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Alexandre Somavilla *Editors*

Neotropical Social Wasps

Basic and Applied Aspects

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Foreword

Vespidology in Brazil: An Appreciation

This is a landmark volume for anyone interested in social wasps and social insects in general. It contains authoritative chapters on a very wide range of topics, from keys for the identification of genera to specific aspects of morphology, ecology, behavior, and evolution. Most of the chapters feature the social wasps of Brazil through the eyes of Brazilian researchers and others who have worked in Brazil or jointly with Brazilian colleagues. The first chapter of the volume describes the lives of some important figures in the history of Brazilian studies of social wasps. Some of them are mentioned in this preface, where I take advantage of the chance to write a personal appreciation of that history.

It would be difficult to overstate the importance of research in Brazil for the history of social-wasp science, especially for studies of Neotropical species. I first began to appreciate this when preparing for fieldwork in Colombia on tropical wasps in the middle of the twentieth century (1964–65). Among the few publications I took along as guides were copies of monographs by Adolpho Ducke (1876–1959) (Fig. 1), the Austro-Hungarian Trieste-born Brazilian biologist, who, before turning to botany (see Egler 1963), was an entomologist at the Museu Paraense (now Goeldi Museum) in Belem. Even though Ducke’s 21 papers with information on social wasps were published many years earlier (during the period 1904–1918), and in three different languages (German, French and Portuguese), they were clearly written and well illustrated. Some contained photographs and drawings of nests, for Ducke considered nests important evidence for studies of vespid phylogeny. His monographs also contained information on natural history and behavior not available elsewhere. Richards and Richards (1951, p. 2) paid tribute to “the great Adolfo Ducke, whose abilities as a naturalist, collector and taxonomist were alike unrivalled” and whose 1910 paper “is still the foundation of all work on S. American POLYBIINAE.” Largely because of Ducke’s papers I still feel a sentimental attachment to now obsolete names of Neotropical social wasp genera such as *Nectarina*, *Tatua*, and *Gymnopolybia* (now *Brachygastra*, *Epipona*, and

Fig. 1 Adolpho Ducke (1876–1959). (From Egler 1963)



Agelaia, respectively). And I regret the loss of the sonorous name *Marimbonda* (now *Leipomeles*) assigned by Richards (1978) to two Brazilian species, one discovered by Richards in the Mato Grosso and the other named by Ducke.

In addition to Ducke's publications, I used early publications by other Brazilians on Brazilian social wasps. Some of those with information on castes and reproduction were by Hermann von Ihering, a German-born naturalized Brazilian, (1850–1930) and his son Rodolpho (1883–1939). (For references to their work on social wasps see Richards and Richards (1951) and Chap. 1 of the present volume.) Like Ducke, the von Iherings published on many biological topics other than entomology and were primarily based in museums, not in teaching institutions. Similarly, R. L. Araujo, who published several important taxonomic papers on Brazilian social wasps, including notes on nests in the 1940s, was based at the Institute of Biology of São Paulo, dedicated primarily to agricultural research and outreach rather than teaching. Jose Francisco Zikán (1881–1949), who published monographs on the taxonomy of *Mischocyttarus* and other social wasps beginning in 1935 (see references in Ross and Matthews 1991), was employed as a naturalist of the Parque Nacional do Itatiaia (from introduction to Zikan 1949 by W. Duarte de Barros). In a paper published posthumously (Zikan 1949) he described several species of *Mischocyttarus* that he believed to be parasitic. To my knowledge this idea has not subsequently been investigated.

The Brazilian authors of the present volume are in large part the second and third intellectual descendants of a later generation of university-based social-wasp researchers who began their work in the 1960s, including Professors Ronaldo Zucchi, Vilma Maule Rodriques, Vera Lúcia Letfzio-Machado, and Carminda do Cruz-Landim. At about the same time there was an influx of important social-wasp researchers from outside. At least some of this surge of activity was due to the promotion of interest in social insects by the charismatic and energetic Brazilian honeybee geneticist Warwick Kerr. It was Kerr who encouraged and advised V.M. Rodriquez, for example, beginning when she was an undergraduate and also during her doctoral work; Kerr was also host to a 1964 visit to Brazil by William D. Hamilton, who then met Rodriquez while he was beginning work on social wasps. Hamilton shared information on the natural history of wasps and supplied

Fig. 2 O. W. Richards (1901–1984) at the campo-cerrado boundary near the Mato Grosso base camp of the Xavantina-Cachimbo expedition of the Royal Society of London and the Royal Geographical Society, March 1968. Richards, a noted naturalist and ecologist, is contemplating a plant, which he identified as *Paepalanthus* (Eriocaulaceae). (Photograph by Maude J. Richards; sent by O.W. Richards to the author in 1971)



difficult-to-obtain reprints of articles (Rodriquez, 1968). Hamilton was in Brazil when he did the final revisions on his influential 1964 papers (Hamilton 1964a, b) on the evolution of social behavior by what was later called “kin selection.” While in Brazil he divided the original manuscript into two parts and added his own observations on Brazilian social wasps (see Hamilton 1996, p.29), including especially *Polistes*. Hamilton’s papers appeared in print while he was still in Brazil and, coincidentally, while I was in Colombia studying *Polistes*. Hamilton’s mention of Brazilian *Polistes* attracted my attention and enabled me to immediately attempt the first field tests of Hamilton’s ideas (see West, 1966, 1967).

O. W. Richards, a leader in taxonomic and biological studies of social wasps (see especially Richards and Richards 1951, Richards 1978) made three trips to Brazil (Richards, 1978, p. 1). The first and longest was in 1968 when he spent 14 weeks at a base camp in the central Mato Grosso maintained by the Royal Society of London-Royal Geographical Society Xavantina-Cachimbo expedition (Fig. 2). That research, and collections made by W.D. Hamilton at the same site, led to the decision by Richards to write a monumental treatise on the social wasps of the Americas (Richards, 1978). He returned to Brazil in 1970 to study type specimens of *Mischocyttarus* species named by Zikán at the Universidade Federal do Paraná, where his host was Padre J. S. Moure. Then, in 1971, Richards travelled to São Paulo to study the historic collections at the Museu de Zoologia da Universidade de São Paulo, hosted by its director Paolo E. Vanzolini. Richards was 77 years old when the book was finally published. He had typed the entire manuscript himself, as I learned from conversations with Richards.

