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Taxonomic Progress and Diversity of Ichneumonoid Wasps (Hymenoptera: Ichneumonoidea) in Southeast Asia

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ABSTRACT.– Taxonomic studies on parasitoid wasps in the superfamily Ichneumonoidea occurring in Southeast Asia (SEA) are reviewed from a historical perspective. A list of all described species in this group until the end of 2019 was compiled for each SEA country and the taxonomic effort expended in each calculated. Taxonomic effort over time differed significantly between countries, probably largely due to historical events. Involvement of local taxonomists started soon after 1900 but the proportion remained extremely low when compared to foreign experts, and although increasing markedly since 1990, remains very low.

KEY WORDS: accumulation curve, Braconidae, estimation, Ichneumonidae, species richness, taxonomists, tropics

INTRODUCTION

Taxonomists have been finding and describing new taxa for several hundred years before the era of Linnaeus, who established the fundamental system of nomenclature that is used universally today (Ereshefsky, 2000; Winsor, 2003). The total number of animal species has variously been predicted to be from 1.8 to 30 million species, depending on the methods of estimation, while the current total number of described species recorded in the Catalogue of Life (CoL) in 2019 was approximately 1.8 million species (Erwin, 1982; Costello et al., 2011; Mora et al., 2011; Roskov et al., 2019). New species are being discovered and described in all major groups of organisms every year, but although discovering new taxa in some charismatic groups, such as mammals, birds and butterflies, is becoming harder, the rate of description in most other groups is rapidly increasing (Bebber et al., 2007; Schipper et al., 2008; Giam et al., 2010; Achterberg and Long, 2010). The vast majority of species remain undescribed, especially in the tropics.

The parasitoid wasps (Hymenoptera: Apocrita excluding most of the Aculeata) are a highly diverse group of insects (Sharkey, 2007; Jones et al., 2009; Yu et al., 2012). They play key roles in terrestrial ecosystems through regulating the populations of their hosts, predominantly other insect species, which they ultimately and invariably kill (Wharton, 1993; Chen et al., 2014; Quicke, 2015). Due to their biology, parasitoid wasps are of interest to applied scientists through their use in biological control and integrated pest management (IPM) programmes to limit damage caused by insect pests both in agricultural areas and in stored products (Schöller et al., 1997; Grieshop et al., 2006; Venkatesan et al., 2007; Wang et al., 2014).

The Ichneumonoidea is the largest superfamily in Hymenoptera in terms of described species (Chen et al., 2014). It comprises two extremely large families, the Braconidae and Ichneumonidae (Quicke, 2012, 2015; Chen et al., 2014), with 18,580 and 23,765 described species, respectively (Roskov et al., 2019), and another small family Trachypetidae has been recently erected in 2020 with seven species (Quicke et al., 2020). However, widely quoted estimates of total global species richness for these are several times larger, 32,000–42,000 and 60,000–100,000, respectively (Townes et al., 1965; Heinrich, 1978; Dolphin and Quicke, 2001; Jones et al., 2009) but even these are probably major underestimates (Rodrigues et al., 2013; Sharkey et al. 2021).

Most ichneumonoids are primary parasitoids and attack the immature stages of Lepidoptera, Hymenoptera, Coleoptera and Diptera, some of which are serious pests causing substantial loss of agricultural productivity (Wharton, 1993; Chen et al., 2014). Further, their role in natural ecosystems is likely to be critical in regulating populations of most species of herbivores from foliage-eaters to wood-borers.

Southeast Asia (SEA) is located in the tropics between the Pacific (in the east) and Indian (in the west) oceans (Sodhi et al., 2004). The region combines four biodiversity hotspots, i.e. Indo-Burma, Sundaland, the Philippines, and Wallacea, making it one of the most world's species-rich areas with 20–25% of the total global plant and animal species (Sodhi et al., 2004; Woodruff, 2010; Bruyn et al., 2014). However, biodiversity in SEA is facing the combined major problems of deforestation and other habitat loss due to economic development and poor resource management. Many species are threatened and it is probable that some will go extinct before ever being recorded (Sodhi et al., 2004; Giam et al., 2010; Webb et al., 2010). Considering to the number of ichneumonoid species in this region, 1,294 species of Braconidae and 710 species of Ichneumonidae have been recorded in Taxapad until 2012 (Yu et al., 2012), much lower than extrapolated numbers (Jones et al., 2009). This indicates that taxonomic work on this superfamily is far from the complete and requires a great deal more taxonomic effort.

