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TAXONOMY AND SISTEMATICS

On the diversity of Neotropical Hymenoptera

Sobre la diversidad de Hymenoptera neotropicales

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ABSTRACT

Hymenoptera is globally one of the most diverse groups of insects. There are no recent estimates nor sound data on the size of the fauna of this order in the Neotropical Region. Based on printed or digital catalogs, lists, as well as reviews of monographs, and other sources, the Neotropics comprises 26 superfamilies, 92 families, 3162 genera, and over 33 640 species of Hymenoptera. Hymenoptera diversity in the Neotropics is greater than in the Nearctic, Palearctic and Australian regions. The Neotropics is probably the richest region in the World in families, genera, and species of the order, with the majority of taxa endemic to this region.

Keywords: Diversity, Hymenoptera, Neotropics, taxonomy.

RESUMEN

Hymenoptera es globalmente uno de los grupos más diversos de insectos. No hay estimaciones o datos firmes recientes sobre el tamaño de la fauna de este orden en la Región Neotropical. Tomando como base catálogos, listas impresas o en forma digital, además de monografías y otras fuentes, el Neotrópico comprende 26 superfamilias, 92 familias, 3162 géneros y un poco más de 33 640 especies. La diversidad de Hymenoptera en el Neotrópico es mayor que en las regiones Neártica, Paleártica y Australiana. Probablemente es el Neotrópico la región más rica del mundo en familias, géneros y especies de Hymenoptera, con la mayoría de taxones endémicos de esta región.

Palabras clave: Hymenoptera, Neotrópico, diversidad, taxonomía.

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Wasps, bees and ants, order Hymenoptera, are one of the most diverse and important groups of insects in terrestrial ecosystems. The vast majority of species are parasitoid wasps that exert a natural control over populations of other insects, many of them phytophagous. Bees are important pollinators of many plants. Ants are key players in the structure and dynamics of forests. Their wealth of behavioral patterns (solitary, communal, subsocial, social, and parasitic) is an obligatory source for the study of the evolution of sociability. In addition, some species are agricultural pests, or may cause veterinary or medical problems. In contrast to the importance of the order, knowledge of its diversity at the global and regional level is key. Knowing how many species there are, what names they have, and where they are found is vital for studies in systematics, phylogeny, biogeography, ecology and conservation.

As Hymenoptera is one of the four hyper-diverse insect orders, it is not easy to establish precise numbers of the described species in the group. It is even more challenging to have estimates of undescribed species, a task that has become increasingly difficult in face of the decline of biological collections and curators, mainly taxonomists. In Hymenoptera, 111 families, 8423 genera (Aguiar *et al.* 2013) and 154 000 living species (Huber 2017) have been described, making it the most diverse order after Coleoptera and Lepidoptera, and close to Diptera. Estimates of total species richness are also variable, generally exceeding one million (Ulrich 1999). One recent study suggests a hidden high diversity of parasitoid wasps (Forbes *et al.* 2018). If true, this planet is flooded not with beetles, but with wasps.

For Coleoptera there is at least one checklist to the Neotropical Region published by Blackwelder between 1944 and 1957 and reprinted by the Smithsonian. In Lepidoptera there are innumerable catalogs with an emphasis on butterflies, being J.B. Heppner the editor of a series that covers most superfamilies and families of the order, with the exception of Geometroidea and Noctuoidea which are covered in other sources (e.g. Scobble 1999 for Geometridae). Nelson Papavero during several decades published the serial catalog of Diptera of the Neotropical region (Klassa and dos Santos 2014).

For Neotropical Hymenoptera there are printed or digital catalogs for specific groups such as sawflies (Taeger *et al.* 2010), ants (Kempf 1972, Bolton 1995, c2022, Bolton *et al.* 2007), bees (Moure *et al.* 2007) and non-bee apoids (Amarante 2002, 2005), or online resources, such as for Chalcidoidea (Noyes c2020). But there are no printed or digital resources that list the entire fauna of Hymenoptera described for the Neotropics. How many species of Hymenoptera have been described for the Neotropics? Fernández (2000) offers a rough assessment, indicating 20 super families, 77 families, 2527 genera and around 24 000 species, estimating the number of species for the region at 60 000. These numbers are now out of date due to the many taxonomic developments since then, but also due to better access to publications and databases with information on poorly known groups at that time (such as Ceraphronoidea) or very rich groups with old and inaccessible literature (such as Chalcidoidea).

