunaceae might be a new record as a host plant family. Overall, *Cyclophora* larvae feed on a wide variety of woody plants.

Larentiinae: Erateinini

Erateina: Two species of this genus were found on Melastomataceae, which is also the only host plant family listed by INBIO (2007) and JANZEN & HALLWACHS (2007) for two more species of this genus. While the data is as yet very scarce, this may hint towards this moth genus having a quite strong affiliation with Melastomataceae as host plants.

Larentiinae: Euphyiini

Euphyia: One species was found on Melastomataceae, a family that is not among the 12 host plant families listed by JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007) for the new world and therefore can be assumed as new. Overall, *Euphyia* larvae feed on a wide range of host plant families, including various herbs in the northern temperate zones.

Larentiinae: Eupitheciini

Eois: Seven species of this genus were found on Piperaceae, which is the only reported host plant family in the Neotropics (DYER & GENTRY 2007, DYER et al. (2007), JANZEN & HALLWACHS 2007, ROBINSON et al. 2007). Some records from the Palaeotropics also list Euphorbiaceae (ROBINSON et al. 2007), but the relatedness of the Palaeotropical and the Neotropical members of this genus remains not fully clear (HOLLOWAY 1997).

Eupithecia: Species from this genus were found on three unrelated plant families (Ericaceae, Myricaceae and Dennstaedtiaceae). Myricaceae are among the four plant families reported from seven species of this genus from the Neotropics by BREHM (2003a) and ROBINSON (2007), the two remaining families can be assumed new for this region. Despite the large number of species in this genus (e.g. SCOBLE 1999), host plant information from the Neotropics remains very scarce, possibly due to the small size and the difficulties in identifying these mainly inconspicuously coloured moths. ROBINSON (2007) lists over 1000 entries, mainly from the Holarctic region, that account for dozens of host plant families. Although polyphagous *Eupithecia* species occasionally feed on ferns in other regions (e.g. *Eupithecia subfuscata* in Europe, see EBERT 2003), this observation may be new for the Neotropical region.

Larentiinae: Hydriomenini

Psaliodes: One species of this genus was found on bracken fern (Dennstaedtiaceae). This appears to be a new plant family for this genus. Further records of three different species by JANZEN & HALLWACHS (2007) are from two more fern families (Cyatheaceae and Lomariopsidaceae) hinting towards a possible specialization on ferns as host plants in this genus.

Larentiinae: Larentiini

Spargania: One species was recorded from an undetermined plant family (either Clethraceae or Actinidiaceae), both of which are among the five plant families listed by JANZEN & HALLWACHS (2007) and ROBINSON et al. (2007) for the New World. In the Old World, representatives of *Spargania* feed on unrelated and partly herbaceous plants in families such as Ericaceae and Onagraceae (EBERT 2003).

Can host plant affiliations of larvae explain small-scale distribution patterns of moths as revealed by light-trapping – some examples

BREHM & FIEDLER (2005a) and HILT et al. (2006) pointed out that for many geometrid species and genera in the study region in Ecuador there are major differences in their abundance between forest and succession or disturbed sites. For some of these taxa that also were addressed in this study, the newly acquired host plant information shall subsequently be used for attempting an explanation of their micro-distributional patterns.

Both afore mentioned studies noted a significant preference of *Pantherodes conglomerata* for disturbed sites, and of *Eois* spp. for forest sites. They explained this observation with the distribution of the known host plants for *Pantherodes* spp. (*Boehmeria* spp. and *Vernonia* spp.; mainly in succession sites) and *Eois* spp. (*Piper* spp.; mainly in forest sites). The newly gathered host plant information provided additional support for this interpretation. Further on BREHM & FIEDLER (2005a) explained the observed prevalence of the genus *Eupithecia* at disturbed sites with data on species of this genus feeding on host plants of disturbed sites. The additional host plant information provided by the present study again fits well into this picture, with all observed host plant species being typical for succession habitats. One further species (*Psaliodes inundulata*) was noted by BREHM & FIEDLER (2005a) to be common at succession sites, but interpretation was at that time impeded by the lack of any host plant information. The newly provided data proves this species to be feeding on bracken fern, one of the most dominant plant species at succession sites (HARTIG & BECK 2003). Hence, host plant data in this case now also provide a functional explanation of the association of the adult moths with open disturbed habitats.

The genus *Bonatea* was one of those noted by BREHM & FIEDLER (2005a) to be rather strongly associated with forest sites. This observation stands in contradiction to the host plants identified by this study and the habitats where caterpillars were found. All caterpillars of *Bonatea viridilinea* were collected in succession or disturbed sites. The species was found to be very polyphagous and most caterpillars were feeding on host plants often observed in succession sites (e.g. *Erato polymnioides* and *Monochaetum lineatum*). No explanation for

this divergence in patterns between micro-distribution of larva and adults can be given at this point.

Special observations on morphology and behaviour

In general, all observed geometrid caterpillars were cryptic in appearance, with brown, green and grey tones predominating their colouration. Some clearly resemble twigs (e.g.: *Pero maculicosta*, Fig. 3), lichens (e.g.: *Perusia* sp. 135, Fig. 38), or mossy bark (e.g. *Phyllodonta semicava*, Fig. 44) in both colouration and shape, while others seem to be only generally inconspicuously coloured to the human eye. Whether this crypsis really pertains also to relevant predators such as visually hunting birds needs further assessment (CHURCH et al. 1998). All geometrid caterpillars encountered showed the typical reduction of the abdominal prolegs to two pairs. Subsequently, I give a more detailed account of some notable observations on individual species.

The caterpillar of ***Pero maculicosta*** (Fig. 3) was elongate and of a stick-like appearance, resembling a dead, broken twig or leaf stalk quite well. Caterpillars of other *Pero* species, depicted by DYER & GENTRY (2007) and JANZEN & HALLWACHS (2007) show a moderate range of morphological variation. One specimen shown by JANZEN & HALLWACHS (2007) as *Pero* 89-SRNP-24 even possesses a fully developed third pair of prolegs and is probably misplaced in this genus. Other specimens figured by the same authors (notably *P. corata*) resemble the one from this study very closely.

