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TAXONOMY AND SPECIES RICHNESS OF AMAZONIAN PIMPLINAE AND RHYSSINAE (HYMENOPTERA: ICHNEUMONIDAE)

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This thesis is based on the following publications and some unpublished results, referred to in the text by their Roman numerals.

I Gómez, I.C., Sääksjärvi, I.E., Veijalainen, A. & Broad, G.R. (2009) Two new species of *Xanthopimpla* (Hymenoptera, Ichneumonidae) from Western Amazonia, with a revised key to the Neotropical species of the genus. *ZooKeys* 14, 55–65.

II Gómez, I.C., Sääksjärvi, I.E., Broad, G.R., Puhakka, L., Peña, C., Castillo, C, Padua D. (2014) The Neotropical species of *Xanthopimpla* Saussure (Hymenoptera, Ichneumonidae). *Zootaxa* 3774 (1): 057–073.

III Gómez, I.C., Sääksjärvi, I.E., Puhakka, L., Castillo, C, Bordera S. (2015) The Peruvian Amazonian species of *Epirhyssa* (Hymenoptera: Ichneumonidae; Rhyssinae), with notes on tropical species richness. *In press Zootaxa*

IV Veijalainen, A., Sääksjärvi, I.E., Erwin, T.L., Gómez, I.C. & Longino, J.T. (2013) Subfamily composition of Ichneumonidae (Hymenoptera) from western Amazonia: insights into diversity of tropical parasitoid wasps. *Insect Conservation and Diversity*, 6, 28–37.

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Table of contribution.

	I	II	III	IV	V
Original idea	IES, ICG	ICG	ICG, IES	AV, IES	ICG, IES
Field work	ICG, TLE	IES, ICG	IES, ICG	IES, TLE, ICG	IES, ICG
Preparation of material	ICG, AV	ICG, IES, CC	ICG, IES, CC	AV, IES, ICG	ICG, IES
Identification of parasitoids	IES, ICG	ICG, IES	ICG, IES, CC	AV, IES, ICG	IES, ICG
Analysis				AV	HT, ICG
Writing the manuscript	IES, ICG	ICG	ICG	AV	ICG, HT
Commenting on the manuscript	GB, AV	IES, GB, LP, CP	IES, LP, SB	TLE, IES, JTL, ICG	IES, PM, MP, GB, CR

ICG= Isrrael C. Gómez, IES= Ilari E. Sääksjärvi, GB= Gavin Broad, AV= Anu Veijalainen,

SB= Santiago Bordera, LP= Liisa Puhakka, CP= Carlos Peña, CC= Carol Castillo,

DP= Diego Pádua, HT= Hanna Tuomisto, PM= Peter Mayhew, TLE= Terry L. Erwin, JTL= John T. Longino, MP= Marc Pollet, CR= Carmen Rey del Castillo

TABLE OF CONTENTS

ABSTRACT

The Amazonian region, the biggest rain forest of our planet, is known for its extraordinary biodiversity. Most of this diversity is still unexplored and new species of different taxa are regularly found there. In this region, as in most areas of the world, insects are some of the most abundant organisms. Therefore, studying this group is important to promote the conservation of these highly biodiverse ecosystems of the planet. Among insects, parasitoid wasps are especially interesting because they have potential for use as biodiversity indicators and biological control agents in agriculture and forestry. The parasitoid wasp family Ichneumonidae is one of the most species rich groups among the kingdom Animalia. This group is still poorly known in many areas of the world; the Amazonian region is a clear example of this situation. Ichneumonids have been thought to be species poor in Amazonia and other tropical areas. However, recent studies are suggesting that parasitoid wasps may be quite abundant in Amazonia and possibly in most tropical areas of the world.

The aim of my doctoral thesis is to study the species richness and taxonomy of two of the best known ichneumonid subfamilies in the Neotropical region, Pimplinae and Rhyssinae. To do this I conducted two extensive sampling programs in the Peruvian Amazonia. I examined also a large number of Neotropical ichneumonids deposited to different natural history museums. According to the results of my thesis, the species richness of these parasitoids in the Amazonian region is considerably higher than previously reported. In my research, I firstly further develop the taxonomy of these parasitoids by describing many new species and reporting several new faunistic records (I, II, III). In this first part I focus on two genera (*Xanthopimpla* and *Epirhyssa*) which were thought to be rather species poor. My thesis demonstrates that these groups are actually rather species rich in the Amazonian region. Secondly, I concentrate on the species richness of these parasitoids in a global comparison showing that the Neotropical region and especially the Peruvian Amazonia is one of the most species rich areas of Pimpliformes ichneumonids (V). Furthermore, I demonstrate that with the data available to date no clear latitudinal gradient in species richness is visible. Thirdly, increasing the macroecological knowledge of these parasitoids I show that some previously unreported ichneumonid subfamilies are present in the Amazonian region (IV). These new insights and the results of the global comparison of ichneumonid inventories suggest that the previous belief of low diversity in the tropics is most likely related to a lack of sampling effort in the region. Overall, my research increases the knowledge of Neotropical ichneumonids highlighting the importance of Peruvian Amazonia as one of the diversity hotspots of parasitoid wasps.

RESUMEN

La región amazónica, la mayor selva tropical del planeta, es conocida por su extraordinaria biodiversidad. La mayor parte de esta diversidad esta aún inexplorada y con regularidad se siguen descubriendo nuevas especies de diferentes taxones. En esta región, como en la mayoría de las áreas del mundo los insectos son uno de los organismos más abundantes. Por lo tanto, el estudio de este grupo es importante para fomentar la conservación de estos biodiversos ecosistemas del planeta. Entre los insectos, las avispas parasitoides son especialmente interesantes porque tienen potencial para su uso como indicadores de biodiversidad y agentes de control biológico en la agricultura y la silvicultura. La familia de avispas parasitoides Ichneumonidae es uno de los grupos más ricos en especies del reino Animalia. Este grupo aún es poco conocido en muchas partes del mundo y la región amazónica es un claro ejemplo de esta situación. Los icneumónidos han sido considerados como poco diversos en la Amazonía y otras áreas tropicales, sin embargo, estudios recientes sugieren que estas avispas parasitoides pueden ser muy abundantes en la Amazonía y, posiblemente, en la mayoría de las zonas tropicales del mundo.

El objetivo de la presente tesis doctoral es el estudio de la riqueza de especies y la taxonomía de dos de las subfamilias más conocidas de icneumónidos en la región Neotropical, los Pimplinae y los Rhyssinae. Para ello se han llevado a cabo dos muestreos a largo plazo en la Amazonia peruana y se han estudiado un gran número de icneumónidos neotropicales depositados en diferentes museos de historia natural. Los resultados sugieren que la riqueza de especies de estos parasitoides en la región amazónica es considerablemente más alta que la reportada anteriormente. En la investigación, en primer lugar, se contribuye al conocimiento taxonómico de estos parasitoides describiendo varias especies nuevas y reportando numerosos registros faunísticos (I, II, III). En esta primera parte han sido estudiados dos géneros que se creían pobres en especies en Amazonía, *Xanthopimpla* y *Epirhyssa*. La tesis demuestra que estos grupos son en realidad bastante ricos en especies en la región. En segundo lugar, se ha estudiado la riqueza de especies de estos parasitoides de forma comparativa a escala global, los resultados demuestran que la región Neotropical y especialmente la Amazonía peruana es una de las zonas más ricas en especies de icneumónidos (V). Además, se demuestra que con los datos disponibles actualmente no es posible concluir si existe una gradiente latitudinal de riqueza de especies a nivel global. En tercer lugar, se contribuye al conocimiento macroecológico de estos parasitoides demostrando que algunas subfamilias de icneumónidos no reportadas previamente están presentes en la región amazónica (IV). Estos nuevos resultados y la comparación global de inventarios de Ichneumonidae sugieren que las hipótesis previas sobre la baja diversidad en los trópicos se deba, posiblemente, a la falta de esfuerzo de muestreo en la región. En general, la presente tesis constituye una contribución relevante al conocimiento de los icneumónidos neotropicales destacando la importancia de la Amazonía peruana como uno de los lugares más diversos en el mundo para estas avispas parasitoides.

TIIVISTELMÄ

Amazonia, planeettamme suurin yhtenäinen sademetsäalue, on tunnettu valtavasta biologisesta monimuotoisuudestaan. Suurin osa tästä monimuotoisuudesta on vielä tutkimatonta, ja alueelta löydetään jatkuvasti tieteelle tuntemattomia lajeja. Amazoniassa, kuten useimmilla alueilla maailmassa, hyönteiset ovat eräs runsaslukuisimmista eliöryhmistä. Tämän ryhmän tutkiminen on tärkeä keino edistää näiden erittäin monimuotoisten ekosysteemien suojelua. Loispistiäiset ovat erityisen kiinnostava hyönteisryhmä, koska niitä voi olla mahdollista hyödyntää indikaattorilajeina ja biologisessa torjunnassa maa- ja metsätaloudessa. Loispistiäisheimo Ichneumonidae on yksi eläinkunnan runsaslajisimmista ryhmistä. Tämä ryhmä on edelleen heikosti tunnettu monissa osissa maailmaa, ja Amazonia on tästä selkeä esimerkki. Ichneumonidae-heimon lajirunsauden on uskottu olevan alhainen Amazoniassa ja muualla tropiikissa. Viimeaikaiset tutkimukset viittaavat kuitenkin siihen, että loispistiäiset saattavat olla huomattavan runsaita Amazoniassa ja mahdollisesti useimmilla maailman trooppisilla alueilla.