The success of such visitors always depends on the experience and hospitality of their hosts, another notable contribution of Brazilian scientists. The hospitality of rural landowners has also facilitated fieldwork on the social wasps. Robert Jeanne, for example, spent more than a year in Brazil as a graduate student. His doctoral

thesis is now well known as a classic study of social wasp *Mischocyttarus drewseni*. In his monograph on that species he acknowledged not only the help of Brazilian scientific colleagues but also the indispensable role of the Haggmann family at Fazenda Taperinha, located on the Rio Ayayá, a branch of the Amazon east of Santarém, Pará. Jeanne wrote that their “assistance, patience, understanding, sympathy, encouragement and hospitality were such as I have never experienced and shall not soon forget” (Jeanne 1972, p.141).

This volume features the special contribution of modern research on social wasps in Brazil. It shows how Brazilian scientists have capitalized on the diversity of species available for study, the opportunity for in-depth studies by people actually living where the wasps live, their special openness to international collaborations, and their own long and rich tradition of research on social wasps.

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Prologue

The Neotropical region has the greatest diversity of social wasps in the world, and this is the reason that, throughout the years, attracted the attention of specialist researchers, who investigated different biological, ecological, behavioral, and evolutionary aspects using the species of these social insects as a model.

In recent decades, studies with Neotropical social wasps have increased significantly, as this group offers fertile ground for many researchers; however, the results of these works are fragmented in thousands of scientific articles, thus hindering an insight into the state of art of the taxon.

In this way, the aim of this book is to share the knowledge obtained by several research groups around different countries (like Belgium, Brazil, Colombia, Costa Rica, Japan, New Zealand, Portugal, the UK, and the USA) whose efforts resulted in a huge amount of information on social wasps. This book provides an updated overview of different aspects of Neotropical social wasps and also pays a tribute to pioneering work, rescuing the natural history of these wasps and pointing out trends in different areas of research.

We hope that the experience shared in this book gives readers an exciting glimpse into the fascinating history of Neotropical social wasps, thereby inspiring a new generation of motivated vespidologists.

Best regards,
The Editors

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Chapter 1

A Brief Review of Studies on Social Wasps in Brazil



Sergio R. Andena, Luis Filipe Lopes, James M. Carpenter,
and Orlando T. Silveira

Abstract Social wasps in Brazil are common elements being important components of interactions with other organisms, acting as predators as well pollinators. In this chapter, we review the study of this group since the discovery of Brazil, in 1500. In the first two centuries (1500–1700), references to this group are rare, being most of the references to Hymenopteran being about ants and bees. During this period, most of the animal descriptions were done by naturalists who focused on their practical use, derived products, and damage caused by them. Later, with the development of natural sciences and onset of taxonomic systems, studies became more systematic. Many foreign researchers and expeditions visited the country to study its wildlife and particularly social wasps. Furthermore, with the establishment of scientific societies and universities in Brazil, many researchers have pursued the study of this group.

Keywords Wasp researchers · Expeditions · Natural history · Naturalists

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Social wasps are widely distributed in the Neotropical Region and are common elements in tropics (Pickett and Carpenter 2010). Also, they are important components of complex interactions with other organisms in neotropical ecosystems (Silveira et al. 2012) as predators – acting in biological control – as well as pollinators (Carpenter and Marques 2001). Research on this important group of insects, sometimes misunderstood by the general public, because some a small fraction of species have huge nests or are very aggressive, has been the key to important theories such as natural selection, where caste differentiation challenged Charles Darwin (1859), inclusive fitness by William Hamilton (Hamilton 1964a, b), and sociobiology by Edward Wilson (1975).

Knowledge about social wasps has been reported since the ancient Greeks, Egyptians, Romans, Native Indians in South and Central America, and the Orient. Wasps, in some places, have played an important role in rituals, legends and symbolism of ancient civilizations. A more detailed account of this part of the history can be found in Edwards (1980).

In this chapter we trace the records of social wasps in Brazil, since its discovery, in 1500, until recently, building from the early reports on Brazilian nature, through the first naturalists, where specific reports on social wasps are scarce, to a period where extensive research work is focused on species of this group.

1.1 Wasp Records in Brazil: Since 1500

Brazil was discovered on April 22 of 1500 by Pedro Álvares Cabral, as part of Kingdom of Portugal marine expansion (Fausto 1996:9). When the Portuguese arrived in Brazil for the first time, they were surprised by the exuberance of the nature in the “new land.” Pero Vaz de Caminha (1450–1501), one of the crew members of the ship, wrote a letter addressed to King Don Manuel I (1469–1521), describing the discovery of the “new land”, including records of the nature, the animals, and the first contact with the culture of Native Indians. In an excerpt from the letter, Pero Vaz describes “the presentation” of some animals to natives and vice-versa:

Mostraram-lhes um papagaio pardo que o Capitão traz consigo; tomaram-no logo na mão e acenaram para a terra, como se os houvesse ali.

Mostraram-lhes um carneiro; não fizeram caso dele.

Mostraram-lhes uma galinha; quase tiveram medo dela, e não lhe queriam pôr a mão. Depois lhe pegaram, mas como espantados.

They showed them a brown parrot that the Captain brings with him, they took him in his hand and beckoned to the earth, as if they were there.

They showed them a ram; they ignored him.

They showed them a chicken; they were almost afraid of her, and they did not want to lay hands on her. Then they took him, but they were astonished.

This first and friendly contact with the native Indians was indispensable for success in the colonization of the Brazil, including the knowledge of nature, although, unfortunately, there is no record of social wasps in this early stage of Brazil.

Records of hymenopterans were rare, and most of the references found are to bees and ants, not specifically to social wasps. However, an anecdote without date, which we thought may be from the time of the early “Brazil Colony,” makes some reference to wasps (Lenko and Pappavero 1996: 169–170).