The three depicted ***Glena*** species (Fig. 5-7) show very little morphological differences. *Glena* sp. B24 (Fig. 6) differs from *Glena* sp. B28 (Fig. 7) and the two specimens of *Glena* sp. B13 (Fig. 5) in having a very dark, in early stages almost black body colouration that contrasted with its red-brown head capsule and partly red-brown legs and prolegs to a varying degree in different instars. However, only four specimen of *Glena* spp. were found and only one of them was of the morphospecies sp. B24. Thus, it remains unclear whether this is a distinct character of this species, or just a part of the natural variation of all *Glena* spp. caterpillars. Pictures of *Glena* spp. by JANZEN & HALLWACHS (2007) show very similar caterpillars.

Iridopsis sp. cf. *subnigrata* was collected in two specimens that differed strongly in colouration (Fig. 9-10). Misidentification is very unlikely, since the adult specimens resemble each other very closely. Interestingly, the colouration of the caterpillars matched that of the respective host plants. One specimen (Fig. 9) was found on an Ericaceae with dark green old leaves, brightly red young leaves and green and dark brown twigs, which are quite well matched by the caterpillar's appearance. The other specimen (Fig. 10) was found on a Viburnaceae with light green to grey-green leaves and white hairs, that the caterpillar resembles with its grey-green colour and white pattern. *Iridopsis* caterpillars depicted by JANZEN & HALLWACHS (2007) are rather similar in some cases (e.g. *I. oberthuri*).

Of the four *Melanolophia* species, the three morphospecies *M.* sp. B34 (Fig. 12), *M.* sp. B35 (Fig. 13) and *M.* sp. B36 (Fig. 14) do not differ markedly in larval appearance. One rather distinct character that they share is the lateral white streak, that appears both on the head capsule and along the first three segments. The fourth species (*M. atigrada*, Fig. 11), in contrast, shows a quite different pattern: it lacks the white streak, and instead has yellow, white and brown dorsal intersegmental markings, black legs and leg bases in all but the anal proleg pair, and two black warts on the last segment. Nevertheless, the described differences in morphology and colouration are well within the limits of variation observed in other genera. The placement of *atigrada* within the genus *Melanolophia* has been marked as uncertain by SCOBLE (1999), and it was excluded from the genus by PITKIN (2002). The observations presented here do neither speak clearly in favour nor against this placement.

Callipseustes sp. B08 (Fig. 16) showed rather bright red colouration that appears quite conspicuous against the green leaves of its host plant, a *Boehmeria* species (Urticaceae), but very well matches its red twigs.

Mychonia violacea (Fig. 17) and *Mychonia* sp. B43 (Fig. 18) were found in one individual each. The caterpillars showed quite similar colouration, but differed distinctly in number and expression of dorsal protuberances. These were more numerous and more strongly developed in all observed instars of *M.* sp. B43 (Fig. 18) than in the corresponding instars of *M. violacea* (Fig. 17). The adult wing pattern and colouration of both specimens (Fig. 93 and Fig. 94) are very similar, but nevertheless show some minor differences. In conclusion it is not entirely certain if these two specimens belong to two species with very similar adults, or rather represent one species with pronounced larval variation. I therefore decided to list both specimens separately.

The caterpillar of *Cargolia arana* (Fig. 19) had a large number of small dorsal and lateral protuberances, some of which are very filigree. Together with the brown and green colouration, this resulted in a remarkably superficial resemblance to mossy bark.

The caterpillars of *Ischnopteris brehmi* (Fig. 20) had lateral bulges at the segment A2. Caterpillars of other *Ischnopteris* species shown by JANZEN & HALLWACHS (2007) are very similar in morphology and some also in colouration and pattern. *I. brehmi* caterpillars shown by BREHM (2003a) are more rich in contrast than those of this study. The pupae of *I. brehmi* (pupae not shown), '*Ischnopteris*' sp. nr. *festi* (pupa not shown) and *Rucana bisecta* (Fig. 23) had the antenna and trunk sheaths extended to a spike that reached down to about half of the free moving part of the pupal abdomen. In the fourth Nacophorini species, *Cargolia arana* (pupa not shown), the antenna and trunk sheaths extended only very slightly beyond the wing sheaths. This feature is not mentioned in RINDGE's (1983) revision of the Nacophorini or by PITKIN (2002, 2005) and may be as yet unknown. PARRA & HENRIQUEZ-RODRIGUEZ (1993) depicted the pupae of two other Nacophorini (*Mallomus falcatus* and *M. tumidus*) that lacked this feature, possibly hinting to a restriction of this character state to a smaller clade within the Nacophorini.

The two reared species of *Bonatea* (Fig. 24-26) both show an enlargement of the second thoracic segment of the caterpillar, thereby either giving the impression of a collar (e.g. Fig. 26 top), or, when the caterpillar is disturbed and pulls the head and first thoracic segment inwards, the impression of a broken twig (Fig. 26 bottom). The colouration of the *Bonatea viridilinea* caterpillars is dominated by grey or brown colours, sometimes with white markings (Fig. 25), while the only found caterpillar of *Bonatea duciata* (Fig. 24) had large whitish areas. Since only one caterpillar of the latter species has been reared, the diagnostic value of this distinction cannot yet be ascertained. Pictures of caterpillars made available by JANZEN & HALLWACHS (2007) as *Bonatea duciata* closely resemble the caterpillars of this study's *B. viridilinea*, as do the adult moths.

The caterpillar of *Nephodia admirationis* displayed a net-like pattern (Fig. 27), that was in a reduced form shared by *Nephodia* sp. nr. *astychiodes* (Fig. 29). The pupa of *N. admirationis*

(Fig. 28) also had rather bright yellow markings and a conspicuous black and yellow pattern on the wing sheaths, while the pupa of *N. sp. nr. astyochiodes* (not shown) had a similar, but less bright colouration and pattern.

