Subfamily composition of Ichneumonidae (Hymenoptera) from western Amazonia: Insights into diversity of tropical parasitoid wasps

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Abstract. 1. Previous studies have found the parasitoid wasp family Ichneumonidae (Hymenoptera) to have an exceptional latitudinal species richness gradient that peaks at mid-latitudes instead of the tropics; however, insufficient tropical sampling and species description may have biased the conclusions. It has been unclear which subfamilies might be species rich in tropical lowland rain forests.

2. This study reports the subfamily abundance composition of a large ichneumonid data set (> 30 000 individuals in 20 subfamilies) collected by Malaise traps and insecticidal canopy fogging in Amazonian Ecuador and Peru and suggests which subfamilies would be important for future study.

3. Relative abundance data from one Peruvian site are compared to similar lowland samples from Costa Rica and Georgia (USA).

4. Contrary to a common assumption, a number of ichneumonid subfamilies are very abundant and presumably species rich in western Amazonia. Cryptinae and Orthocentrinae are noticeably the two most abundant subfamilies, and a number of koinobiont lepidopteran parasitoids, which are generally thought to be scarce in the tropics, are also surprisingly abundant (e.g. Anomaloninae, Banchinae and Cremastinae). However, the subfamilies whose primary hosts are rare in the tropics (e.g. Ctenopelmatinae, Tryphoninae) can still be expected to be more diverse in the temperate than in tropical zone.

5. Further research on the latitudinal species richness gradient within different ichneumonid subfamilies is encouraged to help understand what factors determine macroecological species richness patterns and what is the total number of ichneumonid species on earth.

Key words. Abundance, canopy, idiobiont, koinobiont, Neotropics, parasitoid wasps, tropical rain forest.

Introduction

One of the most striking biogeographical and ecological patterns is the gradient of increasing species diversity from the poles to the equator (Gaston, 2000; Hillebrand, 2004). The earliest explorer-naturalists noticed that the tropics teem with life, the temperate zones have fewer kinds of animals and plants, and the Arctic and Antarctic regions by comparison are stark and barren (Wallace, 1878; Hawkins, 2001). A classical exception to the regular latitudinal pattern is the apparent anomalous species richness gradient of the large family Ichneumonidae (Hymenoptera; e.g. Willig *et al.*, 2003).

Most ichneumonids are parasitoids that develop feeding in (endoparasitoids) or on (ectoparasitoids) other arthropods, finally killing the host. Koinobiont species generally allow the host to continue its development after oviposition, and they have

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become specialised to tolerate the host's immunological and chemical defences, whereas the more generalist idiobionts paralyse the host permanently or even kill it to circumvent its immune system (see Askew & Shaw, 1986; Santos & Quicke, 2011). Unlike most other groups of organisms (Gaston, 2000), several studies have failed to demonstrate an increase in ichneumonid species richness from temperate latitudes towards the tropics (Owen & Owen, 1974; Janzen, 1981; Skillen *et al.*, 2000; but see Gauld, 1987). This is puzzling, because many arthropod groups that ichneumonids utilise as hosts show their highest species richness in tropical regions (Robbins & Opler, 1997; Höfer & Brescovit, 2001; Erwin *et al.*, 2005; but see Kouki *et al.*, 1994). Despite their proclaimed poor representation in the tropics, Ichneumonidae has still been estimated to be possibly the largest animal family on earth (Gauld *et al.*, 2002: over 100 000 species; Yu *et al.*, 2005: ca. 23 300 described species). As a result, their global distribution has prompted discussion and multiple hypotheses to explain the supposed latitudinal species richness gradient anomaly (see Sime & Brower, 1998; Santos & Quicke, 2011).

A recent review by Santos and Quicke (2011) explores the possibility that some large-scale patterns of parasitoid insects may be artefacts owing to biases in species sampling and description, and they explain that much of the current overall picture can follow from differential latitudinal representation of different subfamilies. However, it has not been demonstrated which subfamilies might be more species rich in the tropics than in temperate regions. Indeed, the lowland tropics have been undersampled compared to the temperate zone, and the studies in the tropics have not embraced multiple collecting methods, time periods or habitats. Species accumulation curves and proportions of undescribed species per sample still suggest that a majority of tropical lowland ichneumonid species are yet to be discovered (Horstmann *et al.*, 1999; van Noort, 2004; Sääksjärvi *et al.*, 2004). Certain ichneumonid subfamilies and tribes, for example some idiobionts (Pimplinae, Rhyssinae and Cryptini) and nocturnal koinobionts (Ophioninae), have in fact been observed to be at their richest in tropical regions (Gauld, 1986, 1987; Sääksjärvi *et al.*, 2004; Zúñiga Ramirez, 2004). Whether these are the only groups more diverse in the tropics is still open to debate. For example, Santos and Quicke (2011) highlight the Orthocentrinae, a koinobiont subfamily typically associated with fungivorous dipteran hosts (but see Yu *et al.*, 2005 for other host taxa), whose tropical fauna might be neglected because of the species' small body size.