Väitöskirjani tavoitteena on tutkia kahden tunnetuimman uuden maailman tropiikissa tavattavan Ichneumonidae-loispistiäisten alaheimon (Pimplinae ja Rhyssinae) lajirunsautta ja taksonomiaa. Toteutin tätä varten kaksi laajaa keräystä Perun Amazoniassa. Tutkin myös suuren määrän eri luonnonhistoriallisten museoiden kokoelmissa olevia uuden maailman tropiikista kerättyjä Ichneumonidae-loispistiäisiä. Väitöskirjatutkimuksessani käy ilmi, että näiden loispistiäisten lajirunsaus Amazoniassa on merkittävästi aiemmin luultua suurempi. Työni ensimmäisessä osassa paneudun näiden loispistiäisten taksonomiaan. Kuvaan useita tieteelle uusia lajeja ja raportoin useita uusia havaintotietoja. Keskityn työn ensimmäisessä osassa kahteen sukuun (*Xanthopimpla* ja *Epirhyssa*), joiden on uskottu olevan melko vähälajisia. Väitöskirjatutkimukseni osoittaa, että todellisuudessa Amazonian alueella tavataan runsaasti näiden sukujen lajeja. Työn toisessa osassa keskityn näiden loispistiäisten maailmanlaajuiseen lajirunsauteen ja osoitan, että uuden maailman tropiikki ja erityisesti Perun Amazonia on yksi Pimpliformes-loispistiäisten lajirunsauden keskittymistä. Lisäksi osoitan, että tällä hetkellä saatavissa olevassa aineistossa ei näy leveyspiireihin sidoksissa olevaa lajirunsausgradienttia. Työn kolmannessa osassa laajennan tietämystä tämän lajiryhmän makroekologiasta osoittamalla, että Amazoniassa tavataan eräitä Ichneumonidae-loispistiäisten alaheimoja, joiden ei aiemmin tiedetty esiintyvän alueella. Nämä uudet näkemykset ja lajirunsauden maailmanlaajuinen vertailu viittaavat siihen, että aiempi uskomus tämän ryhmän alhaisesta runsaudesta tropiikissa kuvastaa todennäköisesti alueelta saatavissa olevan keräysaineiston puutteellisuutta. Kokonaisuudessaan työni lisää tietämystä uuden maailman tropiikin Ichneumonidae-loispistiäisistä ja korostaa Perun Amazonian merkittävyyttä yhtenä loispistiäisten lajirunsauden tärkeimmistä keskittymistä.

1. INTRODUCTION

Arthropods are one of the dominant groups of animals on Earth. They are not only far more specious than many other eukaryotic organisms but also far more abundant in numbers. Insects are intrinsically related to many human activities. For example, bees (Hymenoptera) and other wasps are important in the pollination of plants, including many crop species. Bees are also the producers of honey and pollen that humans and other animals consume. Silkworms (Lepidoptera) have been used for thousands of years in the textile industry. Many groups of beetles (Coleoptera) feed on decaying organic matter acting as natural cleaners in different ecosystems and many larvae of this group are a source of food for humans in tropical areas.

Many insect species are known because they are pests, one of the major challenges for agriculture and forestry worldwide (Greathead & Greathead 1992). However, insects also maintain equilibrium in different ecosystems and specialized groups of them control the population of herbivorous insects (Altieri 1994). These specialized groups are the predators and parasitoids. Parasitoids are represented mainly by wasps (Hymenoptera) and flies (Diptera) but also by some beetles (Coleoptera) and even caddis flies (Trichoptera). The parasitoids contribute enormously to preserve balance in natural and non-natural ecosystems and they have also been used in biological control programs against economically important pest species around the world (Altieri 1991).

The aim of my thesis is to provide a tropical contribution to the knowledge of these beneficial organisms. I focus on parasitoid wasps because they are one of the most diverse but at the same time one of the most poorly known groups of insects with great potential in different areas of biological research.

It is possible that the family Ichneumonidae is one of the most diverse groups among parasitoid wasps. This family is may be one of the most species rich animal families that have ever lived on Earth (Gauld 2002). With my thesis I hope to increase the knowledge about the taxonomy and diversity of these parasitoids. Ichneumonids have been suggested to be rather species poor in the highly diverse Amazonian region (Heinrich 1977; Porter 1978). However, recent works suggest that ichneumonid parasitoids may be significantly more species rich in Amazonia than previously thought (Sääksjärvi 2003; Sääksjärvi et al. 2004; Palacio et al. 2010; Broad et al. 2011; Bordera & Sääksjärvi 2012; Khalaim et al. 2013). My work goes along with these efforts and contributes to increase information needed to better understand the diversity of Amazonian ichneumonids.

1.1. The parasitoid wasp family Ichneumonidae (Hymenoptera)

The family Ichneumonidae is with ca. 40 living subfamilies (Gauld 2002; Yu et al. 2012), 1 575 genera and more than 24 000 described species (Aguiar et al. 2013) the most species rich family within the vast insect order Hymenoptera. The most recent published estimation of the species richness of Ichneumonidae suggested that the total number of species may exceed 100 000 (Gauld 2002). Almost all of the species are parasitoids of other arthropods, and the majority of them are quite abundant in most terrestrial habitats. Ichneumonids are also morphologically diverse: some species are very large (e.g. Labeninae, Rhyssinae) while others are hard to see clearly without using a microscope (e.g. Orthocentrinae), some species are brightly colored (e.g. many tropical species) while others are almost entirely black (e.g. high altitude species). The family is also fascinating behaviorally as many parasitoid biological strategies are represented within it (Gauld 1991). The larval stages of ichneumonids can develop internally (endoparasitoids) or externally (ectoparasitoids) and they can develop individually (solitary parasitoids) or, in a few cases, in groups (gregarious parasitoids).

The species of the family can be divided into two large subgroups according to how they treat their hosts. Idiobiont parasitoids permanently paralyze their host when ovipositing while koinobiont parasitoids paralyze the host only temporarily allowing it to continue its development after oviposition (Askew & Shaw 1986; Gauld 1991). In addition, some ichneumonids are known to be hyperparasitoids of other parasitoid species. Interestingly, some species are herbivorous or develop as pseudoparasitoids consuming many host individuals at larval stage (Gauld 1991).

Despite its great species richness and interesting biological traits the family remains mainly unknown, especially in the Neotropics. Currently, a minority of species has been described (Gauld et al. 2000). Therefore, research on this group is needed in order to achieve a better understanding of their role in natural ecosystems.

1.2 Anomalous diversity gradient of ichneumonids

One of the most interesting and long-lasting debates on insect distributions deals with the family Ichneumonidae. This family has been suggested to be less species rich in tropical areas than in higher latitudes (Owen & Owen 1974; Gauld 1986, 1987; LaSalle & Gauld 1993; Gauld & Gaston 1994; Sime & Brower 1998; Horstmann et al. 1999), instead of exhibiting the normal latitudinal diversity gradient found in most other plant or animal groups of higher species richness at lower latitudes (Hillebrand 2004). This case is particularly interesting since most of the ichneumonid hosts (e.g. Lepidoptera and Coleoptera) are known to be very species rich in the tropics (Sime & Brower 1998). Many hypotheses have been proposed to explain this phenomenon: the resource fragmentation hypothesis (Janzen & Pond 1975); the host predation hypothesis (Rathcke & Price 1976); the parasitoid predation hypothesis (Gauld 1987); the interphyletic competition hypothesis (Eggleton & Gaston 1990); and – the most widely studied one – the nasty host hypothesis (Gauld & Gaston 1994). For detailed explanation on these hypotheses see e.g. Sime & Brower (1998) or Santos & Quicke (2011).

Currently, research on the family is increasing the knowledge of these parasitoids and is showing that the diversity and distributional patterns of tropical ichneumonids are far from being well-known (Gauld et al. 2000, 2002ab; Sääksjärvi et al. 2004, 2006; Valera & Diaz 2010; Aguiar & Ramos 2011; Broad et al. 2011; Pham et al. 2011, 2012, 2013; Khalaim et al. 2012; Kasparyan 2012; Veijalainen et al. 2012; Santos & Aguiar 2013; Santos & Quicke 2011; Quicke 2012; I–V). Furthermore, many new species of even well-known groups such as mammals and birds are being found continuously in the Amazonian region (Seeholzer et al. 2012; Solari et al 2012; Jimenez et al.

2013; Mendes et al. 2013) suggesting that, in general, more efforts are needed to have a better understanding of the diversity present in this area of the world.

1.3. Amazonia and ichneumonids

Amazonia is the world's largest rain forest and one of the most unknown and diverse regions on the planet. The Amazon basin has an area of about 6 290 000 km2 (Ter Stegge et al. 2013) and is similar in size to continental USA (McMichael et al. 2012). This basin forms part of most of the South American nations and has been populated by humans for thousands of years (Roosevelt et al. 1996; Pärssinen et al. 2009). Therefore, it is important to take into account that human impact may have been a factor affecting the diversity of this region.

