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SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

Review

Historical Note on the Genus *Trichogramma* (Hymenoptera, Trichogrammatidae) in Brazil, Focusing on Taxonomy and Diversity

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Abstract
The history of the taxonomy of *Trichogramma* parasitoid wasps can be divided into two phases. In the first phase, species identifications were based on external morphological characters; however, these identifications proved to be confusing and inaccurate. In the second phase, starting in the 1970s, taxa were identified based on charcteristics of the male genital capsule , leading to a major advance in *Trichogramma* taxonomy. The history of *Trichogramma* taxonomy in Brazil is recent and mainly related to species that parasitize agricultural pests. In Brazil, the first phase of *Trichogramma* taxonomy occurred in the 1960s, while the second phase occurred from the 1980s onward. In this second phase, *Trichogramma* taxonomy progressed significantly and knowledge of *Trichogramma* diversity as well as associations with lepidopteran pests improved markedly in Brazil as well as worldwide. The last five decades have seen significant progress in studies in Brazil, with taxonomy evolving from identifications based exclusively on morphological characters to integrative taxonomy, encompassing biology (crosses) and morphometry. This historical outline presents the phases of *Trichogramma* taxonomy in Brazil, addressing the hurdles encountered in the first descriptions, erroneous records of the species, and species descriptions since the 1980s. We highlight the importance of accurately identifying *Trichogramma* taxa for their use in biological control, as well as species diversity and associations with lepidopteran hosts.

Keywords Egg parasitoids · Lepidopteran hosts · Parasitoid wasps · Brazilian records

Introduction

Trichogramma taxonomic studies received a major boost from the 1970s onward, with the use of the morphological characters of the male genital capsule for species identification (Nagarkatti and Nagaraja 1971). *Trichogramma* species are the best-studied egg parasitoids in Brazil, due to their efficacy in biological control of lepidopteran pests. Some species have been produced commercially and used in biological programs to control various pests in the country (AGROFIT 2023). In several countries, *Trichogramma* species are also the most intensively researched egg parasitoids as well as the most familiar species to agricultural entomologists. *Trichogramma* taxonomy has advanced considerably in recent decades, revealing the great diversity of the genus worldwide.

In Brazil, *Trichogramma* taxonomic studies based on male characteristics began in the 1980s, for the purpose of using these parasitoids in biological control of forest and agricultural pests. This economic aspect stimulated the need for taxonomic studies to identify *Trichogramma* species for biological control programs. Accurate species identification was essential for the development and success of studies carried out with these egg parasitoids.

Nevertheless, some *Trichogramma* species have been erroneously recorded in Brazil, mainly before the 1960s, and in some cases, incorrect species names have been used inadvertently. The early taxonomic studies in Brazil, including erroneous and dubious records, are discussed here, continuing with investigations in the last five decades.

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This chronological presentation describes the taxonomic studies of the genus *Trichogramma* that have improved understanding of its diversity in Brazil. This information is essential, mainly for researchers and technicians involved in biological pest control, as it covers the history of valid names as well as erroneous or doubtful records, in addition to an overview of the progress of *Trichogramma* taxonomy in Brazil. Species diversity is also discussed, complementing studies on the genus in Brazil. Given its importance to agricultural entomology, mainly to biological pest control, a historical profile of *Trichogramma* taxonomy in Brazil is presented.

Genus *Trichogramma* Westwood

Trichogramma species are tiny wasps (around 0.7 mm in length) (Fig. 1), whose larvae feed on embryos (egg parasitoids) of various insect species, mainly lepidopterans in terrestrial and aquatic environments (Zucchi et al. 2010). Based on our literature survey, approximately 240 species of *Trichogramma* are known worldwide.

The genus *Trichogramma* was created by Westwood (1833) with the description of *T. evanescens*, based on a single female collected in Chelsea, England, in 1828. However, female-based description hampers recognition of the species, as the morphological identification of *Trichogramma* is male-based. Therefore, it is impossible to determine which of several closely related Palearctic species represents *T. evanescens* (details in Pinto 1999). Viggiani and Laudonia (1989) have underscored this hurdle: "Ma le recenti vicissitudini di *T. evanescens* sono continuate, semper ad opera dei ricercatori francesi." There is still no agreement among experts, who have identified two species as *T. evanescens* (Noyes et al. 2000, 2001). Perhaps the first illustration of the male genital capsule of *T. evanescens* was presented by Hintzelmann (1925).

Fig. 1 *Trichogramma* female ovipositing in a lepidopteran posture (photo by Heraldo Negri)

Eventually, Ishii (1941) recognized the importance of male genitalia, in identifying *T. australicum* Girault, *T. evanescens* Westwood, *T. japonicum* Ashmead, *T. chilonis* Ishii, and *T. dendrolimi* Matsumura. However, following Ishii's contribution, the characters of male genitalia were again used in species descriptions only 30 years later (Nagarkatti and Nagaraja 1971).