The Neotropical region is the focus of this study. The Costa Rican Ichneumonidae are relatively well documented (Gauld, 1991, 1997, 2000; Gauld *et al.*, 1998, 2002). Taxonomic papers have also been published on the Mexican and Cuban faunas (Kasparyan & Ruíz Cancino, 2005, 2008; Fernández Triana *et al.*, 2006; González-Moreno, 2011). Elsewhere in the Neotropics, studies are scattered and few (see Yu *et al.*, 2005). Data for Amazonian Ichneumonidae are still markedly wanting. The largest rain forest area in the world spreads across the Amazon River Basin, covering about 6.8 million km^2 (Goulding *et al.*, 2003). Amazonia is an extremely species rich but insufficiently studied ecosystem (e.g. Wilson & Sandoval, 1996). Lowland rain forest canopies in particular are known to harbour numerous undescribed arthropod species (Erwin *et al.*, 2005; Erwin & Geraci, 2009). Amazonian ichneumonids remained basically unexplored up until 10 years ago when the first (and so far only) long-term Malaise trap project was carried out in north-eastern Peru (Sääksjärvi, 2003). Gradually, the ichneumonids at the Andean and Andean–Amazonian interface are also becoming better known (Palacio *et al.*, 2007; Broad *et al.*, 2011; Castillo *et al.*, 2011). A lack of knowledge on the South American ichneumonid fauna restricts our understanding about the family's global distribution and diversity; thus, the situation needs serious attention.

Parasitoids play an important role in tropical trophic interactions and food web dynamics (Lewis *et al.*, 2002; Tylianakis *et al.*, 2007; Dyer *et al.*, 2010), and thus, it is important to have a clear understanding of their diversity. Tropical biodiversity is disappearing at an alarming rate owing to human activities (Bass *et al.*, 2010), accentuating the need for accurate assessment of parasitoid diversity. Shaw and Hochberg (2001) even question the utility of conservation initiatives that do not take parasitic wasps into account.

As the family is of enormous size and encompasses a great variety of parasitoid life history strategies (Gauld, 2000), it seems best to investigate the latitudinal species richness gradient with smaller clades or functional groups within the family. The main aim of this study is to show which subfamilies might have a regular latitudinal species richness gradient in the Western Hemisphere. We hypothesise that some ichneumonid subfamilies are very abundant in the Neotropics – even more abundant than they are in extra-tropical samples from southern USA. This study reports the subfamily abundance composition of a data set collected in the lowland rain forests of Ecuador and Peru. The results of one of the Peruvian sites is compared to published data from Central American lowland rain forest (La Selva, Costa Rica) and North American temperate forest (Hitchiti Experimental Forest, Georgia, USA).

Material and methods

Field sampling was carried out at three study sites in western Amazonia (Fig. 1), under the aegis of three separate biodiversity inventory projects. The sampling was carried out by ground-level Malaise traps in Peru and insecticidal canopy fogging in Ecuador during 1994–2006.