Amazonia is particularly attractive for biologists because of its very high diversity. Many well-known groups of plants and animals, such as mammals, birds, trees and butterflies, have been reported to be at their richest in the world within Amazonia (Gentry 1988, 1992; Robins et al. 1996; Robbins & Opler 1997; Patterson et al. 2006; Ter Steege et al. 2013). Furthermore, it is known that at least western Amazonia has high habitat heterogeneity (Tuomisto et al. 1995) and many different rain forest types (Ruokolainen & Tuomisto 1998) which clearly indicate that Amazonia possesses highly diverse ecosystems.

One would expect then that diverse organisms such as parasitoid insects, with thousands of described species, should be very species rich in Amazonia. However, ichneumonid parasitoids have been suggested to be rather species poor (Porter 1978) or at least poorly populated (Heinrich 1977) in this region. Fortunately, recent studies have improved our knowledge on Amazonian ichneumonids (Sääksjärvi et al. 2003, 2004, 2006; Palacio et al. 2010; Broad et al. 2011; Bordera & Sääksjärvi 2012; Khalaim et al. 2013). These studies have provided valuable insights into the diversity of tropical ichneumonids. However, these efforts have not yet been able to sample any locality extensively enough to achieve an accurate image of the ichneumonid diversity. For this reason, I focused my work on sampling western Amazonia. Combining one year of field work and previous sampling efforts from northern Peruvian Amazonia (Sääksjärvi 2003), my thesis provides information about possibly the most extensively sampled areas of Amazonia.

1.4 Importance of ichneumonids

Ichneumonids have several features that make them especially important for science (see 1.1). The high species richness of this family is important to document since there is currently an extinction process in the planet (Pimm & Raven 2000). Ichneumonids are also important because many species possibly may have potential to serve as biological control agents and indicators of habitat diversity.

a) Biological control agents

Many ichneumonid species are already being used in biological control programs in agricultural and forestry activities. This family possesses an important potential as biological control agents since the majority of species are still undescribed (Greathead & Greathead 1992). The importance of these parasitoids is likely to increase with the growing trend of organic and sustainable food production since many species are excellent for pest regulation (Patel & Habib 1986; Gitau et al. 2007; Dum et al. 2011). The potential of ichneumonids in biological control relies on the fact that many species attack larval or pupal stages of lepidopteran and coleopteran pests. For example, some *Xanthopimpla* Saussure species, idiobiont endoparasitoids of Lepidoptera, are used in the biological control of economically important agricultural pests in different areas of the world (Gitau et al. 2007; Dum et al. 2011). Similarly, some *Campoletis* Forster species, koinobiont endoparasitoids of Lepidoptera, have been found to be efficient biological controllers against pests in commercial crops in South America (Patel & Habib 1986; Gómez 2010).

b) Biodiversity indicators

Many ichneumonid species have potential as biodiversity indicators (Gaston & Gauld 1993; Bartlet et al. 1999; Sääksjärvi et al. 2006). Some species may be good indicators of habitat disturbance since they inhabit mainly secondary forests (Idris et al. 2001a; Idris & Kee 2002). Many sensitive species may be absent in habitats where pesticides are constantly applied whereas other non-sensitive species can be found inhabiting is such areas (Gómez 2010). Some ichneumonid species are being utilized in Central America as indicators in the organic certification process in coffee (*Coffea arabica* L) plantations (Bautista et al. 2013). This last example is a clear indication of a new area of research where ichneumonids may be of economic value in simplifying and reducing costs of the agricultural industry.

1.5 Research aims

Firstly, I aimed to increase the taxonomic knowledge of ichneumonids in the Neotropical region. For this, I focused on the taxonomy and distribution of the most diverse genus of the subfamily Pimplinae, *Xanthopimpla* (I, II). In these works I reviewed the genus in the region describing many new species and providing new faunistic records. I also reorganized the species within the genus and provided new information about their distributional patterns.

Secondly, to study the diversity of ichneumonid parasitoids at the local, regional and global levels, I concentrated on the rhyssine genus *Epirhyssa* (III). Here I focused on the Peruvian Amazonia to test if these parasitoids are species poor in the area as previously stated. The distributional patterns and species richness of the genus are discussed also in this study.

Thirdly, to provide new ecological information on the ichneumonids, I studied the subfamily composition of Ichneumonidae in the Amazonian region (IV). A comparison with other studies from Central and North America provided information about the composition of the family in a broader scale. This study provided a better understanding of the ichneumonid community structure in Amazonia and the Neotropical region.

Fourthly, to evaluate the species richness of tropical parasitoids and the latitudinal diversity patterns of the group I conducted a study of worldwide comparison of species richness (V). This work demonstrated the very high species richness of the group in the Peruvian Amazonia and showed that currently with the available dataset no latitudinal gradient of diversity is detectable for this group.

2. MATERIALS AND METHODS

2.1 The main Peruvian study sites

The main study sites of my thesis are located in northern and southern parts of Peruvian Amazonia (Fig. 1). These areas are located rather close to the Andes. The Andes mountain chain forms the backbone of South America and is the natural limit of Western Amazonia. Both study sites have been recently established as part of the Peruvian conservation area network. This is mainly because research in these areas (e.g. Salo et al. 1986; Tuomisto et al. 1995; Wilson & Sandoval 1996) has demonstrated that they hold very diverse ecosystems in urgent need of conservation. These areas are also of enormous importance since various harmful anthropogenic activities such as deforestation and mining are occurring regularly in the Peruvian Amazonia. Therefore, studying the diversity present there is vital to preserve and protect these highly diverse ecosystems.

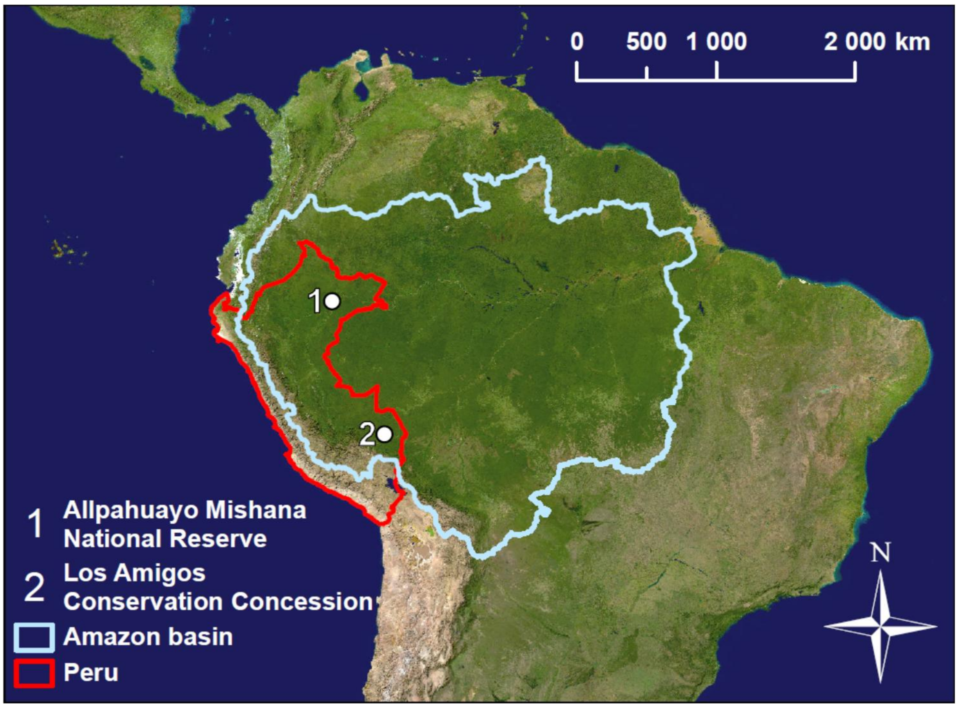

Figure 1. Distribution of sampling localities within the Peruvian Amazonia: Satellite image by NASA Visible Earth. The Amazon basin is shown as defined by Smith & Sandwell (1997).

Allpahuayo-Mishana National Reserve

This National Reserve is located in the northern Peruvian Amazonia (3° 57’ S, 73° 26’ W) in the department of Loreto and it covers an area of about 58 000 hectares (III). The reserve is located rather close to the city of Iquitos which is the biggest Amazonian city in Peru (Fig. 1). The climate is humid and hot; the mean annual precipitation is about 3 000 mm, and the average temperature is

26 °C (Marengo 1998). The environmental conditions of Allpahuayo-Mishana have been described in detail in Kalliola & Flores Paitan (1998).