Six species were found, that according to their adult morphology supposedly belonged to the genus *Isochromodes*, but partly had rather different caterpillar morphology. *Isochromodes duplicata* (Fig. 30) had two black bulges on the fifth abdominal segment of the caterpillar, that were present in all observed instars. The caterpillar appeared very thin and elongated. The caterpillar of *I. sp. nr. polvoreata* (Fig. 31) had the third thoracic leg pair elevated on an enlarged basis and a dorsal and lateral protuberance at the third abdominal segment. Together this made the caterpillar appear like a dead twig with two leaf scars. The *Isochromodes sp. B06* caterpillar (Fig. 32) matched in its colours the foliose lichen that it fed on. Additionally, the pattern made the caterpillar less conspicuous against the background of a lichen covered branch. *Isochromodes sp. B39* (Fig. 34) and *sp. B40* (Fig. 35) had caterpillars that varied in a similar range of green and brown colours with or without white and brown dorsal markings. Both the colouration and the expression of these markings seemed to change between different instars in some individuals. No clear diagnostic characters could be identified. Also rather similar to these two species were the caterpillars of *Isochromodes sp. B12* (Fig. 33), but only brown caterpillars were observed of this species and the overall impression was more elongate. In conclusion, of these six *Isochromodes* species, at least the placement of *sp. nr. polvoracea* and *sp. B06* in the same genus like the other shown species appears doubtful in consideration of caterpillar morphology.

The caterpillar of *Perusia praecisaria* (Fig. 38) had two thin elongated dorsal protuberances: a long one at the second abdominal segment, forking into two points, and a shorter one at the third abdominal segment. The caterpillar's rather bright orange colouration might be either aposematic, hinting towards this species being poisonous, or cryptic, resembling dead leaves. The caterpillar appears somewhat similar to that of *Melinodes subapicata*, depicted by BREHM (2003a). Rather different in appearance was the caterpillar of *Perusia sp. 135* (Fig. 39) that had many smaller protuberances and was coloured in grey-green with brown-orange spots, that perfectly matched the colours of the foliose lichen with its apothecia which the caterpillar fed on. With regard to these pronounced differences, the placement of these two species in the same genus may have to be reconsidered.

The *Microxydia colorata* caterpillar (Fig. 41) was of light brown colouration and had a very slim, stick-like appearance. The morphology of *Microxydia orsitaria* (Fig. 42) and *Microxydia* sp. B37 (Fig. 43), to the contrary, was rather compact in comparison and the colouration dominated by dark shades of grey. Early instars of *M. orsitaria* were black with 4 distinct white dorsal spots on the second abdominal segment (data not shown). During development, the colouration turned to dark grey with a distinct orange pattern on the first five segments, while the white spots turned yellow to a varying degree and became less conspicuous against the orange background. Early instars of *Microxydia* sp. B37 were not observed, but later instars were more lightly coloured and did neither show an orange pattern, nor distinct white or yellow markings. Instead, they displayed less conspicuous pink spots at the very same position as the white spots were in *M. orsitaria*. While the colouration of the caterpillars of *M. orsitaria* and *M. sp. B37* was somewhat distinct, the imagines (Fig. 116-118) are almost identical. Nevertheless, I choose to list them separately for the same reasons as for *Mychonia* sp. Since both the adult and the larval morphology of *M. colorata* is rather distinct from that of the other *Microxydia* species discussed here, the placement within the same genus might deserve further study using additional character sets.

The *Nematocampa* sp. nr. *falsa* (Fig. 44) caterpillar resembled its lichen host very closely in colouration and structure.

Pantherodes conglomerata caterpillars (Fig. 45) were black in all later instars, with mainly lateral white markings. Some caterpillars were observed with red-brown head capsules, legs and first proleg pair. Whether this was related to the caterpillars' instar, part of the morphological variation range or possibly only present at the beginning of any later larval stage could not be determined from the present data. *Pantherodes* spp. caterpillars shown by DYER et al. (2007) are very similar in morphology but have lighter colouration

The caterpillars of *Phyllodonta flabellaria* (Fig. 46) and *P. semicava* (Fig. 47) were both brown with green markings and green warts. Both of them seem to resemble mossy bark in colouration. While both were rather similar in general appearance, *P. semicava* had distinctly stronger developed green warts and *P. flabellaria* more green colouration, allowing for rather

clear distinction between both, provided that it turns out to be a general feature. Pictures of caterpillars of two other *Phyllodonta* species are provided by JANZEN & HALLWACHS (2007). Their *P. indeterminata* looks quite similar to this study's *P. flabellaria*.

The caterpillar of *Prochoerodes pilosa* (Fig. 48) displayed a behaviour of bending the first two segments forward and pulling them together with the third segment to form a uniform knob with the head and thoracic legs (Fig. 48 top). This made the caterpillar appear like a dead twig or leaf stalk. Caterpillars of *P. marciana* shown by JANZEN & HALLWACHS (2007) appear very similar, no caterpillar pictures are provided for those specimens identified as *P. pilosa*.

Sabulodes caberata oberthuri (Fig. 49-51) was found in two individuals. The first one (Fig. 49), which was found as an early instar, developed a rather intensive, dark colouration during development. The other caterpillar (Fig. 50) was found in its last instar and had a very pale colouration with some parts of the pattern of the first caterpillar, like the black markings on the head and most legs, completely missing. The pupae (Fig. 51) were of a pale white appearance, with only the antennal sheaths bearing colour and the eyes visible through the cuticle that seemed partly transparent. Both caterpillars preferred to hide within a leaf-tent most of the time, resulting in a rather hidden way of living, also mentioned by BREHM (2003a) for this genus. This may be the cause for the observed pale colouration of the second caterpillar, while the first caterpillar might have acquired its more dark colouration due to the enforced more open way of living in captivity. Alternatively, it might just as well be only the normal range of variation in this species or caused by differences in host plant suitability. The general pattern of a red head capsule and a dark body with white and orange stripes is also matched by the caterpillar of *S. loba* depicted by JANZEN & HALLWACHS (2007). Pictures of the subspecies of *S. caberata* occurring in northern America could not be obtained for comparison.