Ecuador, Orellana: Onkone Gare and Tiputini

In eastern Ecuador, TLE and his research team used insecticidal canopy fogging to sample arthropods near Yasuní National Park, Department of Orellana, from the rain forest canopy (see Lucky *et al.*, 2002; Erwin *et al.*, 2005). The team worked at two study sites, Onkone Gare (OG; 0°39′25.685″S, 76°27′10.813″W) and Tiputini Biodiversity Station (TBS; 0°37′55.397″S, 76°08′39.204″W), located at about 220 m above sea level. The area consists of primary lowland rain forest, where annual precipitation usually exceeds 2500 mm and the temperature remains above 10 °C (Pitman, 2000). The Yasuní region is
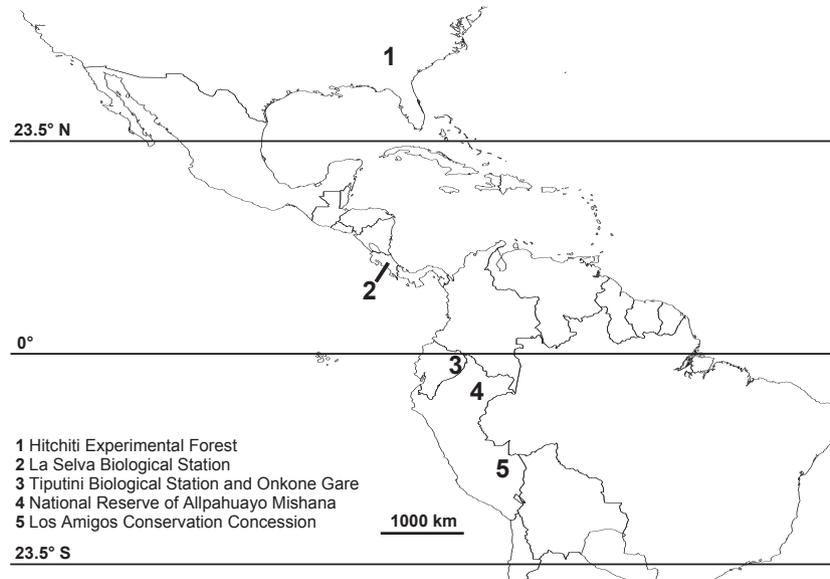
Fig. 1. Field study areas in western Amazonia (3–5) and the areas from where published records were used for latitudinal subfamily abundance comparison (1, 2).

acknowledged to be one of the most biodiverse areas in the entire world; nevertheless, the petroleum industry is regarded as a major threat to its future (Bass *et al.*, 2010).

The canopy fogging projects in Ecuador have so far produced 2100 samples, of which 1079 were studied here. Each sample was obtained with a single fogging from a column (1 m off the ground to as much as 37 m tree height) of rain forest vegetation on a 9-m² collecting surface. The data were collected in three seasons (January–February, July and September–October) across five field work years during 1994–1996 (OG), 1998–1999 (TBS) and 2005–2006 (OG). Both at OG and at TBS, the study area was 100 m × 1000 m in size and included ten 10 m × 100 m transects (1 ha in total). Within each of these transects, 10 collecting sheets of 9 m² size were placed at the same spot on every sampling event. Each site is georeferenced, and all contributing tree species are identified.

Pyrethroid insecticide was fogged up to the canopy using a Curtis DynaFog Golden Eagle Thermal Fogger™ (Curtis Dyna-Fog, Ltd., Westfield, IN, USA). Sampling was carried out in the early morning hours (4–5 a.m.) when air currents are relatively low in tropical rain forests and most insects are least active. The sheet was spread one metre above the ground, tied from its corners to nearby plants, with a collecting jar filled with 80% ethanol placed in the middle and underneath it as a large funnel. A 2-hour drop time was allowed before sample harvesting.

Peru, Loreto: Allpahuayo Mishana (NRAM)

Malaise trap samples were obtained by IES in the National Reserve of Allpahuayo Mishana (NRAM) located about 25 km south-west of the large city of Iquitos, Department of Loreto, Peru (3°57′S, 73°26′W). The NRAM area lies between 100 and 200 m above sea level in a lowland tropical rain forest terrain varying from flat to hilly. The nearby rain forests are extremely heterogeneous in structure and species composition (Whitney & Alvarez Alonso, 1998). The NRAM area is composed of various rain forest types growing on clayish, white sand or loamy soils (Räsänen *et al.*, 1998) that differ from each other in physiognomy and floristic composition (Ruokolainen & Tuomisto, 1993, 1998). All sampling effort was concentrated on non-inundated *tierra firme* sites where primary rain forests represent various forest types with differing geological histories. The environmental conditions and climate of this ca. 57 000-ha national reserve and its vicinity have been described in detail in the study of Kalliola and Flores Paitán (1998).