Dizem que... Durante o período do Brasil Colônia, um dos colonizadores esbarrou descuidadamente em um ninho de vespas. Estas saíram furiosas, em bando, para atacá-lo. Pondo-se em defesa, com a espada desembainhada, o pobre colonizador pôs-se a dar vãs cutiladas no ar, tentando desesperadamente defender-se dos terríveis ferrões. Mas sem resultado – ficou todo disforme e inchado. Bastante vexado, curtindo as picadas, voltou a embainhar a espada, ferido física e moralmente, dizendo: –Ah! Covardes.... Tivessem vindo uma a uma...

They say... During the period of the Brazil Colony, one of the settlers bumped carelessly into a wasp nest. They left, furious, to attack him. Turning in defense, with his drawn sword, the poor colonizer began to whip in the air, trying desperately to defend himself from the terrible stings. But without result – it was all disfigured and swollen. Quite vexed, resenting the stings, he again sheathed the sword, wounded physically and morally, saying: –Ah! Cowards They had come one by one...

The first hymenopteran records, as with those of other species, are mostly based on their practical use, either as a food source (honey) or derived goods (wax), or, as in the previous example, on the threat that they may pose. Some of the early visitors who reported on Brazilian animal species mentioned them.

The German Hans Staden (1525–1576), who was prisoner of the Tupinambás – a tribe of cannibals (Staden 2006) – depicted, in his diary, some landscapes, and records of bees, probably of the species *Tetragonisca angustula* (Latreille, 1825), *Melipona quadrifasciata* (Lepeletier 1836), and *Scaptotrigona postica* (Latreille, 1807) (Almaça 2002). Some species of bees were widely employed by natives for harvesting honey (Staden 2006) (Fig. 1.1).

Jean de Léry was sent by J. Calvin to “Antarctic France,” as was called an island in Guanabara Bay, which was controlled at the time by the French. Later, he refers to bees unlike those in Europe that resemble little black flies and that deposit honey and wax in tree trunks (Almaça 2002). The indigenous people would eat the honey and use the wax to insulate wooden chests. He produced excellent illustrations of the fauna and flora of Brazil in his *Histoire d’un voyage fait en la terre du Bresil, dite Ameriquein*, in 1578.

The priest José de Anchieta (1534–1597) is considered the first major naturalist in Brazil, producing quality descriptions of many animal species (Almaça 2002; Paiva 2000). In May of 1560, in a letter addressed to the general priest of the Companhia de Jesus, he describes about 70 species, among which are some hymenopteran insects, especially ants, considered one of the major destructive forces of the region, as well as a reference to *Atta sexdens* (Linnaeus, 1758), whose winged forms were collected by the indigenous people. A wasp of the Pompilidae



Fig. 1.1 Drawing of a routine of Tupinambás natives' life by Hans Staden (Chapter XLVI)

family is also mentioned, probably *Pepsis elevata* Fabricius, 1804, which is deemed to kill spiders and transport them to the nest (Almaça 2002).

Yves d'Évreux (1577–1632) was sent to Maranhão State, northeastern of Brazil, in 1612, and mentions a wide range of flies, as well as wasps, among those a black wasp that builds complex pottery nests in the tops of trees. Seeking to better observe these nests, he was stung by one and reported feeling excruciating pain and being sick for several days (Almaça 2002).

The publication *Historia Naturalis Brasiliae* must be referred to for this period, as it is considered the first scientific work to be published about Brazilian natural history (Santos 2014; Vanzolini 1996), being published in Leiden and Amsterdam in 1648 (Marcgrave and Piso 1648). The first volume of this publication is of the authorship of Willem Piso on medical subjects and the second of George Marcgrave (1610–1643) about the natural history of Brazil, divided into eight books, entitled *Historiae rerum naturalium Brasiliae libri octo*. Four out of eight chapters are dedicated to zoology and became a work of reference for the Brazilian fauna (Almaça 2002). In Chap. IX (*Infectum volans*), page 255, he pictured the *Paipai guacu*, a Crabronidae).

The little and scattered information about the Brazilian fauna from the 1500s to 1700s is due mainly to the study of natural history in Brazil being hindered by the Portuguese inquisition, which caused a stagnation in science and culture, and by the

limitations imposed by the crown on the publication of knowledge obtained in all areas of the natural history of Brazil, treating it as “a state secret to avoid foreign coveting” (Almaça 2002; Paiva 2000; Santos 2014). Furthermore, Brazil was strictly forbidden from having its own press (Nomura 1998). Therefore, most of the Portuguese texts and descriptions on the natural resources of Brazil were only published many years after they were written. In this period, most of the reports of the Brazilian natural history were published by foreigners, especially from areas that were temporarily controlled by France and the Netherlands. Furthermore, since 1604 foreigners were forbidden to enter Brazil to study its natural resources, as was the case with the famous naturalist Alexander von Humboldt, which further hampered the study of Brazilian zoology (Nomura 1998). Only, much later, in 1801, Count Johann von Hoffmannsegg obtained authorization to send his collector Friedrich Wilhelm Sibber to Brazil to collect insect specimens (Papavero 1971).

Nomura (1998) analyzed the work of 93 naturalists who worked on Brazilian zoology in the eighteenth century, describing animals that occur in Brazil, listing the animals referred to by them and when possible trying to identify its current scientific name. Of those 93 naturalists, only some refer to insects and even fewer species of the order Hymenoptera. Despite the few known expeditions, wasp species, collected in Brazil, were described by Europeans during the eighteenth century, as follows:

Carl Linnaeus (1707–1778) named many South American insect species, among them several Hymenoptera, of the families Formicidae, Vespidae, and Tenthredinidae. The Vespidae species were *Synoeca surinama* (Linnaeus, 1767) and *Polistes canadensis* (Linnaeus, 1758).

Francisco Antônio de Sampaio (unknown birth and death, 1700) referred to several insects, among them two hymenopteran species of the family Apidae, which should correspond to *Melipona scutellaris* (Latreille, 1811) and *Tetragonisca angustula* (Latreille, 1825).

Guillaume Antoine Olivier (1756–1814) referred mainly to species of the order Coleoptera in which he specialized, but included some hymenopterans, of the families Apidae, Formicidae, and Vespidae, namely, *Polistes versicolor*, *Agelaia pallipes*, *Polybia dimidiata*, *Polybia occidentalis*, *Polybia sericea*, etc. (Olivier, 1792).