Over recent years there have been a number of collaborations between western and local researchers that aim to survey and reinforce taxonomic studies on this region, for example, the Thailand Inventory Group for Entomological Research (TIGER) project in Thailand (NSF, 2008). Furthermore, molecular techniques have become an important tool for identification and classification in various organisms, including parasitoid wasps (Hebert and Gregory, 2005; Hajibabaei et al., 2007; Smith et al., 2008, 2009; Butcher et al., 2012).

The species richness of a region is a measure of its biodiversity that can have implications for resource management as well as conservation programmes. However, for many groups of organisms in SEA, taxonomic inventories are far from complete. Taxonomic studies on ichneumonoids in the region began over 200 years ago, but the current number recorded species is still far lower than predictions (DeGeer, 1773; Jones et al., 2009; Quicke, 2012). A marked increase in the rate of species description, especially in Indonesia, Malaysia and the Philippines, took place during the early 20th century which coincides with a period of colonial expansion (Osborne, 2016). Taxonomic effort over time differs significantly between countries probably due to specific historical events. After 2000, description rates and the number of taxonomists involved, substantially increased mainly with the contributions of

taxonomists in Thailand and Vietnam, e.g. Butcher et al. (2012) and Achterberg and Long (2010). The number of local taxonomists is slowly increasing but is still very low when compared to the number of foreign experts.

Here we collate all taxonomic studies of Ichneumonoidea found in SEA and compare taxonomic effort in the component countries.

MATERIALS AND METHODS

Compilation of known taxa

Southeast Asia consists of 11 countries: Brunei, Cambodia, East Timor, Indonesia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Thailand and Vietnam. These are each considered separately except for Timor island, part of which is possessed by Indonesia and part the recently independent country of East Timor, because past much work did not specify from which part of the island material originated. However, all published records for Timor island predate the internationally recognition of East Timor as an independent state in 2002. Hence, localities of wasps found in Timor island are herein treated as a part of Indonesia.

Data of ichneumonoid species and their distributions up until 2012 were largely extracted from Taxapad (Yu et al., 2012). Additional literature relating to the period 2012-19 was gathered from Google, Science Direct, Scopus and Web of Science, using search terms "[name of country] AND Braconidae/Ichneumonidae". The data were then scrutinised to prevent redundancy such as through duplication and synonymy. Taxa not identified to species level were excluded.

Number of taxonomists working in SEA

Names presented in the authorship of binomens and authors who reported the first country records were counted as related taxonomists in SEA. However, there were some species that were firstly found outside SEA, but later recorded in SEA. In those cases, author names were excluded from analyses.

Comparisons of taxonomic efforts

To examine taxonomic efforts in each country, discovery of new species or new country record was compared using the k-sample Anderson-Darling (AD) test, which is a nonparametric statistic for testing the homogeneity of samples (Anderson and Darling, 1952). Cambodia was excluded from the analysis due to the very low number of species records. Statistical analysis was performed using the *kSamples* in R version 4.0.3 (R Core Team, 2020)

RESULTS

Known taxa

Up until the end of 2019, 27 subfamilies, 282 genera and 1,811 species of Braconidae, and 26 subfamilies, 273 genera and 1,119 species of Ichneumonidae had been recorded in SEA (see details in supplementary materials: Tables S1 and S2 and electronic supplement material: https://doi.org/10.5281/zenodo.4467926). Of these, Indonesia had the highest species richness in terms of actual number of known species, while Singapore had the highest recorded species density per area for both families (Tables 1 and 2). Cambodia had the fewest wasp records with only two species of braconids and three species of ichneumonids. Within the Braconidae, the Braconinae had the highest species diversity followed by Agathidinae, Rogadinae and Doryctinae, while for the Ichneumonidae, the Ichneumoninae, Pimplinae and Cryptinae were the top species-rich subfamilies (Fig. 1).

TABLE 1. Number of taxa and taxonomists relating to Braconidae in SEA.

	BN	KH	ID	LA	MY	MM	PH	SG	TH	VN	SEA
No. of subfamilies	11	2	25	9	24	13	19	9	15	20	27
No. of genera	21	2	174	26	129	37	120	19	79	80	282
No. of species	33	2	604	40	482	54	412	27	377	261	1,811
Density (species/km^2)	0.00572	0.00001	0.00032	0.00017	0.00146	0.00008	0.00137	0.03721	0.00074	0.00079	0.00040
No. of taxonomists	21	3	66	21	65	27	57	22	63	45	132

BN = Brunei, KH = Cambodia, ID = Indonesia, LA = Laos, MY = Malaysia, MM = Myanmar, PH = the Philippines, SG = Singapore, TH = Thailand and VN = Vietnam

TABLE 2. Number of taxa and taxonomists relating to Ichneumonidae in SEA.