Two *Cyclophora* species (*C. costiotata*, Fig. 53-54 and *C. viator*, Fig. 55-56) were reared. Both of them had the anteriorly truncated pupae with a silk girdle around the segment A3 (Fig. 72 and 74) typical for all species of the genus *Cyclophora* (HAUSMANN 2004). The placement of these species within this genus, that had been indicated as preliminary by SCOBLE (1999), can therefore be assumed to be correct. Despite the diagnostic value of this

character and several specimens depicted or mentioned by DYER & GENTRY (2007), DYER et al. (2007) and JANZEN & HALLWACHS (2007), no previous comment was found on this feature of the pupae in Neotropical *Cyclophora* species.

Two species of the genus *Erateina* (Fig. 57-59) with diurnally active adult stages were reared. The caterpillars of both species were green with a white and red lateral streak of varying breadth, that sometimes was also reduced to a white line with some red spots. *Erateina siliquata* (Fig. 59) caterpillars were covered with small white dots, that gave them an almost sparkling appearance. Caterpillars of *Erateina radiaria* (Fig. 57-58) also displayed some white dots, but they appeared far less striking. The green and red colouration matched that of the host plants – herbaceous Melastomataceae with mainly red stalks – quite well. Also the white spots of *Erateina siliquata* might serve the purpose of disguising the caterpillar, since the leaves of its host plant *Tibouchina laxa* are covered with whitish hairs.

Caterpillars of probably seven different *Eois* species were found during this study (Fig. 61-70) and either reared to adulthood or identified via barcoding methods. Most *Eois* caterpillars were of some shade of green and in most cases had black, sometimes also white markings. The amount of these markings generally increased with development, but was also found to be very variable between individuals in the species *Eois encina* (Fig. 61-62) and *Eois sp. nr. encina* (Fig. 65-67), of which several specimens were successfully reared. The caterpillars of *E. muscosa* (Fig. 63) were completely black, except for the first two leg and both proleg pairs. Since the caterpillars were found only one day before parasitoid larvae emerged, the depicted appearance may have been influenced by the parasitoid and not totally resemble that of non-parasitized specimens. *Eois olivacea* (Fig. 64) had very distinct white spots, that clearly exceeded the amount of black markings. Since it was only reared once, conclusions on its variability were not possible. This species also had an interesting feeding behaviour in that it only consumed the small, upwardly bulged bits of the rough-textured leaves of its host plant, resulting in a grid-like feeding damage (visible in Fig. 64).

The caterpillar of *Eois sp. B04* (Fig. 68) displayed the largest extent of dark markings, covering most of its body. The caterpillar of *Eois sp. B05* (Fig. 69) showed almost no markings, except for some black dots and two black markings on the head. Caterpillars of *Eois sp. B42* (Fig. 70) were very similar to those of *E. sp. B05*. The adult moths of *Eois sp. B04* (Fig. 138) and *E. sp. B05* (Fig. 139) look similar to each other, while the adults of

Eois sp. B42 (Fig. 140) showed some differences in pattern. Since both caterpillar and adult morphology appears quite variable, the distinction of these three morphospecies is not entirely certain. Images of several *Eois* species shown by DYER & GENTRY (2007), DYER et al. (2007) and JANZEN & HALLWACHS (2007) provide further examples of sometimes pronounced intraspecific variation, while a common feature of almost all *Eois* caterpillars seems to be the short, compact appearance.

The caterpillars of *Eupithecia sobria* (Fig. 71) were feeding inside the flowers of their host plant in the early larval stages, when they were rather lightly coloured (Fig. 71 left). Later instars (Fig. 71 right) fed partly internally on the flowers and fruits. The more intense colouration of the later instars may be an adaptation to this more exposed way of living. The caterpillars of the other observed *Eupithecia* species (*E. yangana*, Fig. 72 ;*E. sp. B15*, Fig. 73; *E. sp. B17*, Fig. 74 and *E. sp. B30*, Fig. 75) were feeding openly on the fronds and leaves of their host plants. While *Eupithecia* sp. B17 had a rather elongate caterpillar, the general appearance of the depicted caterpillars match that of other congeneric species from the Neotropics (BREHM 2003a) and other geographic regions (e.g. EBERT 2003).

Most caterpillars of *Psaliodes inundulata* (Fig. 76-77) were plain green (Fig. 76), but a few showed diffuse dark patterns that made the caterpillar appear almost black (Fig. 77).

Spargania narangilla (Fig. 78-79) displayed an interesting pupation behaviour, in that it built a cocoon into a hole in the leaf and covered it with chewed bits of leaf (Fig. 79). From further away this resulted in the impression of a dead leaf area, rather than a cocoon.

Concluding remarks

With the results of just four months of survey by one single observer, the number of Geometridae species from the Reserva Biológica San Francisco, for which life-history information is now available, rose from 59 to 115. This amounts to a proportion of 9.1% (formerly 4.7%) of the 1266 species recorded so far in the vicinity of that nature reserve (a

global hotspot of species diversity: BREHM et al. 2005b), and to even 10.9% (106 species) if only the 972 species are considered that have been recorded in the elevational belt covered by the samples of this study. Hence, even moderate sampling effort has the potential to unravel many novel facets of the manifold interactions between herbivorous insects and their host plants in Andean rain forests, which suffer heavily from ongoing deforestation (MOSANDL et al. in press) and must be viewed as particularly threatened and vulnerable ecosystems (BECK et al. in press a). Still, much information needs to be gathered in order to make more meaningful comparisons possible with well established study sites in tropical forests, which mostly are situated at lower elevations (e.g. JANZEN & HALLWACHS 2007 and NOVOTNY et al. 2007).