A new assessment of the size of Neotropical Hymenoptera fauna has improved from access to more sources of information, either in old checklists now available online, new lists, or the extraction of information from online catalogs, such as those dealing with bees and chalcidoids. Here is offered the list of Hymenoptera superfamilies and families known in the Neotropical region with the number of genera and described species with the sources before each family (Table 1). In most cases, the numbers are taken from the original references. In most taxa, the data from each list was verified for country or, as in the case of Johnson (1992), for region. Here we report the number of families, genera and species for each superfamily (Table 1). From the Noyes Chalcidoidea database, the names for each family, genus and species were consulted under the "Neotropical" restriction, and lists were compiled for each family. This procedure was followed for the online catalog of bees of the Neotropical Region, which was last updated in 2013.

According to table 1 there are 26 superfamilies, 92 families, 3162 genera and 33645 species for the Neotropics (see also supplementary Figs. S1-4). These figures imply a notable increase regarding the numbers presented in Fernández (2000). Part of these differences are explained by new studies in phylogeny that have created new suprageneric categories (Pilgrim *et al.* 2008, Sann *et al.* 2018, Chen *et al.* 2021, Zhang *et al.* 2022).

The number of described genera and species can be considered reliable for groups in which there is recent, revised and constantly updated information, such as the Chalcidoidea database of Noyes or Bolton's catalog of ants (Bolton c2022).

Table 1. Superfamilies and families of Neotropical Hymenoptera, with number of genera, species and references.

TAXON	Gen.	spp.	References
TENTHREDINOIDEA	**115**	**1027**	Taeger *et al*. 2010
Argidae	32	356	Smith 1992
Cimbicidae	5	9	Smith 1988, Vilhelmsen *et al*. 2018
Diprionidae	3	13	Smith 1988
Pergidae	32	256	Smith 1990, 2006
Tenthredinidae	43	393	Smith 2003ab
PAMPHILIOIDEA	**1**	**4**	Smith 1988
Pamphilidae	1	4	Smith 1988
CEPHOIDEA	**1**	**1**	Smith 1988
Cephidae	1	1	Smith 1988
SIRICOIDEA	**6**	**10**	Smith 1988
Siricidae	6	10	Smith 1988, Malagón-Aldana *et al*. 2014
XIPHYDRIOIDEA	**4**	**18**	
Xiphydriidae	4	18	Smith 1988
ORUSSOIDEA	**5**	**13**	Smith 1988
Orussidae	5	13	Smith 1988, Vilhelmsen and Smith 2002
MEGALYROIDEA	**3**	**4**	Shaw 1990
Megalyridae	3	4	Shaw 1990, 2003
STEPHANOIDEA	**3**	**41**	
Stephanidae	3	41	Aguiar 1998, 2004
EVANIOIDEA	**15**	**296**	Li *et al*. 2018
Aulacidae	2	83	Smith 2001, 2005
Gasteruptiidae	5	35	Macedo 2009, 2011
Evaniidae	8	178	Deans and Hueben 2003, Deans 2005
TRIGONALIOIDEA	**8**	**30**	Carmean and Kimsey 1998
Trigonalidae	8	30	Carmean and Kimsey 1998
CHRYSIDOIDEA	**80**	**1179**	
Bethylidae	26	437	Evans 1964, Gordh and Móczár 1990
Chrysididae	24	278	Kimsey and Bohart 1991
Dryinidae	21	430	Olmi 1984, 1986, 1989, Olmi *et al*. 2000
Embolemidae	2	10	Olmi 1995
Plumariidae	4	19	Roig-Alsina 1994, Diez *et al*. 2007
Sclerogibbidae	1	2	Argaman 1988, Olmi 2005
Scolebythidae	2	3	Evans 1963, Azevedo 1999

(Continued)