The NRAM Malaise trap sampling was conducted in two parts in August 1998–January 1999 and January 2000–January 2001. There were four different sampling areas, one near the village of Mishana and three close to the Iquitos-Nauta road, each containing several rain forest types typical at NRAM. The sampling programme was the same in both sampling periods and in all areas. In total, five Malaise traps (Marris House Nets, UK; also used in Costa Rica, see for example Gauld, 1991) were placed in each study area: two in forests on clayish to loamy soils (high to intermediate in nutrients) and three in forests on nutrient-poor white sand soil with differing humidity and forest structure. They were set up at supposed insect-flying routes and emptied every 2–4 weeks. Trap-specific sampling periods varied because sometimes heavy rains or flooding of small rain forest streams prevented trips to the traps. The total sample size was 185 Malaise trap months (hereafter MTMs): 44 in 1998 and 141 in 2000.

Peru, Madre de Dios: Los Amigos (ACC)

A Malaise trap sampling programme was carried out by ICG at the Los Amigos Conservation Concession (ACC; 12°34′S,

70°05′W), Department of Madre de Dios, Peru. The ACC area covers about 146 000 ha at 260 m above sea level. The soil types of the region show a mosaic of clayey, sandy, silty and gravel materials, and the soil texture can vary dramatically on a small scale, even within a single forest type. Despite the variability in texture, the vast majority of upland soils in the region fall into Ultisols and Inceptisols (Pitman, 2000). The climate of the region is humid and seasonal, with a pronounced 3–4-month dry season in June–September and wet season from October until May, the wettest months lasting from December to February. The mean annual rainfall in 2000–2004 was 2776 mm (ranging from 2613 to 3498 mm), and the mean annual temperature remained around 23 °C (monthly mean temperatures 20–26 °C). Altogether, nine traps ran from May to July 2008, making the total sample size 27 MTMs.

Latitudinal comparison

After mounting and identifying the ichneumonids to subfamilies in the laboratory, the subfamily abundance composition was observed for each study area and for the total data set. The NRAM subfamily abundance composition was contrasted to similar published data from La Selva (Costa Rica; 10°26′N, 83°59′W) and Hitchiti Experimental Forest (HEF, Jones County, GA, USA; 33°03′N, 83°43′W) reported elsewhere (Gaasch *et al.*, 1998; Shapiro & Pickering, 2000). Like the NRAM data, the published studies involved Malaise trap samples collected year-round in lowland forests. Shapiro and Pickering (2000) ran Malaise traps at La Selva for 1 year beginning in January 1997. They placed two traps at each of the two 20-year and two old-growth forest sites, thus resulting in a sample size of 96 MTMs (8 Malaise traps × 12 months) and collecting altogether 10 170 ichneumonid individuals. Gaasch *et al.* (1998) ran one trap in each of the five different forest stands at HEF (1990 clear cut, 30–45-year-old pine, 60–85-year-old pine with prescribed burning, 60–85-year-old without management and 70-year-old riparian deciduous) from January 1993 to December 1994, thus resulting in a sample size of 120 MTMs (5 Malaise traps × 24 months) and collecting 16 584 ichneumonid individuals.

Results

Subfamily composition

In total, 31 733 ichneumonid individuals were collected (NRAM: 21 738, Orellana: 8050, ACC: 1945) belonging to 20 subfamilies. The areas were relatively similar in their proportional subfamily compositions (Fig. 2). Cryptinae (24.7–38.0%) and Orthocentrinae (15.2–34.1%) were clearly the two most abundant subfamilies in all three data sets, followed by the rest in a changing and gradually declining order. All the subfamilies were represented only in the Ecuadorian Orellana data, while Xoridinae was missing from the NRAM, and Lycorininae and Xoridinae from the ACC samples. Some noticeable differences between the areas were the higher proportion of Mesochorinae in Orellana compared to the two other areas (7.6% to 0.4–0.7%) and lower proportions of Anomaloninae (1.0% to 5.0–5.7%) and Cremastinae (2.9% to 6.4–9.2%) at NRAM. To the authors' knowledge, previously unreported subfamilies from Ecuador are Anomaloninae, Cremastinae, Ctenopelmatinae, Lycorininae, Nesomesochorinae (represented by *Nonnus* - a genus of Neotropical distribution recently transferred from Campopleginae to Nonninae by Quicke *et al.*, 2005 and then to Nesomesochorinae by Quicke *et al.*, 2009), Orthocentrinae, Tersilochinae and Xoridinae (Yu *et al.*, 2005), whereas unreported from Peru are Ctenopelmatinae and Tersilochinae (Rodríguez-Berrío *et al.*, 2009).