Three main soil types can be found in Allpahuayo-Mishana. The flat low-lying soils are usually derived from the marine or semi-marine Pebas formation, which yields soils that are clayey in texture, relatively rich in nutrients, and mostly brownish-grey in color (Kalliola & Flores Paitan 1998). On the other hand, soils located on hilltops are white sand which is nutrient-poor and grey to white in color. The third soil type, loamy soil, has intermediate nutrient content and is probably derived from old river terraces (Kalliola & Flores Paitan 1998). The forests growing on these soil types differ from each other in floristic and faunistic composition (Tuomisto et al. 1995; Sääksjärvi et al. 2006). In general, forests growing on nutrient rich clayish soils have large trees and often many canopy layers and a dense shrub layer. In contrast, forests growing on nutrient poor white sand soils usually have slender trees, a less complex canopy structure, and a sparse shrub layer (Tuomisto et al. 2003). This close relation between the soil types and the distributional patterns of the fauna and flora (Vormisto et al. 2000) makes Allpahuayo-Mishana an excellent place to study the diversity of ichneumonids and many other organisms.

Los Amigos Conservation Concession

This conservation area is located in southern Peruvian Amazonia in the department of Madre de Dios (12°34’ S, 70°05’ W) (Fig. 1). It covers an area of about 146 000 hectares. Los Amigos lies between 238 and 268 m above sea level and the climate is humid and seasonal with a pronounced dry season of 3-4 months that occurs during June-September. The wet season lasts from October until May, and the wettest months are from December to February (Pino 2007). The mean annual rainfall between the years 2000 and 2004 was 2 776 mm. The mean annual temperature is around 23 °C with monthly mean temperatures ranging from 20 to 26 °C (Gómez 2009).

The Los Amigos watershed comprises sediments dated from the Neogene and Quaternary that have been deposited during the last 20 million years (Pino 2007). The upper sediments at the concession show a sequence of alluvial, lacustrine and tidal deposits dating from the Miocene, Pliocene and Quaternary (Antoine et al. 2003). It is suggested that some of these were deposited by an inner sea present in this part of the Amazon basin during the upper Miocene. This inner sea and its gradual disappearance may have controlled the past and current biodiversity of the region (Hovikoski et al. 2005).

The soils in the Madre de Dios region show a mosaic of clayey, sandy, silty and gravel materials. Studies in the area demonstrate that upland (terra firme) soils are consistently sandier, more acidic and poorer in nutrients than those of the floodplains (Hovikoski et al. 2005; Antoine et al. 2003).

2.2 Study organisms

The parasitoid wasps of the family Ichneumonidae are the focus of this study. In my research I concentrated on the ichneumonids of the group classified as the Pimpliformes (see Gauld 1991). Wahl & Gauld (1998) included in Pimpliformes eight subfamilies divided into two clades. The first clade, known as the higher Pimpliformes, is comprised of the subfamilies Acaenitinae (Fig. 3), Diacritinae, Cylloceriinae, Diplazontine and Orthocentrinae. The second clade, known as the lower Pimpliformes, is comprised of the subfamilies Pimplinae (Fig. 2), Poemeniinae and Rhyssinae (Fig. 4). In my thesis I focus exclusively on the lower Pimpliformes and will refer to them from herein merely as “Pimpliformes”.

The Pimpliformes is defined by a single autapomorphy which is an accessory tooth in the larval mandible (Wahl & Gauld 1998). This uniquely modified mandible is strong evidence supporting the unification of these subfamilies in a single group. This clade is represented mainly by idiobiont parasitoids, which stop the host’s development at the time of oviposition (Askew & Shaw 1986). This strategy allows the parasitoid larva to consume the host’s tissues without resistance (Gauld 1991). The strategy of idiobiont parasitoids is physiologically relatively undemanding because the parasitoid larva is not exposed to the defensive reactions that a fully active host would generate (Gauld 1991). Therefore, idiobiont parasitoids are in many cases able to exploit a wide range of host taxa (Wahl & Gauld 1998). The major exception in the Pimpliformes parasitoids is the *Polysphincta* genus-group. The species of this group are koinobiont ectoparasitoids of spiders. This is a rather unique strategy within Ichneumonidae (Gauld & Dubois 2006), because most of the koinobiont species are endoparasitoids. Koinobiont ectoparasitoids have to overcome a different set of challenges because they remain on the host’s surface during larval development and are exposed to environmental factors such as desiccation and to biotic challenges caused by the host, e.g. the risk of being sloughed off during the ecdysis of the spider (Gauld 1991).

a) Pimplinae

The subfamily Pimplinae is a relatively large cosmopolitan group with 77 genera and more than 1 500 described species worldwide (Yu et al. 2012; II). The origin of Pimplinae appears to be in the northern hemisphere (Wahl & Gauld 1998; Gauld et al. 2002a) since most of the basal lineages are restricted to areas originating from ancient Laurasia. The Pimplinae species include some of the most commonly collected ichneumonids (Gauld et al. 2002b), e.g. in Amazonia the genera *Neotheronia* Krieger and *Pimpla* Fabricius are usually the most abundant groups in Malaise samples (V). This subfamily is the best-known ichneumonid group in the Neotropical region (e.g. Townes & Townes 1966; Townes 1969; Gauld 1991, 2002; Gauld et al. 1998, 2002ab; Gaston & Gauld 1993; Sääksjärvi et al. 2003, 2004, 2006; Valera & Diaz 2010; Aguiar & Ramos 2011; Palacio et al. 2007, 2010; Kumagai 2002; Kumagai & Graf 2002; I, II). The Pimplinae has caught the attention of many ichneumonologists for several reasons. First, it is possibly the most biologically diverse subfamily within the family Ichneumonidae and shows a great variety of parasitoid-host interactions (Fitton et al. 1988; Gauld 1991, Gauld et al. 1998, 2002a). Second, pimplines may be divided into different biological groups (Gauld 1991; Sääksjärvi et al. 2006; V) which is useful in ecological studies. Third, the phylogeny of this subfamily has been relatively well studied (Wahl & Gauld 1998; Gauld et al. 2002a; Sääksjärvi 2003; Gauld & Dubois 2006; Palacio et al. 2007). Fourth, the potential of the subfamily for biological control is significant since many of the species are parasitoids of important lepidopteran pests (Gauld 1991; II). Finally, this subfamily has an important potential as indicator organisms in biodiversity studies (Gaston & Gauld 1993; Bartlett et al. 1999; Sääksjärvi et al. 2006).

b) Poemeniinae

This subfamily is a relatively small cosmopolitan group with 11 genera and about 84 described species worldwide (Yu et al. 2012). It is represented in the Neotropical region by the tribes Rodrigamini (*Rodrigama* Gauld) and Poemeniini (*Ganodes* Townes) which have nine species in total (Yu et al. 2012; Castillo et al. 2014). The species of Poemeniinae usually inhabit areas close to fallen tree trunks. They are known to be associated with standing dead timber where they are able to attack larvae of the coleopteran families Cerambycidae, Buprestridae and less frequently Curculionidae (Gauld 1991). In this study, despite the extensive sampling in the Amazonian region and the examination of different Neotropical materials, no specimens of this subfamily were found. These species are probably extremely rare or even absent in the lowland Amazonia and inhabit mid or high altitude areas which were out of the main scope of this thesis.

c) Rhyssinae

The subfamily Rhyssinae is a relatively small cosmopolitan group with eight genera worldwide and 258 described species (Yu et al. 2012; Rousse & van Noort 2014; III). According to Kamath & Gupta (1962), it is more species rich in the lowland rain forests of Southeast Asia where other ichneumonid groups are also very diverse (see e.g. Townes & Chiu 1970). In the Neotropical region the Rhyssinae is one of the best-known subfamilies (Porter 1975, 1978, 1982; Gauld 1991; Gauld et al. 1997; Porter 2001; Khalaim & Cancino 2013). Previously, the subfamily was believed to be represented in the region by a single genus, *Epirhyssa* Cresson (Porter 1978; Gauld 1991). However, new records of two other genera have been reported: *Megarhyssa* Ashmead from Mexico (Khalaim & Cancino 2013) and *Rhyssa* Gravenhorst from Honduras (Porter 2001). In the Neotropical region *Epirhyssa* is the dominant Rhyssinae genus with currently 55 described species (III).

Porter (1978) suggested that Rhyssinae might be among the most primitive ichneumonids. The species are believed to be idiobiont ectoparasitoids of immature stages of endopterygote insects boring in wood. Although there are no specific host records in the Neotropical region the species *E. mexicana* Cresson has been reported as a parasitoid of coleopteran larva (Maes 1989).

Figure 2. *Xanthopimpla allpahuaya* Gómez & Sääksjärvi, Pimplinae species found in lowland Peruvian Amazonia.

Figure 3. *Arotes ucumari* Castillo & Sääksjärvi, Acaenitinae species found in Peruvian Andes.

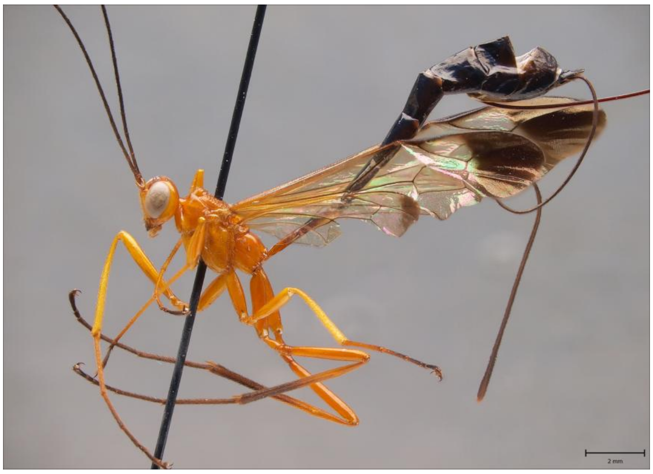

Figure 4. *Epirhyssa iiapensis* Gómez & Sääksjärvi, Rhyssinae species found in lowland Peruvian Amazonia.