	BN	KH	ID	LA	MY	MM	PH	SG	TH	VN	SEA
No. of subfamilies	5	3	21	11	19	16	15	9	17	16	26
No. of genera	7	3	205	44	115	70	68	22	39	92	273
No. of species	42	3	656	114	296	162	175	55	97	344	1,119
Density (species/km^2)	0.00729	0.00002	0.00034	0.00048	0.00090	0.00024	0.00058	0.07579	0.00019	0.00104	0.00025
No. of taxonomists	23	6	76	30	61	35	41	30	45	52	120

BN = Brunei, KH = Cambodia, ID = Indonesia, LA = Laos, MY = Malaysia, MM = Myanmar, PH = the Philippines, SG = Singapore, TH = Thailand and VN = Vietnam

Taxonomic studies in ichneumonoids in SEA have proceeded since the 18th century in which the earliest described species is ichneumonid wasp *Camptotypus rugosus* in 1733 (DeGeer, 1773). Rates of species description showed a marked increase during the 20th century. Braconid wasp species accumulation increased rapidly during the early 1900s which largely reflects the increase of descriptions of Indonesian, Malaysian and Philippine taxa. Subsequently, the rate began declining in 1920 (Fig. 2). The rate of description in SEA increased again starting around 1990 and increased abruptly from 2010 onwards, which primarily reflects taxonomic effort in Thailand and Vietnam.

The SEA ichneumonid species accumulation curve was similar to that of the Braconidae except for the 1930s when there was an abrupt increase due to taxonomic work in Indonesia and Myamar, especially the work of Heinrich (1934) who described over 130 species from these two countries, while the rapid increase of ichneumonid description post 2010 mainly reflected work on the Vietnamese fauna.

Comparisons of description rates indicate that the discovery of new species or new records over time differed significantly between countries for both Braconidae (AD = 529.6, n = 9, $P < 0.001$) and Ichneumonidae (AD = 356.2, n = 9, $P < 0.001$), notably because of work on Thai and Vietnamese taxa (Tables 3 and 4). The current number of wasp species is presented in shaded maps in Fig. 3 which indicated that the numbers of recorded species is higher in island countries than in continental countries.

Number of taxonomists working in SEA

The number of authors publishing new species or records of both braconid and ichneumonid wasps before 1990 was normally between 15 and 30 per decade, with a slight dip from 1931 to 1960 (Fig. 4).