Latitudinal comparison

When the NRAM and previously published subfamily abundances were compared across latitudes, the subfamily
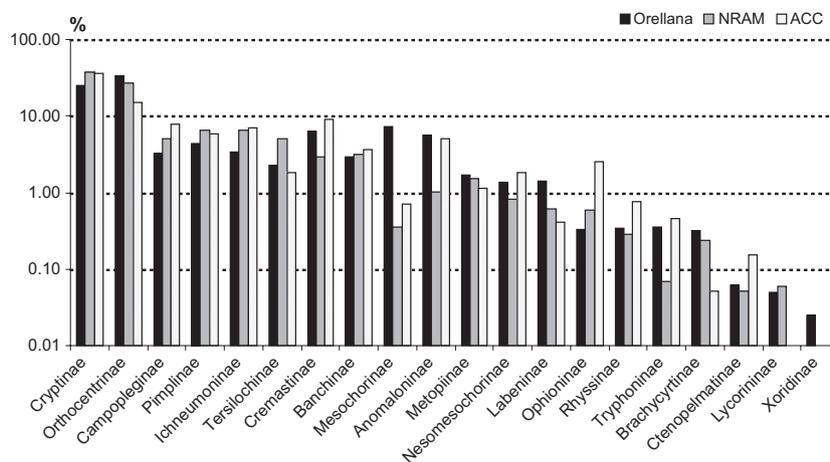
Fig. 2. Proportional subfamily abundances of each study area on a logarithmic scale from the most to least abundant subfamily in the total dataset.

compositions showed somewhat different trends (Fig. 3). On average, 138 individuals were collected per one MTM at HEF, 106 at La Selva and 118 at NRAM. In all areas, among the most abundant families were Orthocentrinae (19.7–27.3%), Cryptinae (15.0–38.0%), Campopleginae (5.0–15.2%), Ichneumoninae (6.5–13.9%) and Pimplinae (3.0–17.6%), followed by Banchinae (2.1–3.2%) and Metopiinae (1.5–3.2%). Proportional abundances were higher in the Neotropics than in HEF for, for example, Tersilochinae (5.0–11.3% to 1.1%) and Cremastinae (2.9–6.1% to 0.9%) and higher at HEF than in the Neotropics for, for example, Ctenopelmatinae (1.0% to <0.1%), Tryphoninae (3.6% to <0.1%) and Mesochorinae (1.4% to <0.6%). Anomaloninae (<1.2%), Labeninae (<0.6%), Lycorininae (<0.1%), Ophioninae (<1.6%) and Rhyssinae (<0.3%) were present but proportionally fairly rare in all the areas. Subfamilies collected in only one area were Acaenitinae (1.0%), Diplazontinae (0.2%), Eucerotinae (<0.1%), Poemeniinae (0.2%) and Xoridinae (0.3%) at HEF, Oxytorinae (0.2%) at La Selva, and Brachycyrtinae (0.2%) and Nesomesochorinae (0.8%) at NRAM.

Discussion

This study clarifies with primary abundance data from the western Amazon Basin which ichneumonid subfamilies might be species rich in the Neotropics and thus interesting for future large-scale diversity pattern studies. Table 1 summarises the life history strategies and sizes of the subfamilies present in western Amazonia and provides further explanations relevant to interpret their Neotropical diversity. Contrary to the common assumption, a number of ichneumonid subfamilies are very abundant and presumably species rich in the western Amazon Basin. However, certain subfamilies (e.g. those whose primary hosts are rare in the tropics: Ctenopelmatinae, Tryphoninae) can still be expected to be more diverse in the temperate than in

the tropical zone. This study resulted in some new surprising findings (e.g. some koinobiont endoparasitoids of Lepidoptera are relatively abundant in the equatorial region) and gave more support to earlier speculation about groups that are likely to be diverse in the tropics (e.g. some idiobiont ectoparasitoids).