Johann Christian Fabricius (1745–1808) was responsible for the description of the largest number of insect species of Brazil from the eighteenth century, including some hymenopterans of the families Apidae, Formicidae, and Vespidae, namely, from this last family, *Synoeca cyanea* (Fabricius, 1775).

João Daniel (1722–1776) referred to many insect species and among them several hymenopterans of the families Apidae, Formicidae, Sphecidae, and Vespidae. The Vespidae referred to would be *Polistes* sp. and *Synoeca cyanea*.

Still in the eighteenth century, under the influence of Sebastião José de Carvalho e Melo (1699–1782), Portuguese prime minister, the influence of the inquisition was limited and public instruction was reformed, including the education at University of Coimbra (Paiva 2000; Simon 1983). This opened the way for the cre-

ation, in Lisbon, of the Academia Real das Ciências in 1779. That same year, Joaquim Veloso de Miranda was sent to Brazil with instructions to collect materials and information pertaining to the natural history of Brazil, to be sent to the Real Gabinete de História Natural da Ajuda (Paiva 2000).

A expedition was prepared to the Brazilian region of Pará, organized by Domingos Vandelli (1730–1816), who proposed Alexandre Rodrigues Ferreira (1756–1815), a Brazilian who studied under his direction in the University of Coimbra, to conduct this expedition (Simon 1983). In his “*Phylosophycal Voyage*”, Alexandre Rodrigues Ferreira described and collected many new animals and amassed an incredible collection of the Brazilian fauna, unique at its time. However, he never got to publish any results, and with the occupation of Portugal by French troops (see below), most of these collections were taken by Etienne Geoffroy Saint-Hilaire to France, including over 500 specimens of insects (Paiva 2000; Simon 1983). Most of the work is focused on other groups, but some references to insects and a picture of a wasp nest were included in the illustrations produced in that expedition (Fig. 1.2). Joaquim José Codina (unknown birth date, 1790) and José Joaquim Freire (1760–1847) were artists accompanying the expeditions headed by Alexandre Rodrigues Ferreira.

In the second half of the eighteenth to early nineteenth centuries, some new scientific academies were formed in Brazil, such as the Academia Brasílica dos Renascidos (1759), in Salvador, and the Academia Científica (1772) do Rio de Janeiro. Later, the Casa de História Natural was created, known as Casa dos Pássaros

Fig. 1.2 A nest of wasp depicted by José Joaquim Freire (1760–1847), in *Desenhos de gentios, animais quadrúpedes, aves, anfíbios, peixes e insetos da Expedição Filosófica do Pará, Rio Negro, Mato Grosso e Cuiabá*. Originais. Volume 1. Deposited at Arquivo Histórico dos Museus da Universidade de Lisboa - Museu Nacional de História Natural e da Ciência, Universidade de Lisboa | PRISC INV. MUHNACMUL-AH, PT-MUL-RMJBA-TC-02-0006



(1784), in Rio de Janeiro, with the objective to collect, prepare, store, and send to the Real Gabinete de História Natural da Ajuda in Portugal. This was the precursor of the current Museu Nacional of Rio de Janeiro, created in 1818 (Paiva 2000) and burned recently, in 2018. In 1810, finally the Royal Press was installed in Brazil, which allowed the publishing of scientific works in Brazil.

All these institutions had a great impact in the Brazil colony, but it was after the move of the Portuguese Court to Brazil that other institutions were created, and science was free to proliferate in the country.

1.2 The Kingdom of Portugal Moves to Brazil in 1808

The Napoleonic Wars, in the nineteenth century, brought serious consequences to Europe. In November 1807 French troops marched into Lisbon, and Prince Dom João, in a few days, decided to move the Portuguese Court to Brazil (Fausto 1996: 75). The transfer of the Court to Brazil involved around 10,000–15,000 people, including ministers, counselors, judges, clergy, armed forces, etc. Furthermore, documents, manuscripts, royal treasure, and libraries were transferred, which later became the National Library in Rio de Janeiro (Fausto 1996:75).

The transfer of the Royal Family to Brazil changed, definitively, the administrative center of the colony to Rio de Janeiro (Fausto 1996: 78). In September 1808, the first newspaper in Brazil was published; theaters, libraries, and literary and scientific academies were also opened to meet the requirements of the royal family and an urban population in rapid expansion (Fausto 1996: 78–79).

After Napoleon's defeat Dom João raised Brazil to the United Kingdom of Portugal and Algarves. He left his son Dom Pedro I (named Pedro IV in Portugal) in Brazil, who assumed the throne. Dom Pedro I later went back to Portugal and left his son, Dom Pedro II, an enthusiast of arts and sciences, as the Emperor of Brazil.

1.3 Dom Pedro II and Science in Brazil

No doubt that the political and intellectual effervescence that characterized the coming of the Royal Family to Rio de Janeiro brought great benefits to Brazil. Here we highlight Dom Pedro II – the most learned emperor of Brazil (from 1831 through 1889). Pedro II's interests included anthropology, geography, medicine, law, religion, philosophy, sculpture, music, theater, poetry, technology, arts, language, and natural science (Lyra 1977). He had an extensive correspondence with the most prominent scientists, artists, and intellectuals of the period, just to cite a few: Richard Wagner, Alexander Graham Bell, Louis Pasteur, and Friedrich Nietzsche (Calmon 1975; Lyra 1977; Gray 2006). Some institutions created under Pedro II

were: Colegio Pedro II (Pedro II School), Ópera Nacional (National Opera), Instituto Histórico e Geográfico Brasileiro (Brazilian Institute of Geography and History), Escola Imperial de Belas Artes (Imperial School of Fine Arts), Instituto Pasteur (Pasteur Institute), and Museu Nacional (National Museum). Another important contribution of Pedro II was to provide means for Brazilian students to attend universities in Europe, fostering the acquisition of new knowledge in the country. These actions had a deep influence on the science of Brazil until the present day.

In the period of the late Empire and early Republic of Brazil (installed in 1889), many naturalists interested in the fauna and flora of Brazil developed their research in the country. Here we emphasize some of those who worked on wasps.