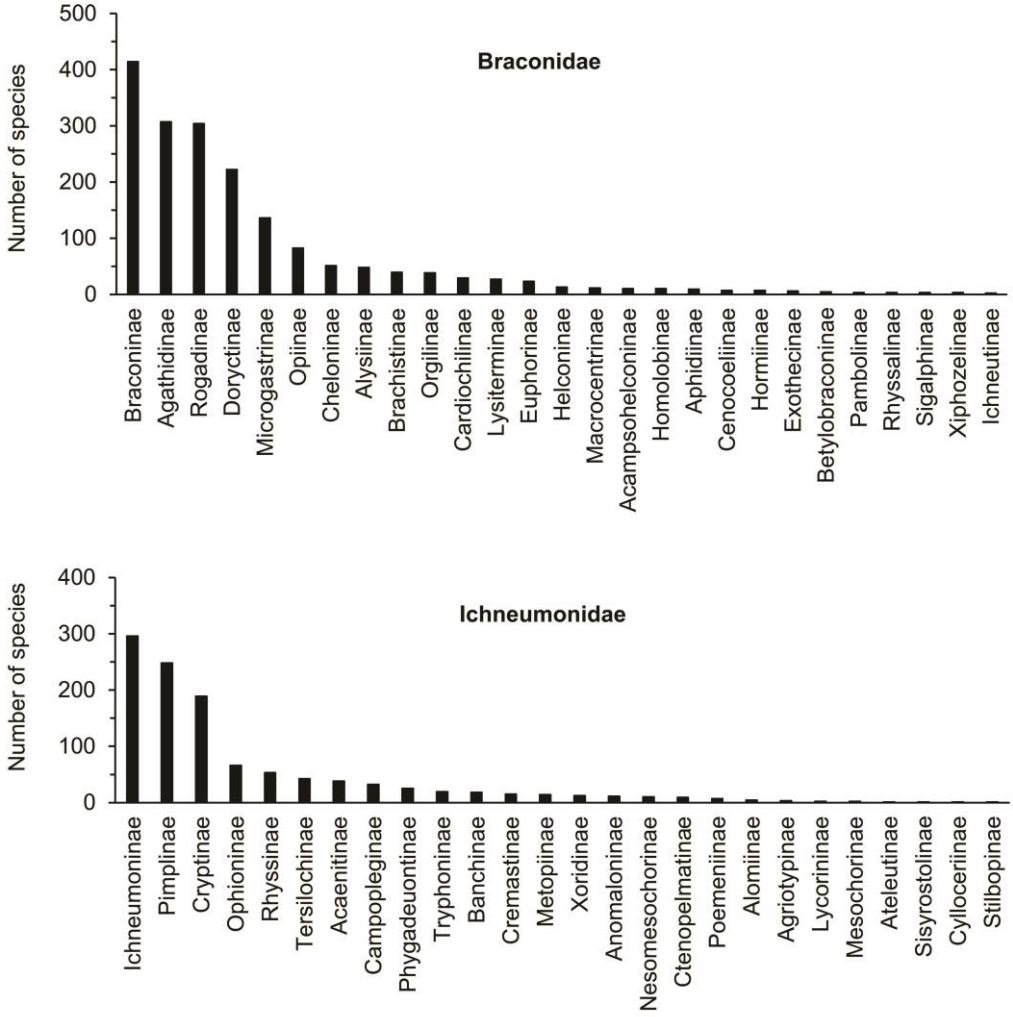

FIGURE 1. Current diversity of the subfamilies of braconid and ichneumonid wasps recorded in SEA.

However, the number almost doubled after 1991. The number of taxonomists working with braconids was consistently higher than for ichneumonids across all years. However, local taxonomists were only involved after 1990 and even though their ratio compared to foreign taxonomists was always much lower (1:13.5 for braconids and 1:8 for ichneumonids).

DISCUSSION

Several earlier studies on the relationship between latitude and species richness indicated that diversity of the family Ichneumonidae revealed an inverse latitudinal cline, so-called anomalous diversity, in which the species richness is positively

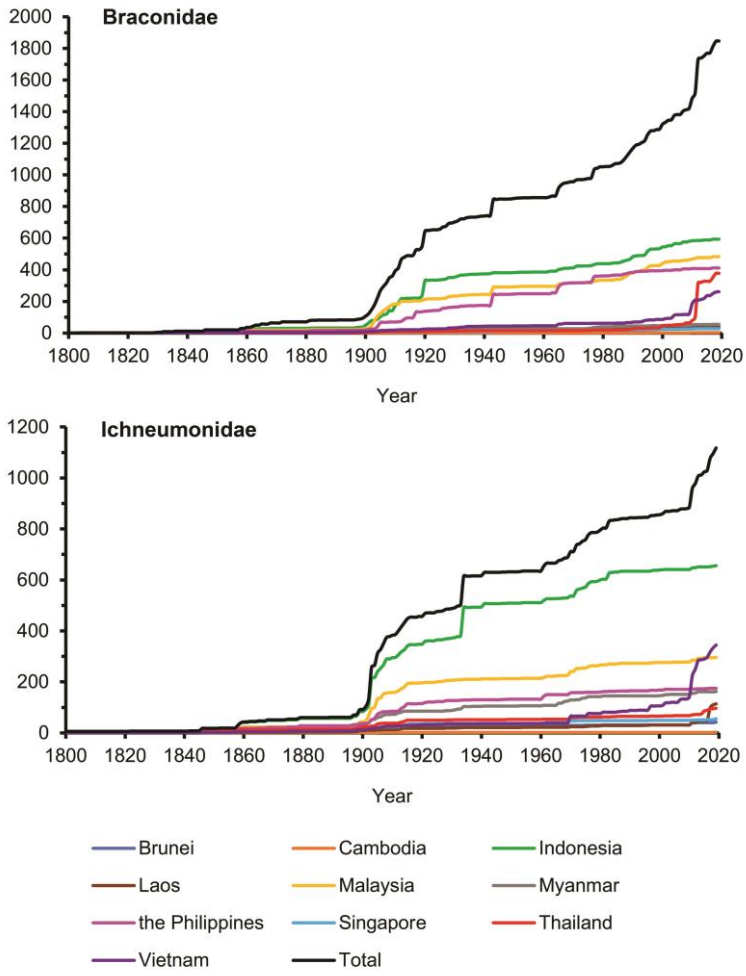

FIGURE 2. Species accumulation curves of Braconidae and Ichneumonidae recorded in SEA.