A striking result was the high Amazonian abundance of many koinobiont subfamilies, especially of those parasitising Lepidoptera. Latitudinally decreasing species richness of koinobionts has been marked several times (e.g. Gauld, 1987; Skillen *et al.*, 2000) and hypothesised to be a consequence of, for example, more fragmented resources, increased predation or higher levels of plant secondary chemicals in the tropics (see Sime & Brower, 1998; Santos & Quicke, 2011). A large proportion of singletons and doubletons is typical of tropical arthropod studies, that is, a high abundance is often an indication of a high number of species (Coddington *et al.*, 2009). Thus, there is reason to expect a high Amazonian abundance to be an indication of a high number of species for, for example, Anomaloninae, Banchinae, Cremastinae and Metopiinae, which are koinobiont parasitoids of Lepidoptera. Two large koinobiont subfamilies also parasitising Lepidoptera, the Campopleginae and Ichneumoninae, were somewhat more abundant in the temperate than in the tropical samples. Gauld (1987) suggested that the diurnally active, commonly black campoplegines lacking aposematic coloration are more prone to predation and thus less diverse in the tropics than at higher latitudes. What the situation for these two subfamilies really is at the species level is left for future studies to uncover.

Recent molecular studies have revealed several cryptic parasitoid species complexes: what were thought to be single species have turned out to be multiple morphologically similar but molecularly and ecologically distinct ones (Smith *et al.*, 2008). Molecular techniques such as DNA barcoding has helped distinguish ichneumonids both in the temperate (Smith *et al.*, 2009) and in the tropical zones. The discovery of cryptic species revises the current understanding of parasitoid geographical distribution ranges, which, for tropical ichneumonids, have been
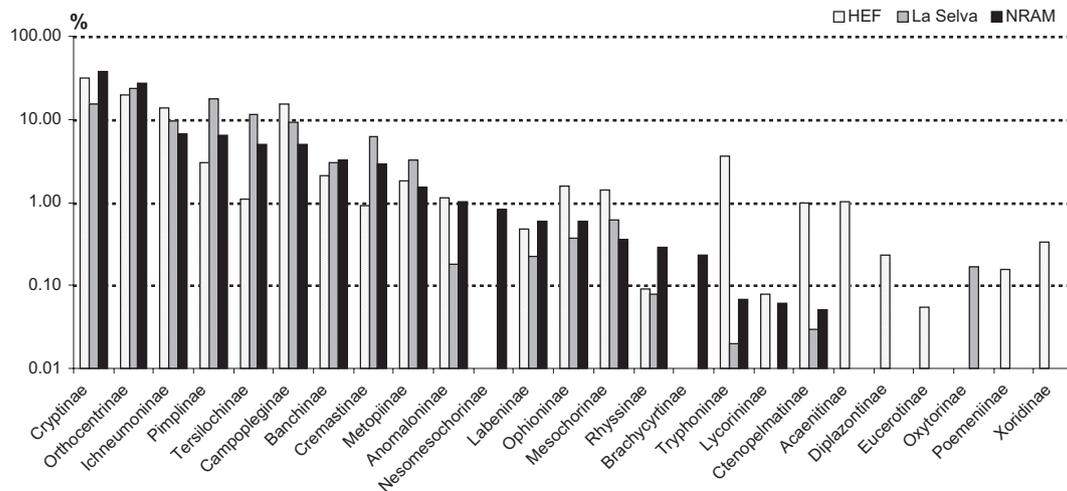
Fig. 3. Latitudinal comparison of proportional subfamily abundances in lowland forest Malaise trap samples collected year-round from HEF (120 MTMs), La Selva (96 MTMs) and NRAM (185 MTMs) on a logarithmic scale from the most to least abundant NRAM subfamily. The original HEF and La Selva data have been published elsewhere (Gaasch *et al.*, 1998; Shapiro & Pickering, 2000).

Table 1. The life history strategies and sizes of the subfamilies present in western Amazonia, with further explanations relevant to interpret their neotropical diversity. Higher classification – 1: Brachycyrtiformes, 2: Ichneumoniformes, 3: Labeniformes, 4: Ophioniformes, 5: Pimpliformes, 6: Xoridiformes. Parasitoid strategy – K: koinobiont, I: idiobiont, ecto: ectoparasitoid, endo: endoparasitoids, hyper: hyperparasitoids, pseudo: pseudoparasitoids. Known/primary hosts – Ara: Araneae, Col: Coleoptera, Dip: Diptera, Hym: Hymenoptera, Lep: Lepidoptera, Meg: Megaloptera, Neu: Neuroptera. Size – approximate number of valid taxa in the world. Data – individuals in the western Amazonian dataset. Comments – further information relevant to the subfamily's neotropical diversity. Higher groups according to Quicke et al. (2009). Biology and size according to Broad et al. (2011), Gauld (1991, 1997, 2000), Gauld et al. (2002), Kasparyan and Ruiz Cancino (2005), Palacio et al. (2007), Sääksjärvi et al. (2004) and Yu et al. (2005).