Appendix – Colour plates

Caterpillar colour plates

The caterpillars of all species collected and reared to adulthood are shown, with the exception of *Eustenophasma fuscata*, where the caterpillar pictures could not be reliably assigned. Most pictures show the last instar larvae (assumed to be the fifth instar L5 for notation). All pictures include a scale bar of 1cm length generated from scaled paper used as background for most pictures; in some cases it may differ from the true scale up to about 10%. Combined pictures showing two caterpillars either have two scale bars, or the scale bar applies to both caterpillars.

Plate 1

Fig. 3: *Pero maculicosta* WARREN, 1897. **Fig. 4:** *Bryoptera* sp. B33. **Fig. 5:** *Glena* sp. B13. **Fig. 6:** *Glena* sp. B24; L4 (top) and L5 (bottom). **Fig. 7:** *Glena* sp. B28. **Fig. 8:** *Iridopsis scolancala* PROUT, 1932. **Fig. 9-10:** *Iridopsis* sp. cf. *subnigrata* WARREN, 1905. **Fig. 11:** ‘*Melanophia*’ *atigrada* DOGNIN, 1893. **Fig. 12:** *Melanolophia* sp. B34. **Fig. 13:** *Melanolophia* sp. B35. **Fig. 14:** *Melanolophia* sp. B36. **Fig. 15:** *Apiciopsis* sp. nr. *maciza* DOGNIN, 1896; probably L4 (top) and L5 (bottom). **Fig. 16:** *Callipseustes* sp. B08; probably L5. **Fig. 17:** *Mychonia violacea* WARREN, 1907; probably L4 (left) and L5 (right). **Fig. 18:** *Mychonia* sp. B43 WARREN, 1907; probably L4 (left) and L5 (right). **Fig. 19:** *Cargolia arana* DOGNIN, 1895. **Fig. 20:** *Ischnopteris brehmi* PITKIN, 2005; probably L4 (top) and L5 (bottom).

Plate 2

Fig. 21: *Ischnopteris* sp. nr. *festa* DOGNIN, 1904; L3 (top) and L5 (bottom). **Fig. 22-23:** *Rucana bisecta* DOGNIN, 1914; L5 (Fig. 22) and pupa (Fig. 23). **Fig. 24:** *Bonatea duciata* MAASSEN, 1890. **Fig. 25-26:** *Bonatea viridilinea* WARREN, 1904; L5 (Fig. 25 and 26 bottom); L3 or L4 (Fig. 26 top). **Fig. 27-28:** *Nephodia admirationis* PROUT, 1911; L5 (Fig. 27) and pupa (Fig. 28). **Fig. 29:** *Nephodia* sp. nr. *astyochiodes* WARREN, 1904. **Fig. 30:** *Isochromodes duplicata* WARREN, 1904. **Fig. 31:** *Isochromodes* sp. nr. *polvoreata* DOGNIN, 1893. **Fig. 32:**

Isochromodes sp. B06; probably F5. **Fig. 33: *Isochromodes* sp. B12. **Fig. 34: *Isochromodes* sp. B39. **Fig. 35: *Isochromodes* sp. B40. **Fig. 36: *Mesedra* sp. nr. *confinis* WARREN, 1904. **Fig. 37: *Mesedra* sp. B16. **Fig. 38: *Perusia praecisaria* HERRICH-SCHÄFFER, 1855.************

Plate 3

Fig. 39: *Perusia* sp. 135. **Fig. 40: *Certima* sp. 97. **Fig. 41: *Microxydia colorata* WARREN, 1904. **Fig. 42: *Microxydia orsitaria* GUENÉE, 1858. **Fig. 43: *Microxydia* sp. B37; probably L5. **Fig. 44: *Nematocampa* sp. nr. *falsa* WARREN, 1906. **Fig. 45: *Pantherodes conglomerata* WARREN, 1894; probably L4 and L5. **Fig. 46: *Phyllodonta flabellaria* THIERRY-MIEG, 1894. **Fig. 47: *Phyllodonta semicava* WARREN, 1904. **Fig. 48: *Prochoerodes pilosa* WARREN, 1897. **Fig. 49-51: *Sabulodes caberata oberthuri* RINDGE, 1978; L5 (Fig. 49-50) and pupa (Fig. 51). **Fig. 52: *Sabulodes* sp. B38. **Fig. 53-54: *Cyclophora costinotata* WARREN, 1900; L5 (Fig. 53) and pupa (Fig. 54). **Fig. 55-56: *Cyclophora viator* PROUT, 1920; L5 (Fig. 55) and pupa (Fig. 56).**************************

Plate 4

Fig. 57-58: *Erateina radiaria* HERRICH-SCHÄFFER, 1853. **Fig. 59: *Erateina siliquata* GUENÉE, 1858. **Fig. 60: *Euphyia* sp. B07. **Fig. 61-62: *Eois encina* DOGNIN, 1899; L3 or L4 (Fig. 51) and L5 (Fig. 52). **Fig. 63: *Eois muscosa* DOGNIN, 1910; probably L4 or L5. **Fig. 64: *Eois olivacea* FELDER & ROGENHOFER, 1875. **Fig. 65-67: *Eois* sp. nr. *encina* DOGNIN, 1899; probably L4 (Fig. 65 top), L5 (Fig. 65 bottom, Fig. 66 and Fig. 67 top) and prepupal L5 (Fig. 67 bottom). **Fig. 68: *Eois* sp. B04. **Fig. 69: *Eois* sp. B05. **Fig. 70: *Eois* sp. B42; probably L4 or L5. **Fig. 71: *Eupithecia sobria* PROUT, 1910; L2 or L3 (left) and L5 (right). **Fig. 72: *Eupithecia yangana* DOGNIN, 1899; L3 or L4. **Fig. 73: *Eupithecia* sp. B15; probably L5. **Fig. 74: *Eupithecia* sp. B17; probably L4.**************************