correlated with latitude (Owen and Owen, 1974; Gauld, 1986; Kindlmann et al., 2007). Sime and Brower (1998) discussed the various hypotheses that had put forward to explain anomalous diversity of ichneumonids by examining taxonomic and geographical distribution in the butterfly hosts, like Papilionoidea and concluded that the diversity pattern of parasitoid wasps is most likely to be explained by chemical defence of their hosts, so-called nasty-host hypothesis, in which the proportion of unpalatable hosts is higher in the tropics resulting in low diversity of associated wasps. However, number of ichneumonid records in SEA is still continually increasing without the sign of asymptote due to the increase of taxonomic efforts in this region (Fig. 2). Therefore, it is not at all clear whether the Ichneumonidae actually do show anomalous diversity (Sääksjärvi et al., 2004; Quicke, 2012; Veijalainen et al.,

TABLE 3. Comparison matrix of description rate of braconid wasps between countries in SEA by using k-sample Anderson-Darling test. Significant differences are indicated in bold ($P < 0.05$) and numbers in parentheses are the numbers of discovery event of new species or new country record until the end of 2019.

	BN	**ID**	**LA**	**MY**	**MM**	**PH**	**SG**	**TH**	**VN**
	(33)	**(604)**	**(40)**	**(482)**	**(54)**	**(412)**	**(27)**	**(377)**	**(261)**
BN		**10.95**	2.07	**8.25**	**5.02**	**22.74**	1.92	**25.97**	**7.81**
ID			**3.04**	**6.46**	**3.68**	**18.39**	2.31	**250.00**	**139.70**
LA				1.93	0.97	**8.96**	0.41	**36.33**	**15.97**
MY					1.49	**17.12**	1.08	**210.10**	**110.00**
MM						**5.44**	0.47	**46.68**	**20.88**
PH							**3.91**	**214.40**	**122.90**
SG								**28.08**	**11.94**
TH									**44.53**

BN = Brunei, ID = Indonesia, LA = Laos, MY = Malaysia, MM = Myanmar, PH = the Philippines, SG = Singapore, TH = Thailand and VN = Vietnam

2012), and if they do, what the underlying reasons might be, and whether it is only a feature of ichneumonid diversity.

An alternative possibility is that the observed low tropical diversity of ichneumonids is due to bias in collecting and/or distribution of taxonomic effort Furthermore, collection bias and description bias is likely to reflect the wasp's body size and this is also related to their biology as well as possibly differing between temperate and tropical zones (Quicke, 2012). As noted in the 'Manual of the New World Genera of the family Braconidae' (Wharton et al., 1997) many genera in North America are thought to contain more undescribed than described species. On the other hand, most areas in the tropics are still unexplored both due to the lack of experts and limited accessibility to the areas (Quicke, 2012; Veijalainen et al., 2012).

Species accumulation curves are a way to compare the progress of taxonomic studies between areas as well as providing a tool for predicting total species richness by fitting the curve to a model (Soberón and Llorente, 1993; Bebber et al., 2007). The accumulation curve of braconids in SEA continually increases with acceleration after 2000 without any sign of an asymptote. Previously, species richness of braconids in tropical Asia has been estimated there would be approximately 2,500 species (Jones et al., 2009). So far, our results showed that the current number of described braconid species is just a half of that prediction. In the case of Ichneumonidae, although the estimation of species richness in SEA no literature has not been reported, from the species accumulation curves in this study, we believed that there are numerous undescribed ichneumonids waiting to be discovered.

The shapes of the species accumulation curves reflect the impact of historical events in a region. Early taxonomic research in many parts of the world are a legacy from the colonial period (Patterson, 2001; Figueiredo and Smith, 2010). SEA was directly affected by western colonialism from the 18th century to the middle of the 20th century with France colonizing what are now Cambodia, Laos and Vietnam, the British Empire dominating from India to

TABLE 4. Comparison matrix of description rate of ichneumonid wasps between countries in SEA by using k-sample Anderson-Darling test. Significant differences are indicated in bold ($P < 0.05$) and numbers in parentheses are the numbers of discovery event of new species or new country record until the end of 2019.