1.4 Amédée Louis Michel Lepeletier of Saint-Fargeau (1770–1845)

Amédée Louis Michel Lepeletier of Saint-Fargeau (1770–1845) was an entomologist in France, dedicating most of his life to the study of Hymenoptera. Also, he was president of the Entomological Society in France, from 1833 until his death, in 1845.

In 1836 Lepeletier published the “Histoire naturelle des insectes – Hyménoptères,” as part of the series “Suites à Buffon,” edited and published by Roret. This work, comprising four volumes, about 2500 pages and 48 plates – drawn by Priest and having excellent coloring for that time – is still, despite its age, an excellent reference for those interested in studying Hymenoptera. Lepeletier (1836) employed the social behavior as the main feature for separating the species into two groups: solitary and social. He named the social vespids the Polistides, with eight genera, including the new *Polybia*, *Agelaia*, *Apoica*, and *Chartergus*, which presently comprise only neotropical species.

1.5 Karl August Möbius (1825–1908)

Möbius was born in Eilenburg in Saxony. In 1844 he passed the exams with distinction and began working as teacher in Seesen, on northwest edge of the Harz mountain range. In 1849 he began studying natural science and philosophy at Humboldt University in Berlin. After he graduated, he taught zoology, botany, mineralogy, geography, physics, and chemistry at the Johanneum High School in Hamburg (<https://peoplepill.com/people/karl-moebius-1/> accessed on December, 01 2019)

Most of his works concerned study of oysters of coastal regions of northern Germany, publishing important titles on this subject, as the *Über Austern- und Miesmuschelzucht und Hebung derselben an der norddeutschen Küste* [About oys-

ters and mussel farming and uplifting on the north German coast], published in 1870, which had the object of the production of oysters commercially.

Despite his dedication to oysters, Möbius also published articles on wasps. His article “Die Nester der geselligen Wespen. Beschreibungen neuer Nester - und einiger neuen Wespen-Arten des naturhistorischen Museums zu Hamburg, nebst Betrachtungen über den Nesterbau im Allgemeinen” [The nests of the social wasps. Descriptions of new nests and some new wasps’ species of the Museum of Natural History in Hamburg, as well as considerations about nest building in general], published in 1856, comprised 51 pages and 19 colored plates devoted to nest architecture (Fig. 1.3).

In 1888, Möbius became curator of the Zoological Collection at Museum für Naturkunde in Berlin, and professor of Systematic and Geographical Zoology at the Kaiser Wilhelm University, also in Berlin, where he taught until he retired at age of 80, in 1905 (<https://peoplepill.com/people/karl-moebius-1/> accessed on December, 01 2019).



Fig. 1.3 Nest of *Angiopolybia pallens*, figured by Möbius as *Polybia ampullaria*

1.6 Hermann (1850–1930) and Rodolpho von Ihering (1883–1939): Father and Son

Hermann Friedrich Albrecht von Ihering was born in Germany and graduated in Medicine (1886–1873) in Berlin and Göttingen. Just after his graduation, he became a zoological assistant of Carl Claus, a crustacean specialist, however von Ihering worked on the ontogeny of *Cyclas* (a freshwater Mollusca), in his PhD thesis, defended at the University of Göttingen. According to Lopes and Podgorny (2014) von Ihering was pressed to publish his articles and get a job, between 1872 and 1880. During this time, he published at least 30 articles in several zoological and anthropological journals. Also, these authors stated that, if several factors of a personal and professional nature must have influenced von Ihering in coming to Brazil, there is no doubt that the competitive environment among German zoologists and the lack of jobs was also an influencing factor. At the age of 30, in 1880, he moved to Rio de Janeiro. From there he settled in Rio Grande do Sul state, southern Brazil, where he started collecting specimens and sending them to museums in Germany and England in exchange for monetary compensation (Nomura 2012). In 1883, he was hired by the Museu Nacional, in Rio de Janeiro, as a “naturalist traveler; 4 years later, in 1887 he was hired by the Museu Paulista, in São Paulo.

The research on the Brazilian fauna, carried out by von Ihering, included a wide range of groups: mammals, birds, reptiles, amphibians, pisces, mollusks, crustaceans, arachnids, helminths, and several groups of insects – Lepidoptera, Coleoptera, Hemiptera, Diptera, Isoptera, Orthoptera, and Hymenoptera (Nomura 2012).

Hermann von Ihering studied ants (Fig. 1.4), bees (especially the stingless bees of Brazil), and wasps, focusing on their behavior, biology, and nest architecture. As pointed out by Nomura (2012), in an article of 1896, “Hermann stated that in Europe the colony of the wasp dissolves in early winter, being similar in *Polistes* in Brazil, and that the *Polybia* species stay into the closed nests. Further, he observed that in Brazil, *Polybia scutellaris* and other species of the same genus form new nests by swarming, as can be observed in bees. In his studies, he observed a great variety of wasp nests in Brazil, reporting that the simplest does not have a cover, but only a layer of cells, (e. g. *Polistes*, *Mischocyttarus*), however other species build complicated nests with a cover that protects them from rain. The life cycle was divided by Hermann into two phases: annual or summer phases as in *Polistes*, *Mischocyttarus*, and perennial phases that multiply by swarming as in *Polybia*, *Apoica*, *Tatua* (= *Epipona*), *Pseudopolybia*, *Synoeca*, *Chartergus* and *Nectarinia*.”

Hermann had four children: Clara, Rodolpho, Wilhelm, and Ida (Nomura 2012). Rodolpho Theodor Wilhelm Gaspar von Ihering (1883–1939) (Fig. 1.5) was born in Taquara do Mundo Novo, Rio Grande do Sul state (<http://dichistoriasaude.coc.fiocruz.br/iah/pt/verbetes/iherrod.htm>, accessed on 30 October, 2019), and was a disciple of his father.