	Subfamily	Biology	Host groups	Size (valid genera; valid spp.)	Data	Comments
1	Brachycyrtinae	Little known; solitary ecto	Neu (Chrysopidae)	Small (1; 20)	77	Morphological diversity highest in tropical America; mostly lowland species.
2	Cryptinae	I ecto; some K endo; pseudo	Lep, Col, Dip, Hym, Ara	Very large (395; 4661)	10 943	Cryptini most species rich in the tropics; biology of tropical species little known.
	Ichneumoninae	K endo	Lep	Very large (438; 4288)	1834	Host-specific species; a little studied subfamily especially in the tropics.
3	Labeninae	I ecto	Wood-boring Col and Hym; Hym (Aculeata)	Moderately small (12; 150)	252	Most species rich in South America and Australia.
4	Anomaloninae	K endo	Lep, Col (Tenebrionidae)	Moderately large (43; 730)	775	Thought to be most species rich in temperate forests; in the Neotropics, highest species richness in lowland areas.
	Banchinae	K endo	Lep	Moderately large (64; 1709)	1000	Most species known from the Holarctic; tropical fauna very little studied but rich.
	Campopleginae	K endo	Lep, phytophagous Col, Hym (Symphyta), Meg	Large (69; 2111)	1508	Little studied subfamily; many species host-specific.
	Cremastinae	K endo	Lep, Col	Moderately large (35; 756)	1320	Mainly a tropical and subtropical subfamily.
	Ctenopelmatinae	K endo	Hym (Symphyta), some Lep?	Large (105; 1253)	19	Symphyta scarce in Amazonia.
	Lycorininae	Unknown	Lep (Microlepidoptera)	Small (1; 28)	17	In Central America, species richness highest in lowland forests.
	Nesomesochorinae	K endo	Lep	Small (1; 22)	324	Nonnus neotropical; in Central America, especially in mid-altitude humid forests.
	Mesochorinae	K endo; hyper	Hym (Ichneumonoidea), Dip (Tachinidae)	Moderately large (13; 876)	680	Hyperparasitoids; little known.
	Metopiinae	K endo	Lep	Moderately large (26; 824)	490	In Central America, species richness highest in lowland to mid-altitude areas.
	Ophioninae	K endo	Lep	Moderately large (33; 1023)	202	High tropical species richness; mainly nocturnal species (attracted to light traps).
	Tersilochinae	K endo	Col, north: rarely Hym	Moderately small (20; 222)	1311	Little studied in the Neotropics.
	Tryphoninae	K ecto	Hym (Symphyta), Lep	Large (59; 1215)	52	Symphyta scarce in Amazonia.
5	Orthocentrinae	K endo	Dip (Mycetophilidae)	Moderately large (29; 462)	8961	Thought to be most species rich in relatively cool and humid areas; in Central America, found abundant in lower montane cloud forests; very little studied, especially in the tropics.
	Pimplinae	I ecto; pseudo; K ecto	Lep, Col, Hym, Ara	Moderately large (76; 1540)	1862	Highest local species richness reported in Amazonia.
	Rhyssinae	I ecto	North: Hym (Siricoidea); tropics: wood-boring Col?	Moderately small (8; 234)	104	Highest local species richness reported in Amazonia.
6	Xoridinae	I ecto	Wood-boring Col and Hym (Symphyta)	Moderately small (4; 204)	2	Only Xorides present in South America; other genera in northern temperate areas.

proposed to be wide (Gaston & Gauld, 1993). For example, three ichneumonid species, *Cubus validus* Cresson, *Creagura nigripes* Townes and *Pimpla croceipes* Cresson, which were thought to have broad geographical distributions over vast tropical areas (Gauld, 1991, 2000; Díaz, 2000; Gauld *et al.*, 2002), were later shown to be complexes of various species (Janzen *et al.*, 2009; Veijalainen *et al.*, 2011). These findings together with the poorly known tropical diversity imply that the true number of ichneumonid species may be even higher than the current – already high – estimates.