	BN	**ID**	**LA**	**MY**	**MM**	**PH**	**SG**	**TH**	**VN**
	(42)	**(656)**	**(114)**	**(296)**	**(162)**	**(175)**	**(55)**	**(97)**	**(345)**
BN		**4.66**	**14.53**	**2.62**	1.45	**3.06**	0.85	1.19	**21.22**
ID			**107.00**	**3.85**	**3.10**	**2.92**	**3.51**	**19.07**	**231.40**
LA				**69.40**	**46.26**	**55.17**	**20.12**	**18.37**	**18.99**
MY					1.81	1.57	2.14	**11.12**	**133.20**
MM						**3.58**	1.71	**6.79**	**85.75**
PH							1.47	**9.82**	**109.80**
SG								2.34	**38.18**
TH									**25.71**

BN = Brunei, ID = Indonesia, LA = Laos, MY = Malaysia, MM = Myanmar, PH = the Philippines, SG = Singapore, TH = Thailand and VN = Vietnam

Myanmar and Malaysia and the Dutch in much of Indonesia. During this period, naturalists and explorers from Europe, for example, Alfred Russel Wallace (in Indonesia during 1854–1862), came to SEA for exploring resources, including plants and animals, and brought those specimens back to museums in Europe causing a speed up of new descriptions in this region during 1900–1920 as shown in Fig. 2 (Wallace, 1869; Wolfe, 2006; Clement, 2016). However, the description rate decreased from the 1930s to the early of the 21st century. Part of this was due to the deaths and retirements of some prolific European ichneumonoid taxonomists who were most active, for example G. Szépligeti in Budapest and P. Cameron in London. World War II (1939–1945) also had a large impact and achieving independence of most countries in SEA resulting in stopping the taxonomic work of European naturalists (Goto, 2003; Osborne, 2016).

Indonesia, Malaysia and the Philippines have the highest number of ichneumonoid records, which is largely due to the colonial legacy. However, geographical characteristics such as the large number of archipelagos in these areas might also be important contributing factors with geographic barriers limiting gene flow between islands, of both parasitoids and their hosts, and so leading to high speciation rates (Witt and Maliakal-Witt, 2007; Santos et al., 2011). Furthermore, Indonesia which has the highest species richness for both families, contains two biogeographic realms, Sundaland and Wallacea, which provides another possible explanation of why its parasitoid diversity is relatively high (Sodhi et al., 2004).

Thailand and Vietnam are the countries that have contributed most to the increase of ichneumonoid records during the 21st century. Thailand was never conquered by western countries during colonial period which had the consequence that the description of parasitoid wasps collected from this country remained very low until recently, with little European involvement and no substantial local infrastructure such as national museum collections on a scale even remotely comparable to the major European institutions. Vietnam experienced much unrest both from wars and invasion of foreign countries which had negative

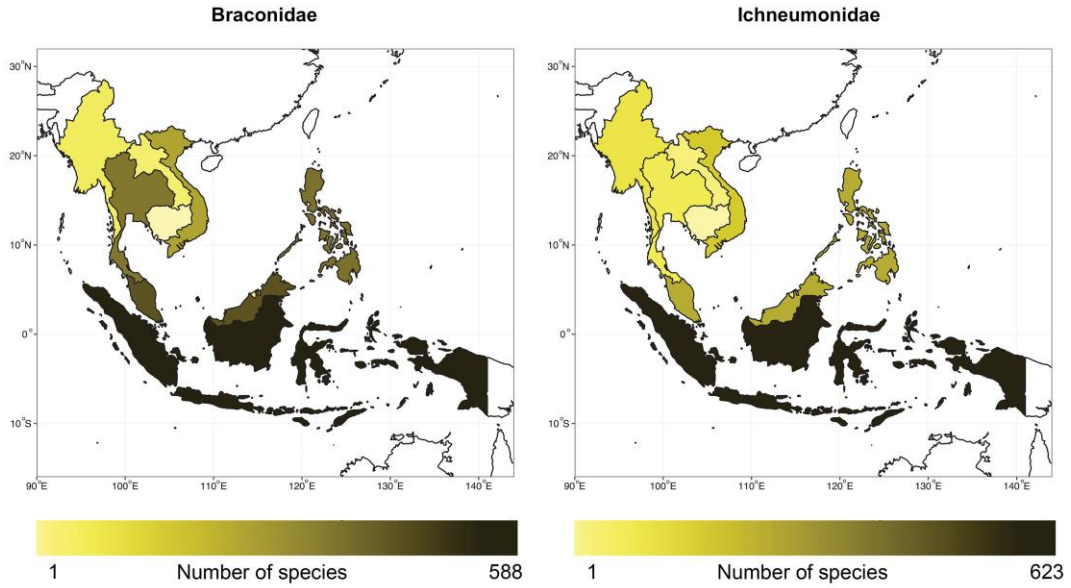

FIGURE 3. Southeast Asian maps shaded to show the current number of braconid and ichneumonid wasp species per country.