TAXON	Gen.	spp.	References
FORMICOIDEA	**142**	**3200**	Fernández *et al*. 2021
Formicidae	142	3200	Bolton c2020
APOIDEA	**475**	**7375**	Sann *et al*. 2018
Non bee apoid wasps	**134**	**2357**	Bohart and Menke 1976, Amarante 2002, 2005
Ammoplanidae	1	1	Bohart and Menke 1976, Amarante 2002, 2005
Ampulicidae	3	26	Bohart and Menke 1976, Amarante 2002, 2005
Astatidae	1	30	Bohart and Menke 1976, Amarante 2002, 2005
Bembecidae	38	389	Bohart and Menke 1976, Amarante 2002, 2005 Nemkov and Lelej 2013
Crabronidae	55	1304	Bohart and Menke 1976, Amarante 2002, 2005
Mellinidae	1	7	Bohart and Menke 1976, Amarante 2002, 2005
Pemphredonidae	12	108	Bohart and Menke 1976, Amarante 2002, 2005
Psenidae	5	79	Bohart and Menke 1976, Amarante 2002, 2005
Philanthidae	4	216	Bohart and Menke 1976, Amarante 2002, 2005
Sphecidae	14	197	Bohart and Menke 1976, Amarante 2002, 2005
APOIDEA ANTHOPHILA	**341**	**5018**	Michener 2007, Danforth *et al*. 2019, Melo c2020
Colletidae	55	632	Michener 2007, Melo c2020
Andrenidae	36	442	Michener 2007, Melo c2020
Halictidae	65	1004	Michener 2007, Melo c2020
Megachilidae	50	1014	Michener 2007, Melo c2020
Apidae	135	1926	Michener 2007, Melo c2020
VESPOIDEA	**77**	**1447**	
Vespidae	74	1427	Richards 1978, Sarmiento and Carpenter (pers. comm.)
Rhopalosomatidae	3	20	Townes 1977a, Fernández and Sarmiento 2002
SCOLIOIDEA	**3**	**52**	
Bradynobaenidae	1	7	Genise 1986, Nonveiller 1990, Pagliano and Romano 2017
Scoliidae	2	45	Bradley 1945, Osten 2005
TIPHIOIDEA	**7**	**87**	
Sierolomorphidae	1	2	Evans 1961
Tiphiidae	6	85	Allen 1972, Kimsey 1991
THYNNOIDEA	**35**	**227**	
Cyphotidae	4	8	Brothers 1970, Pagliano and Romano 2017
Thynnidae	31	219	Genise 1984, Kimsey 1992
POMPILOIDEA	**137**	**2511**	
Pompilidae	60	+1000	Fernández *et al*. 2022
Mutillidae	74	1505	Nonveiller 1990, Brothers and Lelej 2017, Pagliano *et al*. 2018

(Continued)

TAXON	Gen.	spp.	References
Sapygidae	3	6	Pate 1947, Fernández and Sarmiento 2015
ICHNEUMONOIDEA	**937**	**8647**	Quicke 2015
Braconidae	465	4142	Wharton *et al.* 1997, Campos (pers. comm.)
Ichneumonidae	472	4505	Townes and Townes 1966, Yu *et al.* 2012, Palacio (pers. comm.)
CERAPHRONOIDEA	**7**	**36**	Johnson and Musetti 2004
Megaspilidae	5	20	Pezzini and Köhler 2017
Ceraphronidae	2	16	Masner 2006
CYNIPOIDEA	**100**	**704**	Weld 1952, Ronquist 1999, Buffington *et al.* 2020
Ibaliidae	1	1	Azevedo *et al.* 2015
Liopteridae	4	57	Ronquist 1995
Figitidae	69	471	Diaz *et al.* 2002, Fontal-Cazalla *et al.* 2002
Cynipidae	26	175	Diaz *et al.* 2002
PROCTOTRUPOIDEA	**10**	**98**	Johnson 1992
Heloridae	1	2	Townes 1977b
Pelecinidae	1	3	Jonhson and Musetti 1999, Shih *et al.* 2010
Proctotrupidae	8	93	Townes and Townes 1981
DIAPRIOIDEA	**87**	**265**	
Diapriidae	84	229	Masner and García 2002
Ismaridae	1	15	Masner 1976
Monomachidae	2	21	Johnson and Musetti 2012
PLATYGASTROIDEA	**84**	**754**	Johnson 1992, Vlug 1995
Geoscelionidae	1	2	Chen *et al.* 2021
Janzellenidae	1	1	Chen *et al.* 2021
Platygastridae	34	406	Johnson 1992, Vlug 1995, Arias 2002, Buhl 2011
Scelionidae	44	332	Johnson 1992
Sparasionidae	4	13	Chen *et al.* 2021
MYMAROMMATOIDEA	**1**	**1**	Gibson *et al.* 2007
Mymarommatidae	1	1	Gibson *et al.* 2007
CHALCIDOIDEA	**813**	**5618**	De Santis 1979, 1983, 1989, Noyes 2020
Agaonidae	7	100	Ramirez 1970
Aphelinidae	22	347	Hayat 1983, Kim and Heraty 2012
Azotidae	1	17	Noyes c2020
Chalcididae	21	472	Delvare and Bouček 1992, Arias and Delvare 2003
Encyrtidae	170	1200	Noyes 1980, c2020
Eucharitidae	18	138	Heraty 2002

(Continued)

TAXON	Gen.	spp.	References
Eulophidae	120	1541	Gauthier *et al.* 2000, Hansson 2009
Eupelmidae	31	206	Gibson 1989, 1995
Eutrichosomatidae	2	3	Boucek 1975, Zhang *et al.* 2022
Eurytomidae	32	306	Noyes c2020
Leucospidae	2	36	Bouček 1974
Megastigmidae	2	3	Noyes c2020
Mymaridae	77	349	Yoshimoto 1990, Huber 1986
Ormyridae	1	4	Hanson 1992
Perilampidae	4	45	Noyes c2020
Pteromalidae	228	473	Noyes c2020
Rotoitidae	1	1	Bouček and Noyes 1987
Signiphoridae	4	52	Noyes c2020
Tanaostigmatidae	5	72	LaSalle 1987
Tetracampidae	1	1	Noyes c2020
Torymidae	13	126	Noyes c2020
Trichogrammatidae	51	126	Pinto 2006, Noyes c2020