Inadequate sampling can easily give biased results about the true number of species. Previous studies on NRAM Pimplinae and Rhyssinae suggest Amazonian ichneumonid species to be rare or rarely collected (Sääksjärvi *et al.*, 2004). To sample tropical ichneumonids efficiently even on a local scale requires persistent work, yet a majority of the family's tropical surveys have been small or modest in extent. Future research must embrace multiple biogeographical regions, tropical rain forest types, vegetation strata, years, seasons, collecting methods and identification techniques. Encouragingly, alongside the Neotropical fauna, the afrotropical ichneumonids are becoming better known as a part of a large-scale study on the wasps of Africa south of the Sahara (S. van Noort, pers. comm.). Species not collected by traditional sampling methods may again turn out in rearing projects. These host records together with improving molecular host identification methods can be used to evaluate the level of specialisation (Hrcek *et al.*, 2011) – one of the key variables when estimating the number of ichneumonid and other parasitoid species in temperate and tropical regions.

When discussing latitudinal species richness patterns, one should also consider the longitude (Santos & Quicke, 2011). Asking why a drop in ichneumonid species richness has been found after mid-latitudes might be more appropriate than assuming – without adequate data – that the richness does not rise again in Amazonia or in other tropical rain forests. Similar to Janzen's (1981) results for Ichneumonidae, Quicke and Kruft (1995) found a mid-latitude peak in species richness for the sister-family Braconidae (Hymenoptera) when studying published records from North America. They discussed whether the aridity of southern United States and northern Mexico, or scarcity of dew as suggested by Townes (1972), could be one factor depressing the braconid numbers at these latitudes. Skillen *et al.* (2000) also returned to Janzen's (1981) results and sampled campoplegines and ichneumonines along a latitudinal gradient in Ontario, Maryland, Georgia and Florida. They found a similar but broader mid-latitude peak, the number of species decreasing from Georgia to Florida. Furthermore, Heinrich (1977), in his publication on the Ichneumoninae of Florida, highlights the state's exceptionality in terms of the ichneumonine fauna, geological history and lack of humid and shady forests that he had noticed the subfamily members typically inhabit in large numbers. Aridity, or scarcity of humid and shady forested habitats, might indeed affect ichneumonid diversity. Further evidence comes from Barro Colorado Island, where a more pronounced dry season in comparison to La Selva was thought to explain the lower subfamily abundances (Shapiro & Pickering, 2000). The island's ichneumonoids were also discovered to avoid gaps in the rain forest vegetation both in the wet and in the dry season (Richards & Windsor, 2007). Interestingly, some of the first latitudinal species richness gradient studies sampled tropical ichneumonids in open and disturbed, garden or field-like habitats (Owen & Owen, 1974; Janzen & Pond, 1975). Thus, samples also from the species-rich primary tropical rain forests ought to be incorporated into future temperate–tropical comparisons.

Quicke and Kruft (1995) realistically remind that it would be unwise to extrapolate the trend observed for Braconidae in North America to more general latitudinal species richness and diversity questions. However, one finds the widely cited Janzen (1981) study on North American ichneumonids often generalised. The assumption of an anomalous ichneumonid species richness cline is firmly established among scientists: it is applied to give further support to study results (Traynor & Mayhew, 2005; Archibald *et al.*, 2010) and serves as a classical textbook example (Grimaldi & Engel, 2005, p. 13). Perhaps the works of some influential ichneumonologists who had, however, studied relatively little material from tropical lowland areas further supported adopting a rather simplified understanding of the gradient too early (see Heinrich, 1977; Porter, 1978; Gupta, 1983). Nevertheless, as Santos and Quicke (2011) already suspected, the results presented here show that there would now be reason to call such generalisations to a halt and focus on revising the true extent of tropical ichneumonid diversity.

Based on this study, primarily interesting ichneumonid subfamilies for further large-scale Neotropical species richness studies would be the small-bodied Mesochorinae, Orthocentrinae and Tersilochinae and the koinobiont lepidopteran parasitoids in the relatively abundant Anomaloninae, Banchinae, Campopleginae, Cremastinae, Ichneumoninae and Metopiinae. Regardless of whether Ichneumonidae as a whole will turn out to be more diverse in the Nearctic or Neotropical realm, the fact that certain subfamilies and tribes are abundant and species rich in Amazonia should no longer be neglected. Careful investigation will tell whether these groups have a regular latitudinal species richness gradient (even if not necessarily as sharp as that of their hosts). Answering these questions will ultimately clarify what factors determine macroecological species richness patterns and what is the total number of ichneumonid species on earth.

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