2.3 Field work

The main field sampling of this thesis was conducted in two localities in the Peruvian Amazonia separated by about 1 000 kilometers (Fig.1). The first sampling was conducted in southern Peru in Los Amigos Conservation Concession outside of the rainy season during three months (May- July) in 2008. In this locality, sampling was done by Malaise trapping and hand netting in three different slopes, covering a variety of forest types. The sampling of parasitoids was mainly conducted in non-inundated rain forest within about five kilometers from the CICRA biological station (Fig. 5). The sampling was limited to this area mainly because of two factors: the condition of the trails and the presence of groups of illegal gold miners who hunted in nearby areas.

The second field inventory was done in northern Peru in the Allpahuayo-Mishana National Reserve (AMNR). In this area the sampling was conducted outside of the rainy season over nine months (April – December) in 2011. A variety of sampling methods were applied to collect the parasitoid fauna. Some of these methods e.g. light trapping (Fig. 6) were unsuccessful in catching parasitoids and they were not considered in the dataset of this thesis. The sampling was conducted mainly in non-inundated secondary forest within about three kilometers from the Allpahuayo-Mishana biological station. The sampling points within the reserve were chosen to include a variety of forest types in both nutrient poor white sand forests and nutrient rich clay soil forests. During the sampling, a few Malaise traps were stolen, probably by local people who enter the reserve to hunt or to extract trees illegally. In the biological station I conducted a lepidopteran larvae rearing project (V) where the natural history of the larvae and some parasitoids was recorded at detail. Many of these results are not included in this thesis; however, they are ongoing projects that will be published in the future.

2.4 Sampling methods

The most common methods to sample Hymenoptera are Malaise traps, yellow pan traps, sweep-nets, and light-traps (e.g. Noyes 1989). Various studies testing different sampling methods in catching parasitoid wasps have been conducted (Noyes 1989; Idris et al. 2001b; Garcia 2003; Aguiar & Santos 2010). These studies reveal different results and usually the efficiency varies according to the investigated taxa. In general, the most used method in sampling ichneumonids is Malaise trapping (eg. Gauld 1991; Gaston & Gauld 1993; Palacio et al. 2007; Kumagai 2002, Kumagai & Graf 2002; Gonzalez-Moreno & Bordera 2012; Sääksjärvi et al. 2004; I, II, III, V). In both study sites I focused mainly on Malaise trapping. However, to obtain a representative sample of the parasitoid assemblage present in each area and to minimize the possible bias of collecting with a single method I also tried other collecting methods. These methods are explained briefly below:

Figure 5. Canopy view of primary rain forest in Los Amigos Conservation Concession.

Figure 6. Field work in secondary rain forest in Allpahuayo-Mishana National Reserve.

a) Yellow Pan Trap (YPT): This is a plate-like yellow trap (Fig. 7a) where arthropods which are attracted by the yellow color of the dish are trapped in a liquid solution. A total of 100 YPTs were established weekly during 23 weeks in Allpahuayo-Mishana. Each week the traps were located in different areas of the reserve and the samples were collected after 24 hours.

b) Hand netting: Collection with a standard entomological net (Fig. 7b) was done weekly during 13 weeks in Los Amigos and during 23 weeks in Allpahuayo-Mishana. During each week, the sampling consisted of four hours of random hand netting in the nearby rain forests.

c) Larval rearing: In order to study the host-parasitoid interactions, a total of 3 298 lepidopteran larvae were collected from the forests of Allpahuayo-Mishana and reared for adult Lepidoptera or parasitoids (Fig 8a). Each larva was reared individually in a plastic jar of one liter and detailed information about the biological cycle was recorded daily (Fig 8b). The reared material is also used for biochemical analyses of haemolymph in collaboration with the Department of Chemistry, University of Turku (Vihakas et al. in press).

d) Pupal rearing: A total of 113 lepidopteran pupae were collected from the forests of Allpahuayo-Mishana and reared for adult Lepidoptera or parasitoids. Each specimen was held in a one-liter plastic jar and observed daily in order to record whether a parasitoid or a Lepidoptera adult emerged from the pupa.

e) Malaise trapping: The Malaise trap is a tent-like insect trap (Fig. 7c) widely used in parasitoid studies for its efficiency in collecting strong flying insects such as ichneumonids (Gauld et al. 1998, 2000; Kumagai & Graf 2002; Sääksjärvi et al. 2003, 2004; Palacio et al. 2007; Mayhew et al. 2009; Gonzalez & Bordera 2012; Mazon et al. 2014). The data collected by Malaise trapping was used in global comparisons between different studies (V), including a measure of sampling effort expressed in Malaise trap months (MTM). One MTM is defined as the effort of one trap collecting in the field continuously for one month.

Nine Malaise traps were employed in Los Amigos during May-July 2008 with a total effort of 27 MTM. In Allpahuayo-Mishana 14 Malaise traps were employed during April-December 2011 (some traps were stolen) producing a sampling effort of 45 MTM. In order to evaluate the complete Malaise sampling effort in the Peruvian Amazonia, two previous Malaise sampling inventories from Allpahuayo-Mishana reported in Sääksjärvi (2003) were added to the data. The first of these inventories was conducted from August 1998 to January 1999 with a total effort of 41 MTM and the second one from January 2000 to January 2001 with a total effort of 144 MTM. The total sampling effort, combining all periods, was 257 MTM.

Table 1. Sampling methods and effort applied in the two Peruvian Amazonian sites

Site	Allpahuyo-Mishana			Los Amigos
Collection year	1998	2000	2011	2008
Malaise sampling	41 MTM	144 MTM	45 MTM	27 MTM
Yellow pan trap	_	_	76.7 trap months	_
Hand netting	_	_	92 hours	52 hours
Larval rearing	_	_	3298 larvae	_
Pupal rearing	_	_	113 pupae	_

Figure 7. Different sampling methods applied in Allpahuayo-Mishana in 2011. a) Yellow pan trapping. b) Hand netting. c) Malaise traps in different forest types.

Figure 8. Lepidoptera rearing project in Allpahuayo-Mishana in 2011. a) Rearing jars inside the field station. b) Example of the biological cycle documentation done to each collected Lepidoptera larva. The photographs show the cycle of the Hesperiidae *Chioides catillus catillus* (Cramer). c) Variety of larvae reared in the Allpahuayo biological station.

2.5 Other examined material

Most of the ichneumonid material examined in my thesis is based mainly on the long-term sampling conducted in the Peruvian Amazonia as detailed above. In addition, I examined samples collected in the tropical Andes of Peru by my collaborators (Department of Cusco, sampled by Carol Castillo and Department of Junín, sampled by Santiago Bordera and collaborators). Descriptions of these study sites can be found in (III). I also studied a large number of Malaise samples collected from the tropical forests of French Guiana (by the Société Entomologique Antilles Guyane, SEAG team). To broaden the scope of my research outside of Amazonian region I also examined Malaise samples collected from Central America (LLAMA project, led by John Longino); from Chile (Marc Pollet and collaborators) and from Uganda (Heikki Roininen project). In addition, I examined samples collected by canopy fogging in Ecuadorian Amazonia (IV). Lastly, I studied some of the Neotropical Pimpliformes specimens deposited in the following collections:

American Entomological Institute, Gainesville, Florida, USA. (AEIC)

Natural History Museum, London, U.K. (BMNH)

Canadian National Insect Collection, Otawa, Canada. (CNC)

Florida State Collection of Arthopods, Gainesville, Florida, USA. (FSCA)

Philadelphia Academy of Natural Sciences, Philadelphia, USA. (PANS)

Museo de Entomología Klaus Raven, La Molina, Peru. (MEKRB)

Museo de Historia Natural de San Marcos. Lima, Peru. (UNSM)

Museo de Historia Natural de Tamaulipas, México. (TAMUX)

Swedish Museum of Natural History, Stockholm, Sweden. (NHRS)

Colección Entomológica de la Universidad San Antonio Abad de Cusco, Peru.

Colección de Entomología, Universidad de Alicante, Spain. (CEUA)

Instituto Nacional de Pesquisas da Amazonia. Manaus, Brazil. (INPA)

Museu de Zoologia Universidade de Sao Paulo, Brazil. (MZUS)

2.6 Identification of parasitoids

The identification of tropical parasitoid wasps is challenging mainly because of their high diversity but also because most of the species are unknown to science. In addition, the taxonomic attention is not well distributed towards this and other hiperdiverse invertebrate groups (May 2010). Initially, all the individuals were pin and label and first sorted into subfamilies. Then the Pimpliformes subfamilies (Pimplinae and Rhyssinae) were identified into genera and further sorted into species or morphospecies. The specimens were sorted using mainly the identification keys of Gauld (1991), Gauld et al. (1997, 1998) and Porter (1978).