Plate 5

Fig. 75: *Eupithecia* sp. B30; L4 or L5. **Fig. 76-77: *Psaliodes inundulata* GUENÉE, 1858; probably L5. **Fig. 78-79: *Spargania narangilla* DOGNIN, 1893; L5 (Fig. 78) and cocoon (Fig. 79).****

Moth colour plates

The taxonomy of Neotropical Geometridae is still in flux and many species have either not been depicted in any readily available form in the literature or, if so, are depicted there with incomplete, incorrect, or outdated names. A large number of species has not even been described yet. Therefore it is often difficult to determine what species a name refers to, and impossible in cases where identification to species level was not achieved, as it is the case in several of the specimens presented here.

To facilitate the permanent connection of data on caterpillar host plants and morphology with a specific species or at least morphospecies, pictures of the adult moths of all species addressed in this study are presented here.

Each picture shows both upper- (on the left) and underside (to the right) of one specimen. In order to maximise the diagnostic value, the best preserved side of each specimen was used for the generation of these plates and formatted to fit the general scheme. For every specimen a scale bar was placed under both depicted halves indicating the length of either 1cm, or – where explicitly noted by a ‘1/2’ sign – 0.5cm.

Plate 6

Fig. 80: *Pero maculicosta* WARREN, 1897. **Fig. 81:** *Bryoptera* sp. B33. **Fig. 82:** *Glena* sp. B13. **Fig. 83:** *Glena* sp. B24. **Fig. 84:** *Glena* sp. B28. **Fig. 85:** *Iridopsis scolancala* PROUT, 1932. **Fig. 86:** *Iridopsis* sp. cf. *subnigrata* WARREN, 1905. **Fig. 87:** ‘*Melanophia*’ *atigrada* DOGNIN, 1893. **Fig. 88:** *Melanolophia* sp. B34. **Fig. 89:** *Melanolophia* sp. B35. **Fig. 90:** *Melanolophia* sp. B36. **Fig. 91:** *Apiciopsis* sp. nr. *maciza* DOGNIN, 1896. **Fig. 92:** *Callipseustes* sp. B08. **Fig. 93:** *Mychonia violacea* WARREN, 1907. **Fig. 94:** *Mychonia* sp. B43 WARREN, 1907. **Fig. 95:** *Cargolia arana* DOGNIN, 1895. **Fig. 96-97:** *Ischnopteris brehmi* PITKIN, 2005. **Fig. 98:** *Ischnopteris* sp. nr. *festu* DOGNIN, 1904. **Fig. 99:** *Rucana bisecta* DOGNIN, 1914. **Fig. 100:** *Bonatea duciata* MAASSEN, 1890.

Plate 7

Fig. 101: *Bonatea viridilinea* WARREN, 1904. **Fig. 102:** *Nephodia admirationis* PROUT, 1911. **Fig. 103:** *Nephodia* sp. nr. *astyochiodes* WARREN, 1904. **Fig. 104:** *Isochromodes duplicata* WARREN, 1904. **Fig. 105:** *Isochromodes* sp. nr. *polvoreata*.B26 DOGNIN, 1893. **Fig. 106:** *Isochromodes* sp. B06. **Fig. 107:** *Isochromodes* sp. B12. **Fig. 108:** *Isochromodes* sp. B39. **Fig. 109:** *Isochromodes* sp. B40. **Fig. 110:** *Mesedra* sp. nr. *confinis* WARREN, 1904. **Fig. 111:** *Mesedra* sp. B16. **Fig. 112:** *Perusia praecisaria* HERRICH-SCHÄFFER, 1855. **Fig. 113:** *Perusia* sp. 135. **Fig. 114:** *Certima* sp. 97. **Fig. 115:** *Eustenophasma fuscata* WARREN, 1907. **Fig. 116:** *Microxydia colorata* WARREN, 1904. **Fig. 117-118:** *Microxydia orsitaria* GUENÉE, 1858. **Fig. 119:** *Microxydia* sp. B37. **Fig. 120:** *Nematocampa* sp. nr. *falsa* WARREN, 1906. **Fig. 121:** *Pantherodes conglomerata* WARREN, 1894.

Plate 8

Fig. 122: *Phyllodonta flabellaria* THIERRY-MIEG, 1894. **Fig. 123:** *Phyllodonta semicava* WARREN, 1904. **Fig. 124:** *Prochoerodes pilosa* WARREN, 1897. **Fig. 125:** *Sabulodes caberata oberthuri* RINDGE, 1978. **Fig. 126:** *Sabulodes* sp. B38. **Fig. 127:** *Cyclophora costinotata* WARREN, 1900. **Fig. 128:** *Cyclophora viator* PROUT, 1920. **Fig. 129-130:** *Erateina radiaria* HERRICH-SCHÄFFER, 1853. **Fig. 131-132:** *Erateina siliquata* GUENÉE, 1858. **Fig. 133:** *Euphyia* sp. B07. **Fig. 134:** *Eois encina* DOGNIN, 1899. **Fig. 135:** *Eois muscosa* DOGNIN, 1910. **Fig. 136:** *Eois olivacea* FELDER & ROGENHOFER, 1875. **Fig. 137:** *Eois* sp. nr. *encina* DOGNIN, 1899. **Fig. 138:** *Eois* sp. B04. **Fig. 139:** *Eois* sp. B05. **Fig. 140:** *Eois* sp. B42. **Fig. 141:** *Eupithecia sobria* PROUT, 1910. **Fig. 142:** *Eupithecia yangana* DOGNIN, 1899.