In 1901 Rodolpho graduated in Science and Modern Language, in São Paulo, and, in 1902, he was nominated by his father as Assistant Director of Finances of the

Fig. 1.4 Hermann von Ihering with his wife, Meta Buff von Ihering, possibly in the Reserva Florestal do Alto da Serra, São Paulo State. Available at <http://www.kb.dk/images/billed/2010/okt/billeder/object147776/en/>



Fig. 1.5 Picture of Rodolpho Theodor Wilhelm Gaspar von Ihering (1883–1939). (Modified from Paiva and Mesquita (2013))



Museum Paulista (<http://dichistoriasaude.coc.fiocruz.br/iah/pt/verbetes/ihenrod.htm>, accessed on 30 October, 2019; Nomura 2012). In 1905 he went to Europe to study natural sciences; however, after 6 months he had to come back to Brazil after the death of his brother and his mother (Nomura 2012).

Rodolpho, since 1904, dedicated his studies to the freshwater fishes of Brazil including taxonomy, reproduction, behavior, systematics, etc. (<http://dichistoriasaude.coc.fiocruz.br/iah/pt/verbetes/ihenrod.htm>, accessed on 30 October, 2019).

Despite his dedication to fishes, he also worked on invertebrates and published several articles and books on zoology and biogeography. He traveled to several parts of Brazil for more than 30 years collecting specimens and records about rituals and stories regarding the Brazilian fauna. One of his most prominent works was the *Dicionário dos animais do Brasil* [Dictionary of animals of Brazil], in 1940.

In 1904, Rodolpho published the article “As vespas sociais do Brasil” [The social wasps of Brazil]. In this revision, he pointed out that “the present review of the Brazilian species shows 11 genera and 130 species.” Furthermore, he provided an identification key to the social wasps of South America.

1.7 William J. Fox (Unknown Birth and Death)

Fox was not a researcher on wasps; he was hired at the Academy of Natural Sciences, in Philadelphia, as an assistant librarian. “Nothing is recorded of Fox’s early life, but the fact that his first paper, published in 1891, dealt with a trip to Jamaica made in company with C. W. Johnson suggests that his interest in insects may have been first aroused, or at least encouraged, by that beloved dipterist who, as is well known, initiated and nurtured an interest in insects in several boys who later became well known entomologists” (Bradley 1959).

Despite Fox having worked most on the fauna of Hymenoptera of North America, he also published a report on the Hymenoptera collected by Donaldson Smith on an expedition in Africa and a very important series of papers on the Hymenoptera collected by Herbert H. Smith during some years’ residence in Brazil (Bradley 1959). His knowledge of the neotropical fauna of social wasps was mainly based on the collection made by Herbert H. Smith, of which he described the genus and species *Charterginus fulvus* (Fox 1902), and 12 more species from other polistine genera. In Vespidae, Fox described nearly 80 species, mostly in Eumeninae. Bradley (1959) stated that Fox’s work on Hymenoptera was discontinued in 1898, not because of loss of interest but, he was told, because he was officially discouraged by his superior officer from continuing it; however he, later, published an article about the Eumenidae of Brazil in 1902.

1.8 Henri de Saussure (1829–1905)

Born in Switzerland, Saussure graduated from University of Geneva, where he was introduced to entomology by François Jules Pictet de la Rive and got his PhD at the University of Giessen (Yung 1905; de Claparède 1905).

“Beside entomology, de Saussure surprised those who approached him by the extent and variety of his knowledge; a naturalist educated in all the fields of zoology, he was also a geologist, archaeologist, historian, and geographer; he stood at the heart of the progress of agronomy as well as of physics or alpinism, and very few were the questions to which he could not immediately give a precise and thorough answer” (Yung 1905).

Under the direction of Dr. Pictet, he began his great monograph of *Guêpes Sociales*, which he pursued in Paris, where he spent several years, following courses at the Sorbonne, often in the laboratories of the museum, making friends with the professors of this establishment (de Claparède, 1905). In 1854 he and his friend Henri Peyrot set out on a long voyage of exploration in the Antilles and Mexico, a difficult journey through the Mexican provinces, then in permanent revolution, during which time he amassed considerable numbers of objects (Yung 1905).

This voyage was an important event in the career of de Saussure; he engaged in research on hydrology, volcanoes, insects, and myriapods; and he made several first-rate discoveries. “Among these were his notes on the Volcan de Jurullo et le pic d’Orizba, his Description des ruines d’une ancienne ville mexicaine, his Observations sur les mammifères et sur divers oiseaux du Mexique, his Recherches sur les orthoptères de l’Amérique moyenne, his Divers Crustacés nouveaux du Mexique et des Antilles, his Essai d’une faune des myriapodes du Mexique and letters which he addressed to our journal, describing in a sober and captivating style the events of which he was the witness and the remarkable men he met during his perilous expedition. His letters on Mexico were for all those who read them a true revelation.” The interest was still exceeded, if possible, by the tales de Saussure loved to tell to his friends about this decisive period of his life (Yung 1905; Léréjallien 1906).

He returned from Mexico in 1856, after visiting the United States, where he established friendly relations with Louis Agassiz, Professor Henry, head of the Smithsonian Institute, and other eminent scholars of the New World. De Saussure became a great authority, not only on the Hymenoptera, a group on which he wrote thousands of pages and hundreds of cleverly drawn figures, but also on the Orthoptera, of which he had formed an unrivaled collection. He was sent insects from all the parts of the globe to determine, and his correspondence was immense. While engaged in an investigation of the anatomical forms, he did not lose sight of the living insect, and his observations on the nesting of the *guêpes* will remain a model of the study of the manners of the animals (Yung 1905).

The travels of de Saussure resulted in important collections, which, together with the material deposited in European collections, were the base of his great monograph on the vespids, describing around 50 genera (Van der Vecht and Carpenter 1990). His most important work *Études sur La famille des Vespides*,

published in three volumes from 1852 to 1858, divided the Vespidae into three tribes – Masariens, Euméniens, and Vespiciens – based on the level of sociality, which, according to the author, would be enough to separate the groups. Besides taxonomic work, de Saussure presented extensive biological data, as well as detailed studies on nest architecture. Some terms created by him to describe general architectural features like “stelocytтарous” and “phragmocytтарous” were widely employed by Richards and Richards (1951) and Richards (1978) and are still in use.

1.9 Adolpho Ducke (1876–1959)

The naturalist Adolpho Ducke (born in Trieste, Italy) became one of the most prominent botanists/entomologists working in the Amazon region in the early 1900s.