Male specimens were sorted after females, since many reliable morphological characters are found in the structure of the female ovipositor (Gauld 1991). The extensive material examined from different parts of the Neotropical region allowed me to observe the intra- and interspecific variation of the species. Emphasis was made on identifying all the Pimpliformes into described or undescribed species because some of the aims of my study were to provide new faunistic records (I, II, III), describe new species from the region (I, II, III) and evaluate the proportion of known and unknown taxa in Peruvian Amazonian sites (V). The voucher specimens of the Peruvian samples are deposited in the Zoological Museum, University of Turku, Finland (ZMUT). In the future, part of the vouchers will be moved the Natural History Museum of the National University of San Marcos (UNSM), Lima, Peru.

2.7 Analysis

a General analysis

To estimate the general completeness of the field sampling and the total richness of the sampled community, as an overall, species accumulation curves were plotted as a function of sampling effort. Curves that reach an asymptote indicate well sampled assemblages whereas curves that continue to rise are indicative of incomplete sampling. For comparability with previous works, only Malaise trap samples were used for this analysis. In order to estimate the total (observed and unobserved) species richness of the sampled communities, non-parametric estimators were used on both the abundance (Chao1 (Chao 1984), ACE (Chao et al. 1993)) and incidence data (Chao2 (Chao 1987). The ICE and the first and second order jackknifes (Jack 1 and Jack 2 (Burnham & Overton 1979)) were also used. The Chao and Jack 2 estimators use the abundance or incidence of both singletons and doubletons to estimate the unsampled species, whilst Jack1 uses only singletons. ACE and ICE use the number of singletons and other rare species as well as common species. The estimators were calculated by using the program EstimateS (Colwell 1997; Colwell et al. 2012). For a comprehensive review and definition of the estimators and procedures used here see Colwell and Coddington (1994).

b Data analysis on species richness

To document species accumulation patterns as a function of sampling effort in the Peruvian sites, for which time series data were available. Each sampling interval (originally 1 or 2 weeks) from each trap was used as a separate sampling unit. In addition, consecutive sampling intervals from the same trap were aggregated into progressively longer time periods. In this way, sampling units representing a range of sampling efforts were obtained. Entire traps were then randomly pooled, within habitat types only, to observe patterns of species accumulation at the site level (V). To also take into account species abundance patterns, the effective numbers of species was calculated, true diversities sensu Tuomisto (2010). These are also known as Hill numbers after Hill (1973). They equal the reciprocal of the weighted mean of the proportional species abundances, with the speciesabundances themselves used as the weights. Two different means were used, the geometric mean and the arithmetic mean. The former gives a diversity value that equals the exponential of the well-known Shannon index, and the latter gives a value that equals the reciprocal of the Simpson index.

The Chao-1 estimator was used to assess how many additional species could be expected at the site, given the number of species observed only once or twice with a given sampling effort. The estimated number of additional species was then compared with the corresponding sampling effort to check for indication that species sampling was approaching completeness. Division of the Peruvian data to subsets of different sampling efforts made it also possible to compare richness values from 95 parasitoid inventories elsewhere in the world with Peruvian data of similar sampling effort (V). Species accumulation was plotted against both sampling effort in the strict sense (the length of the sampling interval in MTM) and sampling efficiency (the number of Pimplinae and Rhyssinae individuals captured). All analyses were done in the R environment using either the 'vegan' package (Oksanen et al. 2013) or code written by Dr. Hanna Tuomisto.

3. RESULTS AND DISCUSSION

3.1. Increasing the knowledge of Neotropical parasitoids

Xanthopimpla is one of the largest and best studied genera of the family Ichneumonidae. This genus is most species rich in the Oriental and Afrotropical regions and prior to this study it was represented by five described species in the Neotropical region (I). In my thesis I reviewed all the Neotropical species of the genus and described in total six new species, doubling the number of described species and providing 10 new distributional records for the region (I, II). I reorganized the classification within the genus by redefining the only preexisting Neotropical species-group, the *aurita* species-group. In addition, I proposed a new species-group, the *amazonica* group, to accommodate five new species with some unique characters and hypothesized that another species-group will be established when more material from the Andean-Amazonian interface becomes available (II). These studies not only increased the taxonomic knowledge of *Xanthopimpla* but also gave important insights into the distributional patterns of the genus demonstrating that many of the species are actually widely distributed in the region.

Epirhyssa is the largest genus of the subfamily Rhyssinae (III). This genus is believed to be more species rich in tropical Asia (Kamath & Gupta 1972) than in other regions of the world. Interestingly, the Amazonian region was claimed to be rather species poor in *Epirhyssa* species (Porter 1978, 1982). However, Sääksjärvi et al. (2004) reported many *Epirhyssa* morphospecies from Allpahuayo-Mishana showing that these species are potentially abundant in the region. To investigate the species richness of this group I studied the *Epirhyssa* species of Peruvian Amazonia (III) and demonstrated that this area harbors at least 24 valid species and is actually one of the most diverse centers of *Epirhyssa* in the world. In this work 10 new species are described from the Peruvian Amazonia and 15 new distributional records are provided for the Amazonian region. Furthermore, the distribution of the species in the Neotropical region is discussed and it is demonstrated that these species are widely disperse in two main assembles in the Neotropical region.

At the local and regional level, my studies contributed to the increasing knowledge of these parasitoids in Peruvian Amazonia. The most recent checklist of Peruvian ichneumonid species reported a total of 73 Pimpliformes (Rodriguez et al. 2009). In my thesis, just from the two Amazonian sites, a total of 128 Pimpliformes species are reported (V). Furthermore, in my work 22 Pimpliformes species records are added to the Peruvian fauna (I, II, III) and I am currently describing new species from this country in ongoing studies that will be published soon.

In general, these results suggest that the Neotropical region and especially Amazonia is still not well-documented for parasitoid wasps. In Central America, the extensive inventories conducted by the late Ian D. Gauld and collaborators have already demonstrated how superficial the studies of ichneumonid wasps are in the tropics. These researchers increased enormously the knowledge of ichneumonids, describing more than 850 species (Gauld 1991, 2002; Gauld et al. 1997, 1998, 2000) and providing an invaluable baseline for studies of these parasitoids in the Neotropical region.

In the taxonomic part of the thesis, together with my supervisor we gave the public in Finland and Peru an opportunity to propose names for some of the new species (see III). The idea was to draw attention to the unknown but fascinating world of tropical parasitoid wasps. In both countries we launched contests to name the new species of parasitoids, announcing the contests in major newspapers. This idea resulted in an audience of several hundred people participating, albeit in a small way, in tropical biodiversity research and conservation.

3.2. Species richness estimates

Even though the Peruvian Amazonian sites are not the most intensively inventoried areas for ichneumonid wasps to date, they show consistently higher species richness than other localities in the world (V). Indeed, in possibly the most extensively sampled locality in the world, Santa Rosa in Costa Rica, with a huge sampling effort of 576 MTM a total of 40 Pimpliformes species were reported (Gaston & Gauld 1993). This number of species is lower than that found in each of the Peruvian localities (V). In both Peruvian study sites the species richness estimates showed that there are still many ichneumonid species to be collected. The species accumulation curve does not show any signs of stabilizing in either of the sites. Curves that continue to rise beyond the level of present sampling are indicative of incomplete sampling. Furthermore, the proportion of singleton species remains high throughout the collection periods (Fig. 9), indicating that a greater sampling effort is needed in the Peruvian Amazonia**.**

In Los Amigos, a total of 51 Pimpliformes species were sampled and the predicted total number of species according to different estimators was: 91.4 species (ACE), 98.7 species (ICE), 80.0 species (Chao1, SD 14.9), 91.1 species (Chao2, SD 19.5), 79.4 species (Jack-knife 1, SD 12.6), and 97.5 species (Jack-knife 2) (Fig. 9b). The estimators give a mean of 89.7 (SD 8.3 and population SD 7.6) Pimpliformes species for Los Amigos. The values of the commonly used diversity indexes are: Alpha = 33.22, Shannon = 3.58 and Simpson = 25.11.

In Allpahuayo-Mishana, a total of 105 Pimpliformes species were sampled and the predicted total number of species according to different estimators was: 120. 6 species (ACE), 118. 5 species (ICE), 138 species (Chao1, SD 9.8), 122. 3 species (Chao2, SD 9.8), 126.4 species (Jack-knife 1, SD 4. 1), and 136. 2 species (Jack-knife 2) (Fig. 9a). The estimators give a mean of 127 (SD 8.3, population SD 7.5) Pimpliformes species for the Allpahuayo-Mishana. The values of commonly used diversity indexes are: alpha= 25.79, Shannon= 3.89 and Simpson= 30.7.