Plate 9

Fig. 143: *Eupithecia* sp. B15. **Fig. 144:** *Eupithecia* sp. B17. **Fig. 145:** *Eupithecia* sp. B30. **Fig. 146:** *Psaliodes inundulata* GUENÉE, 1858. **Fig. 147:** *Spargania narangilla* DOGNIN, 1893.

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Fig. 3: *P. maculicosta*



Fig. 4: *Bryoptera* sp. B33



Fig. 5: *Glena* sp. B13



Fig. 6: *Glena* sp. B24



Fig. 7: *Glena* sp. B28



Fig. 8: *I. scolancala*



Fig. 9: *I. sp. cf. subnigrata*



Fig. 10: *I. sp. cf. subnigrata*



Fig. 11: *M. atigrada*



Fig. 12: *Melanolophia* sp. B34



Fig. 13: *Melanolophia* sp. B35



Fig. 14: *Melanolophia* sp. B36



Fig. 15: *A. sp. nr. maciza*

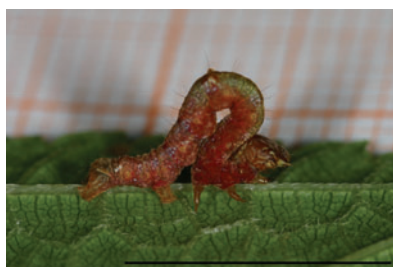


Fig. 16: *Callipseustes* sp. B08



Fig. 17: *M. violacea*



Fig. 18: *Mychonia* sp. B43



Fig. 19: *C. arana*



Fig. 20: *I. brehmi*



Fig. 21: *I. sp. nr. festa*



Fig. 22: *R. bisecta*



Fig. 23: *R. bisecta*

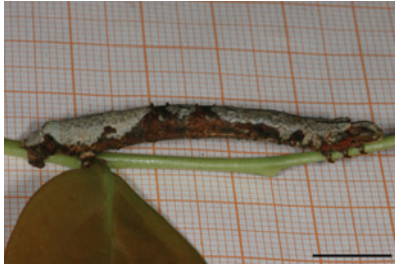


Fig. 24: *B. duciata*



Fig. 25: *B. viridilinea*



Fig. 26: *B. viridilinea*



Fig. 27: *N. admirationis*



Fig. 28: *N. admirationis*



Fig. 29: *N. sp. nr. astyochiodes*



Fig. 30: *I. duplicata*



Fig. 31: *I. sp. nr. polvoreata*

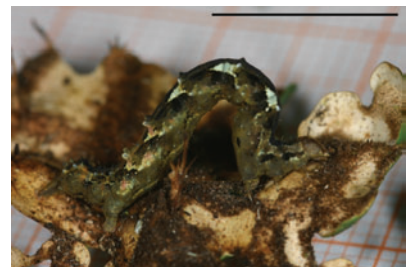


Fig. 32: *Isochromodes sp. B06*

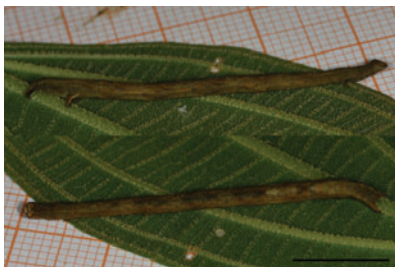


Fig. 33: *Isochromodes sp. B12*



Fig. 34: *Isochromodes sp. B39*



Fig. 35: *Isochromodes sp. B40*



Fig. 36: *M. sp. nr. confinis*



Fig. 37: *Mesedra sp. B16*



Fig. 38: *P. praecisaria*



Fig. 39: *Perusia*, sp. 135



Fig. 40: *Certima* sp. 97



Fig. 41: *M. colorata*



Fig. 42: *M. orsitaria*



Fig. 43: *Microxydia* sp. B37



Fig. 44: *N. sp. nr. falsa*



Fig. 45: *P. conglomerata*



Fig. 46: *P. flabellaria*



Fig. 47: *P. semicava*



Fig. 48: *P. pilosa*



Fig. 49: *S. caberata*



Fig. 50: *S. caberata*



Fig. 51: *S. caberata*



Fig. 52: *Sabulodes* sp. B38



Fig. 53: *C. costinotata*

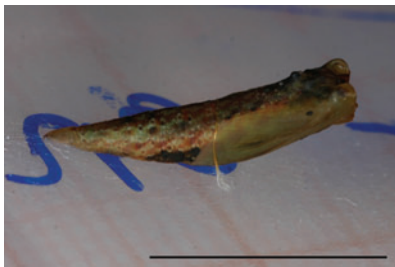


Fig. 54: *C. costinotata*

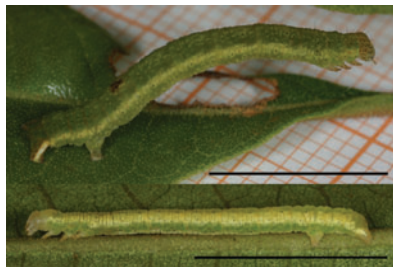


Fig. 55: *C. viator*



Fig. 56: *C. viator*



Fig. 57: *E. radiaria*



Fig. 58: *E. radiaria*



Fig. 59: *E. siliguata*

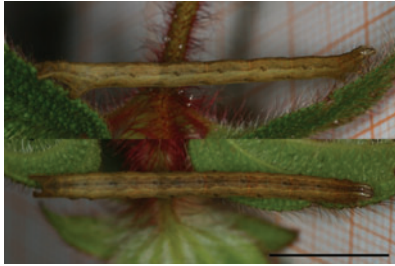


Fig. 60: *Euphyia* sp. B07

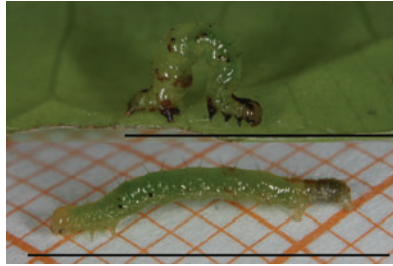


Fig. 61: *E. encina*



Fig. 62: *E. encina*



Fig. 63: *E. muscosa*



Fig. 64: *E. olivacea*



Fig. 65: *E. sp. nr. encina*



Fig. 66: *E. sp nr. encina*



Fig. 67: *E. sp nr. encina*



Fig. 68: *Eois* sp. B04



Fig. 69: *Eois* sp. B05



Fig. 70: *Eois* sp. B42



Fig. 71: *E. sobria*