However, in key groups such as bees or microhymenoptera (excluding Chalcidoidea) there is no updated information. In some cases (such as Diaprioidea and Platygastroidea), efforts have been made to scan recent literature. In the case of Cynipoidea, one of the important groups of unlisted wasps, the work of making a checklist based on original literature is being undertaken. There are a few families of Hymenoptera for which there are no catalogs or lists available, such as Tiphiidae or Thynnidae.

In the megadiverse superfamily Ichneumonoidea, the task of establishing updated numbers of genera, and especially of species, is difficult. Making estimates of diversity is even more complicated, due to the apparent large number of species that remain undescribed in the tropics (e.g. Zaldívar-Riverón *et al.* 2010, Fernández-Florez *et al.* 2013, Marsh *et al.* 2013, Sharkey *et al.* 2021). However, the high numbers of new species reported with molecular techniques, as in the case of the 403 new species of Braconidae described in Sharkey *et al.* (2021) using COI barcode clusters should be viewed carefully. Meier *et al.* (2021) show that many of Sharkey *et al.*'s species are unstable when the underlying data are analyzed using different species delimitation algorithms. This creates a new problem, that of the proliferation of new names weakly supported (the "superficial description impediment": Meier *et al.* 2021).

The most species-rich families are Ichneumonidae (4505), Braconidae (4142), Formicidae (3200), Crabronidae (1304), Apidae (1926), Eulophidae (1541), Mutillidae (1505), Vespidae (1427), Encyrtidae (1200), Megachilidae (1014), Halictidae (1004) and Pompilidae (nearly 1000) (Table 1, Supplementary Fig. S1). Regarding the number of genera, the richest families are Ichneumonidae (472), Braconidae (465), Pteromalidae (230), Encyrtidae (170), Formicidae (142), Apidae (135), and Eulophidae (120) (Table 1, Supplementary Fig. S2). There are families rich in species, but not in genera, such as Crabronidae, or rich in genera and not in species, such as Pteromalidae. Others occupy the first places in any criterion of number of genera or species, such as Ichneumonidae and Braconidae, groups considered hyper-diverse.

Despite the limitations noted above, and the certain lack of recent information on some groups (such as Tiphiidae), the numbers offered here are a good estimate of the described richness of the order Hymenoptera. When

making adjustments (new taxa vs synonymized taxa), the number of described genera should be close to 3200 and the number of described species close to 34 000. These numbers respectively represent 38 % of World genera and 22 % World species. Even though there is no recent and comparable information on the diversity of Hymenoptera in each of the large natural regions, the following data gives an idea of the sizes of their fauna: About 13 000 species in Australia (8 % of the World, Britton c2018), 17 429 in the Nearctic (12 % of the World, Danks and Smith 2009), just over 21 000 in the Palearctic (14 % of the World, Korotyaev *et al.* 2017). Even without knowing the numbers for the other two great regions, the Afrotropical and Oriental, it is highly probable their combined Hymenoptera fauna is the richest in the world, with almost 34 000 described species.

Another matter is estimating the total number of species in the Neotropics and other regions. For the Nearctic, Grissell (1999) estimates the number of species may be about 36 000 (50 % more). This author cites 17 000 described species only for Costa Rica and estimates total number between 20 000 and 40 000. If these numbers and approximations are accurate, the Neotropical fauna could easily reach 100 000 species, more than 60 % of which is not described. Since global estimates of the richness of Hymenoptera is highly variable (between 30 000 and 2.5 million species) the estimated number for the Neotropics can vary between 100 000 and almost a million. In the most recent approach Forbes *et al.* (2018) extrapolate information on the diversity of parasitoids and estimates 1 152 127 species of Hymenoptera for the World.

It is striking that the Neotropics are home to a rich fauna, with a high number of endemism, but at the same time it is facing serious problems that threaten the future of biological diversity (Mundy 2020). Deforestation, change in land management, illegal and legal mining, climate change, introduction of invasive species, new pathogens, overpopulation and pollution are exerting strong damaging pressures on the diversity of the region, from humid lowland forests to páramos (e.g. Alroy 2017). The disappearance of Hymenoptera species, as well as other insects (Wagner *et al.* 2021), not only compromises the stability of ecosystems, but also ecosystem services of interest to humans, such as the natural control of forest pests or the pollination of plants of economic interest.

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CONFLICT OF INTEREST

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