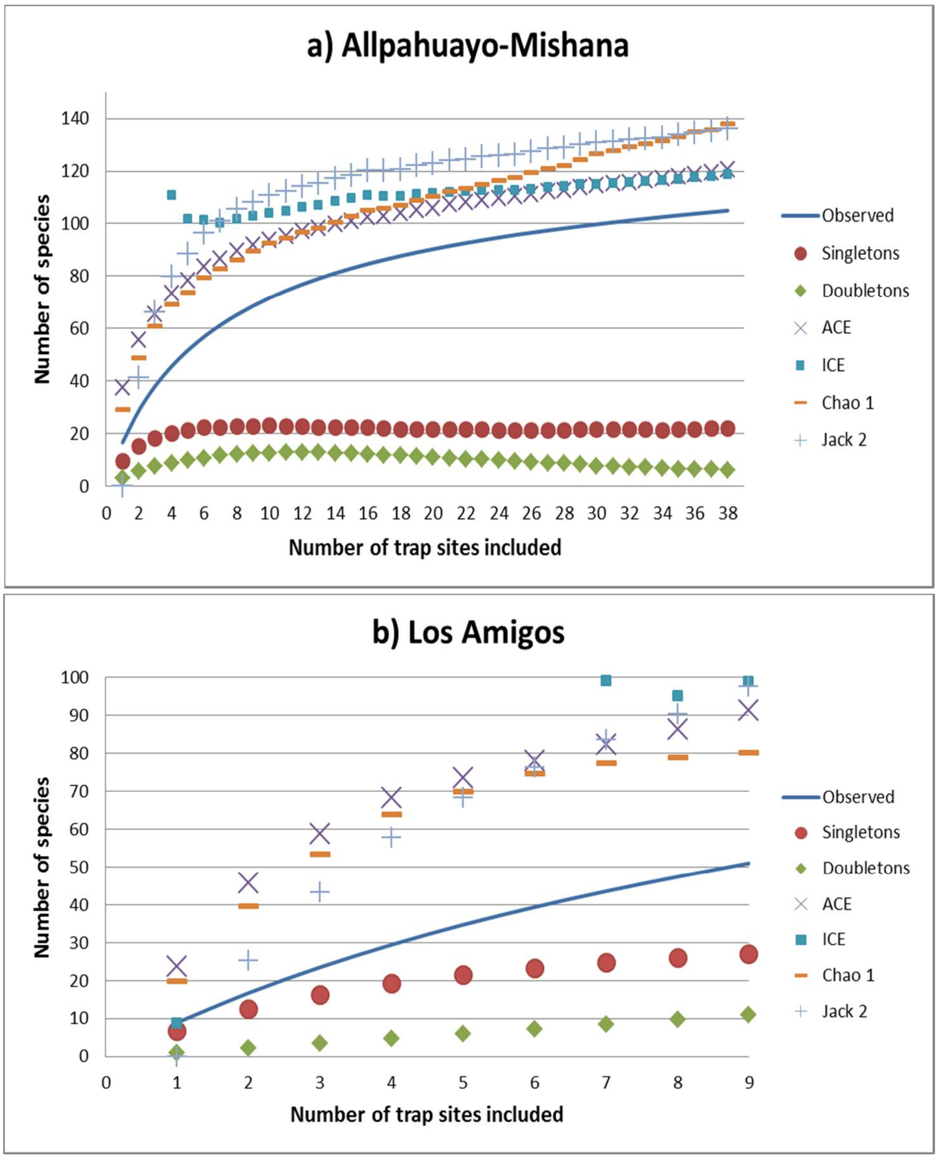

Figure 9. Species richness estimators for the Malaise samples. a) Allpahuayo-Mishana collection from the years 1998, 2000 and 2011. b) Los Amigos collection from the year 2008.

3.3 Highest diversity of Pimpliformes in the world

Combining all the sampling done in the two Peruvian Amazonian localities, a total of 26 390 ichneumonid individuals belonging to 19 subfamilies were collected between the years 1998-2011. The subfamily Pimplinae was represented by 1 622 individuals and the subfamily Rhyssinae by 96 individuals; no Poemeniinae individuals were collected. Overall, 128 Pimpliformes species were identified; all of these were collected by Malaise trapping.

According to the comparative analysis (V) Allpahuayo-Mishana is currently the most species rich locality reported for Pimpliformes parasitoids in the world. Indeed, in the most extensively sampled

Costa Rican study locality, Santa Rosa, with an enormous effort of 576 MTM, only 40 Pimpliformes species were reported (Gaston & Gauld 1993). In the case of Allpahuayo-Mishana, 105 species were found with an effort of 230 MTM. Furthermore, in Los Amigos, a remarkable 51 Pimpliformes species were recorded with a smaller effort of 27 MTM. This number, despite the relatively low sampling effort, is higher than in most of the other localities around the world (V).

Additionally, if the Pimpliformes species richness is compared with an equivalent sampling effort between all the studies the two Peruvian localities show in general higher number of species caught (V). This high richness in Allpahuayo-Mishana and Los Amigos becomes even more evident when the comparison is made with equivalent sampling effort measure by number of individuals against the total number of species (V).

Of the collected Pimpliformes, four genera (*Neotheronia*, *Hymenoepimecis* Viereck, *Epirhyssa* and *Acrotaphus* Townes) seem to be more diverse in the sampled Peruvian localities than in the other localities included in the comparative analysis (V).

On a broader scale, a comparison of ichneumonid studies suggests that the Neotropical localities contain the highest numbers of Pimpliformes species. This result questions the extensively studied phenomenon of the anomalous latitudinal gradient of ichneumonids. To my understanding none of the studies that supported this phenomenon considered in their analysis a wide set of ichneumonid studies from different latitudes. My study shows clearly that the Peruvian localities are among the most diverse localities in the world for Pimpliformes parasitoids (V).

The ichneumonid species richness in Amazonia is possibly very high. The Amazon basin, with a vast extension of 6 290 000 km2 (Ter Stegge et al. 2013), is still mostly unsampled. For example, the two sampled localities combined represent a tiny part (about 0.0003 %) of the Amazon basin. The two Ichneumonid subfamilies alone (Pimplinae and Rhyssinae) are represented by at least 128 species, most likely many more (Fig. 9), in this small part of the region. What could be then the real number of ichneumonids for the whole Amazonia?

To answer this at least two factors need to be considered. First, there is a lack of long term inventories in the region, not only in lowland Amazonia but also in the high and mid altitude areas of the Andean-Amazonian interface which may be inhabited by a different ichneumonid assemblage. The second challenge is the general lack of knowledge about the distributional ranges of ichneumonids in Amazonia which mainly derives from the first factor.

I examined the Pimpliformes species from the two Peruvian localities Allpahuayo-Mishana and Los Amigos, which are separated by about 1000 km, and found that about 22 % of the species were shared between these localities. I was not able to find any distributional study of ichneumonids in Amazonia to provide more insights on this matter and therefore this area of research should be investigated in the future. Townes (1969) estimated that the Neotropical region holds about 17 000 ichneumonid species. Later, Gauld (2002) increased this estimate by a factor of two claiming that about 35 000 species is a more realistic estimate. Here I do not dare launch an estimate of the species richness for the region since I consider that there is not yet enough data, at least for South

America, to provide a reliable figure. Nevertheless, with my short experience studying this group, I hypothesize that the number of ichneumonid species is likely higher than the estimates given by Townes (1969) and Gauld (2002).

3.4 Anomalous diversity gradient and sampling deficiency of ichneumonids

Most of the published studies of ichneumonid parasitoids in the world sampled with Malaise trapping have had a rather low sampling effort (V). This has probably created a bias in the assessment of parasitoid diversity. Clearly, any study on these parasitoids is valuable; however, most of the efforts in the Neotropics have not included long term sampling that could have provided more comprehensive information about the community structure and diversity of these parasitoids.

The anomalous diversity gradient of ichneumonids was proposed by Owen & Owen (1974). This study started an extensive debate on the distributional patterns of ichneumonids. Owen & Owen (1974) studied samples from the temperate region (Sweden and UK) and from the tropical region (Uganda and Sierra Leone). These authors reported that “a quite extraordinary number of species was found once only and no species was really common” in their samples. In fact, in each of the collected sites singleton species accounted for about a third of the total number of species. This suggests that the sampling effort applied, besides of been extensive, was not enough to provide reliable indications about the species richness present in each study locality. Most importantly the data was inadequate to provide such generalization on the latitudinal distributional patterns of ichneumonids because it did not represented sites distributed in a proper latitudinal gradient. Moreover, in diverse areas such as the tropics, inadequate sampling may lead to erroneous conclusions on the distribution of species in different habitats (Tuomisto et al. 1995). Similarly, Gauld (1991) suggested that short term studies may underestimate ichneumonid abundance, especially in the tropics. This author also proposed that reliable estimates of ichneumonid species richness will only be possible when extensive data are amassed.

The results of this thesis about the species richness in the Peruvian Amazonia agree with previous studies suggesting that the widely studied phenomenon of the anomalous diversity gradient of ichneumonids is partly a result of inadequate sampling (Hespenheide 1978; Morrison et al. 1979; Gauld 1991; Sääksjärvi et al. 2004; Santos & Quicke 2011; Quicke 2012; IV; V). In my thesis I tackle this issue and provide, for the first time, a study that gathers almost a hundred sampled localities distributed in a proper latitudinal gradient (V). The results of this work lend no support for the existence of a latitudinal species richness gradient in ichneumonids parasitoids.