As part of the scientific development of the Museu Paraense – in Belém, Pará State, northern Brazil – in 1899, Dr. Emilio Goeldi, head of the Museum, hired several technicians, among them, Adolpho Ducke, at that time at the age of 23. Ducke initially worked in the Zoology Department, as collector and curator of the entomological collection (Miranda 1999), being the first Hymenoptera taxonomist resident in the Brazilian Amazon.

In several articles published in the first two decades of the nineteenth century, Ducke (1904, 1905, 1907, 1908a, b, 1910a, b, 1914, 1918) carried out important work on the neotropical fauna, creating nine new genera of social wasps – most used until very recently and three of them still being valid nowadays. With these new taxa, Ducke promoted the recognition of considerable diversity of form, social organization, and architecture in natural groups traditionally treated as parts of *Polybia*. Ducke’s last work on wasps was a catalog of the Brazilian fauna (Ducke 1918). Despite his works on wasps, Ducke was also a botanist. Jacques Huber (1909) *apud* Miranda (1999) says that “Mr. Ducke, entomologist at the Museu Goeldi, collect in his travels to country of the state, in behalf of the Museu Goeldi, to collect, besides insect, a great number of dried plants.” In 1914 he started the collection of botany, and, in 1918, he became the head of the Botanical Sector of the Jardim Botânico do Rio de Janeiro (Botanical Garden of Rio de Janeiro), where he produced his last work about wasps. From Rio de Janeiro, Ducke, in 1933, moved back to Northern Brazil, to Manaus, to study the region called “Alto Amazonas.”

According to Miranda (1999), in the 1950s, Ducke proposed, along with other botanists, the preservation of the area surrounding Manaus, due to the great floristic diversity. In 1956 that area became the Center of INPA (Instituto Nacional de Pesquisas na Amazônia, National Institute for Amazon Research) Forest Surveys. In 1962, the 10,000 hectare Center of INPA was donated to INPA, receiving the name of the Adolpho Ducke Forest Reserve.

1.10 Joseph Francisco Zikán (1881–1949)

Joseph Francisco Zikán was one of the most important taxonomists of the neotropical social wasps during the twentieth century. Zikán was born in Teplitz-Schönau, present-day Czech Republic, and completed his basic studies in his native country. Migrating at a young age to Brazil, in 1902, he initially settled in São Paulo. He lived for some time in Minas Gerais, where he worked as a teacher and an insect collector, carrying out expeditions there and in Espírito Santo State, where he lived from 1911 until 1923 when he finally settled with his family in Itatiaia, Rio de Janeiro. During the years 1927 and 1928, he made collections in the Amazon, invited by the Rio Negro Prelature. He was then hired as a technical assistant to the current Itatiaia National Park, where he was later promoted to naturalist, having devoted 26 years of his life to the study of the insects in that region (Fundação Oswaldo Cruz – Adolfo Lutz Virtual Library; www.bvsalutz.coc.fiocruz.br; accessed on 06.viii.2019).

Zikán published about 60 works on, besides social wasps, insects of the orders Coleoptera, Lepidoptera, and Diptera. He published two works of major impact on the taxonomy of wasps of the genus *Mischocyttarus* de Saussure, with emphasis on the fauna of the Itatiaia region and other locations in southeastern and southern Brazil. The first of these studies was published in 1935, where he described 27 new species. Besides, the study contained detailed descriptions of nest architecture and other aspects of the biology and distribution of these wasps. The second article was published in 1949, the year of his death, where he described 82 new species of *Mischocyttarus*. The mere consideration of the number of new taxa described by Zikán leaves no doubt about the importance of his work in this field, but it is further reinforced by the notable insect collection he produced, currently deposited in the collection of the Instituto Oswaldo Cruz, in Manguinhos, Rio de Janeiro. It contains close to 150,000 specimens, mainly from the fauna of Itatiaia National Park, in which we highlight the collections of Lepidoptera (57,329 specimens), Coleoptera (56,744 specimens), and Hymenoptera (32,785 specimens). It was acquired by the Instituto Oswaldo Cruz in 1952 (Instituto Oswaldo Cruz Entomological Collection; <http://ceioc.fiocruz.br/>; assessed on 17.x.2019; Academia Itatiaense de História; https://acidhisoficial.blogspot.com/P/acidhis_patrons.html; assessed on 17.x.2019) (see also Richards 1978).

1.11 Renato Lion de Araujo (1912–1978)

Renato Lion de Araujo was born in Lambarí, Minas Gerais State, and moved to São Paulo to pursue his studies. In 1931 he graduated as an accountant and was hired by the Instituto Biológico, Secretaria da Agricultura, as a supervisor. Three years later, in 1934, he started working in the Museu Paulista, where he developed most of his

studies. Initially, Araujo dedicated most of his time working on Isoptera; however, he also worked on wasps and birds. He traveled to most parts of Brazil collecting, especially Isoptera, and compiling a vast collection, presently deposited in the Museu Paulista, São Paulo.

In 1937, Silvestri, visiting Brazil, suggested the creation of a Brazilian society to serve entomologists. Araujo followed through to create the Sociedade Brasileira de Entomologia, of which he was the head from 1947 to 1951.

Regarding Araujo's work on Hymenoptera, one of his most prominent projects was the revision of the genus *Metapolybia*, describing two new species (Araújo 1945). Moreover, he proposed a new name, *Angiopolybia*, for the new concept of *Stelopolybia* (Ducke 1914) (see Araújo 1946) and other important works about Vespidae, such as his work of 1951, in which he expands the knowledge of *Clypearia angustior*, about Polybiinae (=Epiponini) (Araújo 1960), and also the knowledge of *Synoecoides* (Araújo 1944).

1.12 Owain Westmacott Richards (1901–1984)

Richards was born in Croydon, United Kingdom, in 1901, had a long interest in natural history, and, according to his own record, had from “about the age of 10” been determined to take up entomology (Southwood, 1987). In 1912, he moved with his family to Cardiff and was sent as a boarder to Hereford Cathedral School, but on his weekends at home, he roamed the countryside on his bike collecting butterflies and plant specimens for his youngest brother Paul Westmacott Richards (Southwood 1987; http://herbariaunited.org/wiki/Owain_Westmacott_Richards).