In North America, the early taxonomic treatment of *Trichogramma* was also confusing, as identification was based on body coloration and wing setae. An additional complication was the use of European species names—*T. evanescens* and *T. embryophagum* (Hartig)—for North American species (*T. pretiosum* Riley and *T. minutum* Riley). Over time, the North American species were properly identified and a taxonomic revision was presented by Pinto (1999).

As mentioned, *Trichogramma* taxonomy advanced following the work of Nagarkatti and Nagaraja (1971), based on morphological characters of the male genital capsule (Fig. 2). Since then, new species have been described, synonyms have been established, and several taxonomic issues have been clarified.

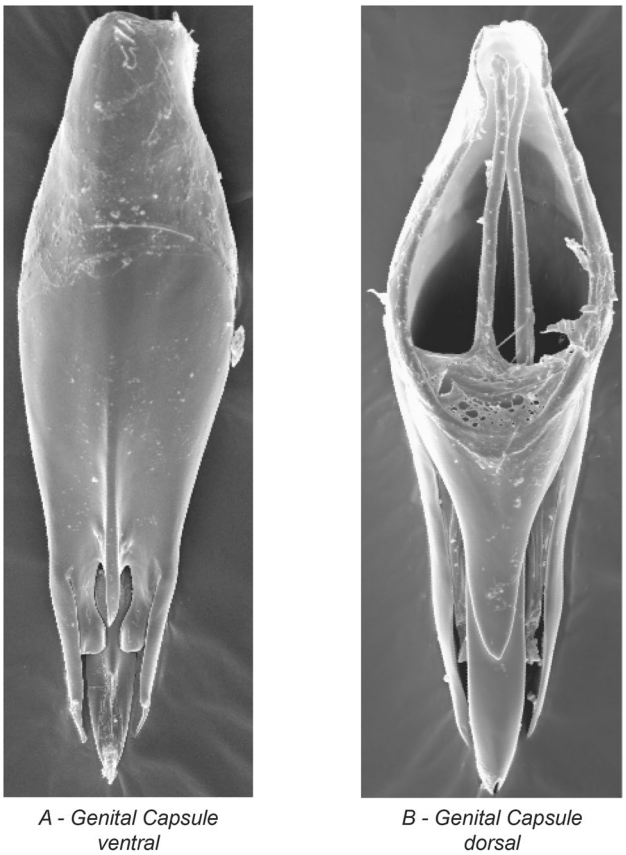

Fig. 2 **A**, **B** Genital capsule of *Trichogramma pretiosum* male. **A** Ventral view. **B** Dorsal view (photo by Ranyse Querino)

In the 1980s, *Trichogramma* species identifications in Brazil began to use reliable morphological characters, opening a new phase in taxonomy in the country. Currently, in addition to morphological characters, *Trichogramma* species have been identified and characterized through biological, morphometric, and molecular analyses, integrating different types of information and increasing the reliability of taxonomic studies of the genus.

Taxonomic studies in Brazil

The first references for *Trichogramma* species were based on species names mentioned in articles published in North America. The species were named based on the name available in the literature, without preparation, examination, and deposition of specimens in a collection. Thus, it is impossible to know which *Trichogramma* species were discussed in the initial reports (see Silva et al. 1968). Until the 1960s, records referred exclusively to *T. minutum* Riley parasitizing eggs of various agricultural pests. However, these records did not actually correspond to *T. minutum*, which is now understood not to occur in Brazil (Querino and Zucchi 2007). On the other hand, it is not possible to confirm the identity of *Trichogramma* species in the initial phase of studies in Brazil, since no material was deposited in collections (voucher specimens) to confirm the species. References to *T. minutum* in that period are due to the availability of that name in the literature, mainly in the United States. Subsequently, three species were cataloged in Brazil, namely, *T. fasciatum* (Perkins) (see De Santis 1979), *T. bennetti* Nagaraja & Nagarkatti, and *T. brasiliensis* (Ashmead) (see De Santis 1980), but these species were not present in the catalog of De Santis (1989). Unfortunately, the typographic formatting of the species list and of the bibliographic citations in the catalogs of De Santis (1979, 1980) hampers the association of species records with hosts and with the respective authors of the publications. However, regardless of additional information from these first records in Brazil, current knowledge of *Trichogramma* allows for some clarifications of these three species.

Trichogramma bennetti Nagaraja and Nagarkatti was cataloged by De Santis (1980), but not in later catalogs (De Santis 1981; De Santis and Fidalgo 1994). The record of this species in Brazil may relate to another trichogrammatid, *Trichogrammatoidea bennetti* Nagaraja, which was originally described from specimens collected in Brazil. *Trichogramma bennetti*, originally described from Trinidad and Tobago, does not occur in Brazil (Querino and Zucchi 2007) and has not been collected in this country to date.