The most completely sampled locality in Amazonia (Allpahuayo-Mishana), according to the global comparative analysis (V), currently holds the highest reported Pimpliformes species richness. However, as expected, Allpahuayo-Mishana is still incompletely sampled (Fig. 9a) even after two full years of sampling effort. This situation is still common in the Neotropical region, especially with hyperdiverse organisms such as parasitoid wasps. Furthermore, only a small fraction, certainly less than 20 %, of tropical insects have been found and described (Godfray et al. 1999). As stated earlier, the subfamilies Pimplinae and Rhyssinae are among the best-known ichneumonid taxa in the Neotropical region. Of the 128 Pimpliformes species reported from the Allpahuayo-Mishana and Los Amigos, according to my identifications, the majority represent undescribed species. Therefore, if the majority of ichneumonid species is still unknown from the best-studied subfamilies most probably the diversity gradients of ichneumonid parasitoids have been investigated without sufficient knowledge of their species richness (Hespenheide 1978; Morison et al. 1979; Quicke 2012).

3.5 Testing different sampling methods for ichneumonids

During the field work conducted in Allpahuayo-Mishana in 2011 I used five sampling methods to obtain a representative sample of the ichneumonid assemblage present in the area and to test which methods were most efficient in capturing parasitoid wasps.

In general, Malaise trapping was the most efficient method, collecting 1 961 ichneumonid individuals, 74 % of the total catch (2 640 individuals) with significant proportions in all the subfamilies (Table 2). All the Pimpliformes species encountered in the inventory as a whole were found in the Malaise traps. This finding is in agreement with those of Gauld (1991); Gaston & Gauld (1993) and Hanson & Gauld (1995) who claimed that Malaise trapping is probably the best method to collect large numbers of ichneumonid parasitoids.

Yellow pan trapping (YPT) collected 19 % (511 individuals) of all ichneumonids. In the specific cases of the subfamily Nesomesochorinae, YPT was more efficient than Malaise trapping with 68 % (55 individuals) of the total 81individuals captured. YPT collected important quantities also in two other subfamilies, Cryptinae with 33 % (386 individuals), and Ichneumoninae with 20 % (50 individuals) of the total captured in each subfamily. These results are partially due to the YPT being established next to the trail systems in Allpahuayo-Mishana: according to my field observations, individuals of these two subfamilies are usually encountered flying along trails close to the forest edge. In the case of the Pimpliformes subfamilies, not a single specimen was caught by YPT. However, in a study in Poland (Piekarska-Boniecka et al. 2009) 34 Pimpliformes species were collected using this method, suggesting than YPT may be efficient in trapping Pimpliformes in other regions. The result of YPT collecting large numbers of Cryptinae is similar to the findings of Aguiar & Santos (2010) in Brazil. These authors found that in general, YPT collected more Cryptinae than Malaise traps. Under this evidence YPT could be considered an effective method, at least in the Amazonian region, for studies targeting the subfamilies Cryptinae, Ichneumoninae or Nesomesochorinae.

Hand netting collected 5% (142 individuals) of the ichneumonids. However, the sampling effort made with this method was considerably lower (one net) in comparison with the Malaise or YPT (many traps in both cases). Interestingly, from the total subfamily catch, hand netting collected 24% (20 individuals) of the Anomaloninae, 21 % (4 individuals) of the Rhyssinae, and 8% (17 individuals) of the Pimplinae. Therefore, hand netting is worth applying in ichneumonid studies since this method is useful when targeting specific groups of parasitoids. For instance, in the case of Rhyssinae, expending time close to fallen trunks yielded some individuals of *Epirhyssa*. If the focus is on Anomaloninae or Cremastinae, using the net in grass-like vegetation is likely to yield many individuals of these subfamilies.

Larval rearing, with a total of 3 298 larvae, resulted in less than 1 % of the total ichneumonids collected. Moreover, it did not contribute any specimen of Pimpliformes. This result is strongly in agreement with the literature since Pimpliformes are known to be mainly idiobiont ectoparasitoids of concealed hosts or idiobiont endoparasitoids of pupal stages of Lepidoptera (Gauld 1991). Pupal rearing, with a low effort (113 rearings), contributed three individuals of Metopiinae and one of Pimplinae. This method is not commonly applied in ichneumonid studies and because of this it could yield new taxa.

Table 2. Subfamily catches with different sampling methods in Allpahuayo-Mishana 2011.

Subfamily	Sampling method										Subfamily total	
	Malaise trapping		Yellow pan trapping		Hand netting		Larval rearing		Pupal rearing			
	individuals	%	individuals	%	individuals	%	individuals	%	individuals	%	individuals	%
Anomaloninae	49	2,5	10	2,0	20	14,1	3	13,6	0	0	82	3,1
Banchinae	79	4,0	3	0,6	0	0,0	5	22,7	0	0	87	3,1
Brachycyrtinae	18	0,9	0	0,0	1	0,7	0	0,0	0	0	19	0,7
Campopleginae	103	5,3	1	0,2	0	0,0	4	18,2	0	0	108	4,1
Cremastinae	239	12,2	1	0,2	6	4,2	2	9,1	0	0	248	9,4
Cryptinae	712	36,3	386	75,5	70	49,3	0	0,0	0	0	1168	44,2
Ichneumoninae	186	9,5	50	9,8	11	7,7	3	13,6	0	0	250	9,5
Labeninae	41	2,1	0	0,0	3	2,1	0	0,0	0	0	44	1,7
Lycorininae	5	0,3	0	0,0	0	0,0	1	4,5	0	0	6	0,2
Mesochorinae	10	0,5	0	0,0	0	0,0	0	0,0	0	0	10	0,4
Metopiinae	22	1,1	0	0,0	0	0,0	4	18,2	3	75	29	1,1
Nesomesochorinae	24	1,2	55	10,8	2	1,4	0	0,0	0	0	81	3,1
Ophioninae	68	3,5	0	0,0	3	2,1	0	0,0	0	0	71	2,7
Orthocentrinae	154	7,9	4	0,8	3	2,1	0	0,0	0	0	161	6,1
Pimplinae	187	9,5	0	0,0	17	12,0	0	0,0	1	25	205	7,8
Rhyssinae	15	0,8	0	0,0	4	2,8	0	0,0	0	0	19	0,7
Tersilochinae	49	2,5	1	0,2	2	1,4	0	0,0	0	0	52	2,0
Total per trap	1961		511		142		22		4		2640	100
Trap catch (%)	74,3		19,4		5,4		0,8		0,2		100	

3.6 Future research

The results of my thesis and previous studies (Gauld 2000; Sääksjärvi et al. 2004) suggest that the study of tropical ichneumonids is still in an initial stage. The main reasons for this situation are probably the enormous diversity of the family (Gauld 2002, V) and the generalized small sampling effort in high altitude regions or in vast lowland areas such as the Amazonian region (I, II, V). Further research on tropical ichneumonids is needed in e.g. the following areas:

1) Taxonomic studies: Although they are often disregarded and overlooked, taxonomic studies are crucial in improving knowledge of ichneumonids (I, II, III). This area of research is the baseline for any type of biological studies. The role of taxonomy is especially important in this group because the majority of species are still unknown. Therefore, the production of taxonomic studies is important to improve this situation. Furthermore, without this area of research many species of insects may continue to go extinct without even being described loosing invaluable knowledge.

2) Further sampling and species richness studies: The sampling effort applied in most ichneumonid inventories (V) is still not large enough to provide reliable data to estimate the real size of the largest family of Hymenoptera. The lack of long term sampling is most probably the major weaknesses in tropical parasitoid studies (IV, V). The sampling effort applied for my thesis, although being likely the most extensive conducted in Amazonia, was demonstrably insufficient to document most species present in this area. Therefore, further sampling is required different areas especially in highly diverse tropical areas of the world (V).

   Different studies have shown that Malaise trapping is the most efficient method to sample ichneumonid parasitoids and my results (V) support these claims. I suggest, as previous researchers have done (e.g. Gauld 1991; Sääksjärvi et al. 2004; Fraser et al. 2008), that Malaise traps should be widely used in ichneumonid studies. This would allow comparability between studies in different areas of the world. Optimistically, future long term inventories will provide a deeper understanding of the real distributional patterns and species richness of the family Ichneumonidae.

3) Applied studies: Knowledge of the natural history of ichneumonid parasitoids is very limited, particularly in tropical areas. Ichneumonids may provide many useful applications to e.g. pharmacological studies due to the different toxins that they possess.

   Some ichneumonid species have potential to be of economic importance for agriculture (e.g. *Xanthopimpla* species) and forestry (e.g. *Epirhyssa* species). Studies of the natural history of ichneumonids may propose species that will be important biological control agents for these industries.

   Some ichneumonid species are also used as indicators of habitat perturbation in tropical organic plantations. This role is important in, for example, the organic coffee and cacao (*Theobroma cacao*) industries which are rapidly expanding in tropical areas such as

Amazonia. The growing industry of organic agriculture is likely to benefit from studies on key parasitoid species that could be used to control economically significant pests. The resultant decrease in the use of pesticides and other harmful chemicals would contribute to preserving the biodiversity of the Amazonian region.

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