impacts on all aspects of biodiversity research (Osborne, 2016). In these two countries, collaboration between western experts (such as DLJQ, Cornelis van Achterberg and Michael J. Sharkey) and local taxonomists (such as Buntika Areekul Butcher, Khuat Dang Long and Nhi Thi Pham) combined with increasing integration of molecular techniques for identification (DNA barcoding), began after 1990. For example, the description of 179 new Thai braconid species from one genus (*Aleiodes*) in a single publication by Butcher et al. (2012), and the description of three new genera and 42 new species of Vietnamese braconids by Achterberg and Long (2010). These works alone represent large percentage increases in ichneumonoid records within a short period of time.

Accessibility to the areas, the prevailing political situation and impoverishment probably had a marked negative influence on taxonomic effort in countries such as Cambodia, Laos and Myanmar. Transportation to rural areas and forests is limited and requiring laborious work and an associated high level of expense. Some parts of the region are still too dangerous to access due to the wartime legacies of land mines, and unexploded bombs together with other national security reasons such as drug trafficking (Chandler, 2008; Osborne, 2016). For example, the very low number of wasp species recorded from Cambodia is largely due to the numerous unrest events following WWII, such as Cambodian Civil War (1968–1975), Cambodian genocide by the Khmer Rouge regime (1975–1979) and Cambodian–Vietnamese War (1978–1989). Although current politics are more stable than in the past, it will likely be a long time before some areas can be explored in depth for entomology.

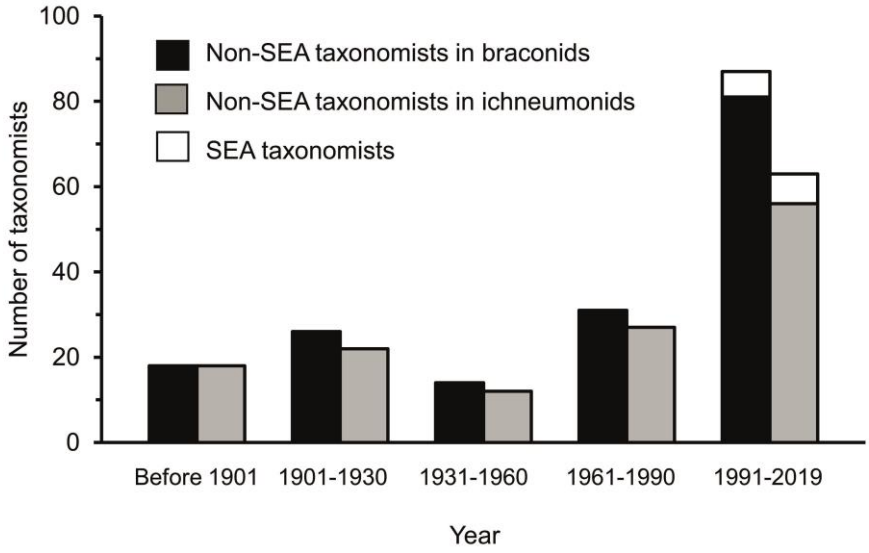

FIGURE 4. Number of taxonomists involved in new species description or new records in SEA over periods of time.

The taxonomic study of ichneumonoids in SEA is increasing and, especially in Thailand and Vietnam, gaining more attention than the past. The number of taxonomists involved is considerably larger now than before 1990. Moreover, there is now participation by local taxonomists which never occurred before 1990. Although the proportion of the local taxonomists is still much lower relative to the foreign experts, this is a good sign of taxonomic studies in parasitoid wasps in the region. Perhaps education and training local people to be taxonomists can improve information of parasitoid wasp diversity and emphasize SEA as an important diversity hotspot in the world. However, it seems likely that revolutionary approach to how species are described will be needed, such as primary reliance on DNA barcode data and basic images (Meierotto et al. 2019). Significantly, the first applications of this procedure have involved ichneumonoid wasps (Meierotto et al. 2019; Sharkey et al. 2021), and whilst not without criticism, should be applied to the SEA fauna to greatly expand the number of species recorded from this region.