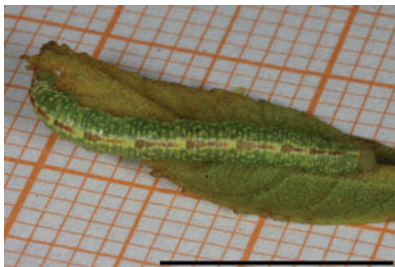


Fig. 72: *E. yangana*



Fig. 73: *Eupithecia* sp. B15



Fig. 74: *Eupithecia* sp. B17



Fig. 75: *Eupithecia* sp. B30



Fig. 76: *P. inundulata*



Fig. 77: *P. inundulata*

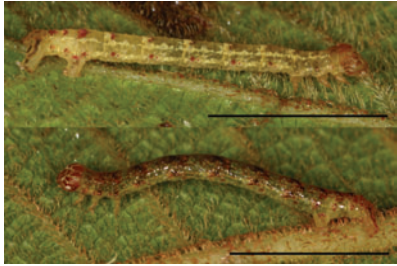


Fig. 78: *S. narangilla*

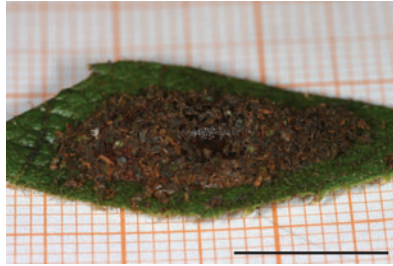


Fig. 79: *S. narangilla*



Fig. 80: *P. maculicosta*



Fig. 81: *Bryoptera* sp. B33



Fig. 82: *Glena* sp. B13



Fig. 83: *Glena* sp. B24



Fig. 84: *Glena* sp. B28



Fig. 85: *I. scolancala*



Fig. 86: *I. sp. cf. subnigrata*



Fig. 87: *M. atigrada*



Fig. 88: *Melanolophia* sp. B34



Fig. 89: *Melanolophia* sp. B35



Fig. 90: *Melanolophia* sp. B36



Fig. 91: *A. sp. nr. maciza*



Fig. 92: *Callipseustes* sp. B08



Fig. 93: *M. violacea*



Fig. 94: *Mychonia* sp. B43



Fig. 95: *C. arana*



Fig. 96: *I. brehmi*



Fig. 97: *I. brehmi*



Fig. 98: *I. sp. nr. festa*



Fig. 99: *R. bisecta*



Fig. 100: *B. duciata*



Fig. 101: *B. viridilinea*



Fig. 102: *N. admirationis*



Fig. 103: *N. sp. nr. astyochiodes*



Fig. 104: *I. duplicata*

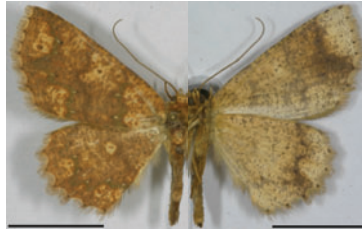


Fig. 105: *I. sp. nr. polvoreata*



Fig. 106: *Isochromodes sp. B06*



Fig. 107: *Isochromodes sp. B12*



Fig. 108: *Isochromodes sp. B39*



Fig. 109: *Isochromodes sp. B40*



Fig. 110: *M. sp. nr. confinis*



Fig. 111: *Mesedra sp. B16*



Fig. 112: *P. praecisaria*



Fig. 113: *Perusa sp. 135*



Fig. 114: *Certima sp. 97*



Fig. 115: *E. fuscata*



Fig. 116: *M. colorata*

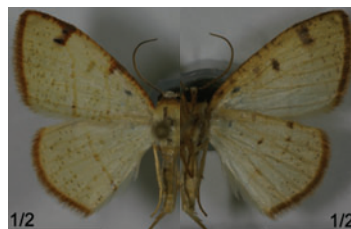


Fig. 117: *M. orsitaria*



Fig. 118: *M. orsitaria*



Fig. 119: *Microxydia sp. B37*



Fig. 120: *N. sp. nr. falsa*



Fig. 121: *P. conglomerata*



Fig. 122: *P. flabellaria*



Fig. 123: *P. semicava*



Fig. 124: *P. pilosa*



Fig. 125: *S. caberata oberthuri*



Fig. 126: *Sabulodes* sp. B38



Fig. 127: *C. costinotata*



Fig. 128: *C. viator*



Fig. 129: *E. radiaria*



Fig. 130: *E. radiaria*



Fig. 131: *E. siliquata*



Fig. 132: *E. siliquata*



Fig. 133: *Euphyia* sp. B07



Fig. 134: *E. encina*



Fig. 135: *E. muscosa*



Fig. 136: *E. olivacea*



Fig. 137: *E. sp. nr. encina*



Fig. 138: *Eois* sp. B04



Fig. 139: *Eois* sp. B05

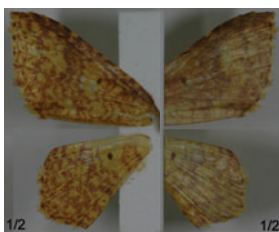


Fig. 140: *Eois* sp. B42



Fig. 141: *E. sobria*



Fig. 142: *E. yangana*



Fig. 143: *Eupithecia* sp. B15



Fig. 144: *Eupithecia* sp. B17



Fig. 145: *Eupithecia* sp. B30



Fig. 146: *P. inundulata*



Fig. 147: *S. narangilla*

Curriculum vitae

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