Richards graduated from Oxford (Southwood 1987). After leaving Oxford he worked at Imperial College where he remained until 1967 when he retired from the Headship of the Department of Zoology and Applied Entomology and from the Directorship of the College Field Station at Silwood Park (Waloff 1986). In 1959 he was elected to the Fellowship of the Royal Society, and it was his achievements, rather than any other person's, that sustained the international reputation of this department of entomology (Waloff 1986).

Richard approached fieldwork as one of the milestones in the development of ecology and he contributed much to the understanding of quantitative life budgets (Waloff 1986). He firmly believed that a good grounding in basic taxonomy is essential for an ecologist and liked to point out that even closely related species differ in their ecological behavior and physiological requirements (Waloff 1986).

Despite most Hymenopterists knowing Richards as a taxonomist of wasps, he also worked on other groups of insects, such as Diptera and Orthoptera. His wide biological interests lay in ecology, taxonomy, and the theory of evolution (Waloff 1986). He was a world authority on the taxonomy of Diptera, Sphaeroceridae in

particular, and, of course, on aculeate Hymenoptera, which were his life-long interest and on which his long list of papers and monographs culminated in 1978 in the publication of his *opus magnum*, *The social wasps of the Americas, excluding the Vespinae* (Waloff 1986).

Between 1950 and the mid-1970s, Richards travelled widely, always collecting, identifying, observing and often shaming local biologists with the extent of his knowledge of their flora and fauna (Southwood 1987). International congresses and meetings were one cause, perhaps one might say excuse, for such trips (Southwood 1987). More extensive journeys included a visit to the Rukwa Valley in Tanzania in 1952, to advise the International Red locusts Control Service on methods of estimating red locusts (*Nomadacris septemfasciata*) (Southwood 1987). Also, his travels included two expeditions to Guyana, in the first of which his ecological and youngest brother – Professor Paul W. Richards – also participated. The two brothers derived much pleasure and inspiration from discussions of their common interests (Waloff 1986). In 1968, he and his first wife Maud, a well-known entomologist, joined the Royal Society Mato Grosso Expedition to Brazil. Later he visited there alone and paid numerous visits to North and South America in his pursuit of the aculeate Hymenoptera (Waloff 1986).

Most of this work was undertaken in the British Museum (Natural History), where he was an Honorary Associate (Southwood 1987). When he retired from his chair at Imperial College, he was offered and accepted space in the Hymenoptera Section at the Museum and worked there full-time, except for the day or so a week he spent in Silwood (Southwood 1987). He was a prodigious worker and even long after his retirement confessed to feeling shame-faced when he spend time away from his studies on insects (Waloff 1986). He donated to the Museum his collection of 69,000 Hymenoptera and 14,000 Diptera and incorporated much of this material to the museum collection (Southwood 1987).

O.W. Richards was the author or joint author of more than 180 papers and six books, the first of which, *The Variations of Animals in Nature*, was written with J.C. Robson and published in 1936. In 1957 and again in 1977, together with R.G. Davies, he revised the entomologists' bible, *Imm's Textbook of Entomology* (Waloff 1986; Southwood 1987). With his wife, Maud Jessie Richards, he published in 1951 a study about social wasps of South America, especially based on his Guiana work. In 1978 he published *The Social Wasps of the Americas, excluding the Vespinae* (see above), his most important publication on social wasps. In his publications, he described 15 new Vespidae genera (Van der Vecht and Carpenter 1990) and around 150 species and subspecies of Neotropical Polistinae, the taxonomic revision of *Mischocyttarus* de Saussure, and others.

Despite all the advances in the field since its publication, *The social wasps of the Americas, excluding the Vespinae* still remains a fundamental reference for those studying the New World's social wasps and certainly has been inspiring generations since then.

1.13 Universidade de São Paulo (USP, Ribeirão Preto) and Universidade Estadual Paulista (UNESP, Rio Claro): Two Groups Involved in the Study of Wasps in Brazil

These two universities employed important hymenopterists that have been involved in the most recent studies on Brazilian wasps. Most of these researchers were deeply influenced by or were disciples of Warwick Estevam Kerr (1922–2018), who worked in both universities. Kerr was born in 1922 in Santana de Parnaíba, São Paulo State, and started his academic career at a time when there was an extraordinary development of this field in São Paulo, thanks to the presence of Carlos Arnaldo Krug, Friedrich Gustav Brieger, André Dreyfus, and Theodosius Dobzhansky (Coelho and Kerr 2005).

In 1955 Kerr became head of the Rio Claro Department of Biology at the UNESP, when this University was created. In 1965, he became head of the Department of Genetics at the Faculty of Medicine of USP – Ribeirão Preto, where he became a full professor in 1971.

In these two universities, Kerr began the study of Hymenoptera, and although he worked mainly on stingless bees, some of his students were stimulated to work on social wasps.

In the 1960s, Ronaldo Zucchi, one of Kerr's students, started his studies on the behavior of social wasps in Rio Claro and later moved to Ribeirão Preto, having published more than 130 articles on bees and wasps. Zucchi was also influenced by Shôichi F. Sakagami (1927–1996), Emeritus Professor of Hokkaido University, who was a visiting Professor during 1971–1977 and studied stingless bees and social wasps. Zucchi was the advisor of Dércio Simões, Nivar Gobbi, and Sulene Noriko Shima, who were hired by UNESP Rio Claro and all have worked with social wasps. Presently all of them are retired.

Also, in the 1960s Vilma Maule Rodrigues (1938–2019) and Vera Lígia Letfizio Machado were precursors of a generation of wasp researchers at UNESP Rio Claro. Their former students José Roque Raposo Filho and Edilberto Giannotti (all retired) supervised many of the current generation of researchers presently working in Brazil.

1.14 Final Remarks

This brief review attempts to compile the historic research on wasps carried out in Brazil for the last 520 years, from the early naturalists, whose reference to this group was scarce and focused on eminently practical faunistic features, to the most recent academic research. Even with an increase of researchers and publications devoted to the group in the last decades, there is still much to be done in this field, considering the country's vast territory and the environmental variability it holds,