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SUPPLEMENTARY MATERIALS

TABLE S1. Number of braconid wasp species recorded in each country of SEA.

Subfamilies	Indo-Burma					Sundaland + Wallacea				The Philippines	SEA
	KH	LA	MM	TH	VN	BN	ID	MY	SG	PH	
Acampsohelconinae							4	4		2	10
Agathidinae		5	9	109	72	4	87	57	6	54	307
Alysiinae	1	1	6	4	6		21	10	1	10	48
Aphidiinae				8	1		1	2	1	1	9
Betylobraconinae					3		1				4
Brachistinae		10		1			8	16		11	39
Braconinae	1	16	11	18	7	9	214	153	3	59	414
Cardiochilinae		2		1	11	1	13	7	2	4	29
Cenocoeliinae							5	2			7
Cheloninae			2	6	1	7	20	18	7	21	51
Doryctinae		1	3	6	52	1	52	79	3	90	222
Euphorinae			1	1		1	9	6		5	23
Exothecinae							1	5			6
Helconinae			5				4	2		2	13
Homolobinae			2	1			4	2		3	10
Hormiinae				2	3	2		3		2	7
Ichneutinae					1		1				2
Lysiterminae			1	1	5		10	11		5	27
Macrocentrinae		1			1		7	4	1	2	11
Microgastrinae			10	9	46	1	48	48	3	61	136
Opiinae		1		14		5	38	19		32	82
Orgilinae			2		14	4	13	17		11	38
Pambolinae					2			3			3
Rhyssalinae					1		1	1			3
Rogadinae		3	1	196	27	3	40	12		37	304
Sigalphinae					2		1				3
Xiphozelinae			1		1		1	1			3
Total species of each country	2	40	54	377	261	33	604	482	27	412	1,811
Total taxonomists working in each country	3	21	27	63	45	21	66	65	22	57	132
Total species of each biodiversity hotspot			650				993			412	1,811
Species density of each hotspot (species/km^2)			0.00034				0.00044			0.00137	0.00040

BN = Brunei, ID = Indonesia, KH= Cambodia, LA = Laos, MY = Malaysia, MM = Myanmar, PH = the Philippines, SG = Singapore, TH = Thailand and VN = Vietnam

TABLE S2. Number of ichneumonid wasp species recorded in each country of SEA.

Subfamilies	Indo-Burma					Sundaland + Wallacea				The Philippines	SEA
	KH	LA	MM	TH	VN	BN	ID	MY	SG	PH	
Acaenitinae		1			31		2	4			38
Agriotypinae			1		2						3
Alomiinae		4									4
Anomaloninae			1	1	1		8	4		4	11
Ateleutinae								1			1
Banchinae		1	4	1	3		14	2	1	1	18
Campopleginae			4	3	9		24	10	2	6	32
Cremastinae			1	2	4		14	4	1	3	15
Cryptinae	1	2	10	3	12		142	68	7	18	190
Ctenopelmatinae		1		3	7		1			1	9
Cylloceriinae			1	1							1
Ichneumoninae		63	73	8	39		196	38	2	13	296
Lycorininae							1	1			2
Mesochorinae					1		1				2
Metopiinae			1	2	9		3			5	14
Nesomesochorinae							7	3		2	10
Ophioninae		17	15	10	23	27	45	33	11	36	66
Phygadeuontinae	1		1	2		3	14	6	3	4	24
Pimplinae	1	16	39	53	160	1	119	84	27	70	248
Poemeniinae		1	1	1			5	5			7
Rhyssinae		1	2	1	11		36	22	1	7	53
Stilbopinae					1						1
Sisyrostolinae							1	1			1
Tersilochinae		7		1	27	8	3	2		1	42
Tryphoninae			6	3		3	15	1		2	19
Xoridinae			2	3	5		5	7		2	12
Total species of each country	2	40	54	377	261	33	604	482	27	412	1,811
Total taxonomists working in each country	3	114	162	97	344	42	656	296	55	175	1,119
Total species of each biodiversity hotspot			6				30			35	45
Species density of each hotspot (species/km^2)			513				792			175	1,119

BN = Brunei, ID = Indonesia, KH= Cambodia, LA = Laos, MY = Malaysia, MM = Myanmar, PH = the Philippines, SG = Singapore, TH = Thailand and VN = Vietnam