Trichogramma brasiliensis (Ashmead) was described from a single female collected from a cotton field in "Bahia," Brazil, in "Mar 83" (Pinto 1997), deposited in the collection of the National Museum of Natural History, Washington, D.C. However, it was transferred to the genus *Trichogrammatoidea*, based on the morphological characters of the antennae and wings, by Pinto (1997), who considered *Trichogrammatoidea brasiliensis* as nomen dubium, as the taxonomic characters of the female do not allow specific identification. Therefore, one of the first trichogrammatids collected in Brazil is a member of the genus *Trichogrammatoidea*.

Trichogramma fasciatum (Perkins) stands out for its dark color, but its identity was clarified only at the end of the 1970s, with the lectotype designation (Pinto et al. 1978). Therefore, record of *T. fasciatum* in Brazil, such as that cataloged by De Santis (1979) should be disregarded, as it probably refers to other species. Anyway, surveys in recent decades in Brazil have not found *T. fasciatum*. Furthermore, *T. fasciatum* is record in Costa Rica, Mexico, Venezuela, southwestern Canada (Pinto 1999), and Ecuador (Querino and Zucchi 2019).

Trichogramma minutum Riley was the most commonly cited species in Brazil and the only species recorded in the country until the 1960s, parasitizing eggs of numerous agricultural pests (Silva et al. 1968; De Santis 1980). Lima (1962), in his classic "Insetos do Brasil – Hymenoptera," stated that *T. minutum* was well known throughout the Americas. The use of the name *T. minutum* in the Brazilian literature of the period was due to the availability of this name in North American literature; thus, the use of this name was based on a literature citation, without a taxonomic study to support it. At that time, identification was based on external characteristics, as reported by Souza (1961): "*Trichogramma minutum* was identified in our laboratories by comparing the prints presented by Clausen in Entomophagous Insects (page 108) with the preparations for wings, antennae, etc. of the insect." Furthermore, at that time, there were no reliable taxonomic characters for *T. minutum* identification. Only after the designation of the *T. minutum* neotype by Pinto et al. (1978) could this species be characterized and identified. In all egg parasitoid surveys carried out in Brazil from the 1980s onward, *T. minutum* was never collected (Querino and Zucchi 2007). This finding remains valid to this day.

The catalog by De Santis and Fidalgo (1994) lists 29 *Trichogramma* species, with 11 species for Brazil, including *T. australicum* Girault, *T. chilotraeae* Nagaraja & Nagarkatti, and *T. japonicum* Ashmead. Due to the catalog formatting, associating the records of these species with the respective authors of the information is extremely difficult. However, these three records are doubtful, as there have been no records of these exotic species in recent decades in Brazil. Nevertheless, the CIBC (1976) report lists these three species, stating that 200 host eggs (without species information) parasitized by *T. japonicum*, 200 by *T. australicum*, and 200 by *T. chilotraeae* were sent to the state of Amapá, northern Brazil (no details on the location), where a new sugarcane

mill was to be installed. Yet, no other information was given about this shipment of parasitoids; thus, it is likely that these species did not establish, as there are no other references about these *Trichogramma* species in Brazil besides the above records. Therefore, we consider that *T. australicum*, *T. chilotraeae*, and *T. japonicum* do not occur in Brazil.

Therefore, seven *Trichogramma* species have been erroneously recorded in Brazil (De Santis 1979, 1980; De Santis and Fidalgo 1994; Noyes 2019), resulting in inaccurate information on the geographic distribution of the species. These species were recorded in Brazil due to erroneous identifications or lack of taxonomic studies (*T. bennetti*, *T. brasiliense*, *T. fasciatum*, and *T. minutum*) or introductions of parasitoids that failed to establish (*T. australicum*, *T. chilotraeae*, and *T. japonicum*) (Table 1).

Present stage of taxonomic studies in Brazil

This stage began in the 1980s, when taxonomic studies on *Trichogramma* were based on morphological characters, mainly of the male genitalia, which conferred reliability to identifications. Furthermore, the deposit of preparations of *Trichogramma* species on microscope slides in entomological collections, such as the collection of the Luiz de Queiroz Museum of Entomology (MELQ) at the Luiz de Queiroz College of Agriculture (ESALQ) in Piracicaba, São Paulo State (Brazil), is another characteristic of the current phase, as no voucher specimens were deposited in the pioneering studies of *Trichogramma* in Brazil.

The first identifications of *Trichogramma* species in Brazil to be based mainly on male genitalia were carried out at the Federal University of Minas Gerais (UFMG) in Belo Horizonte, state of Minas Gerais, and at the Luiz de Queiroz College of Agriculture (ESALQ). At UFMG, studies on *Trichogramma* aimed to control forest pests, while studies at ESALQ were focused on agricultural pests. These studies led to the first descriptions of *Trichogramma* species in Brazil, roughly 150 years after the initial description of the genus *Trichogramma*.

Taxonomic studies at UFMG

Trichogramma studies were implemented in the 1980s with the participation of Jean Voegelé, then a researcher at INRA (Institut National de la Recherche Agronomique) in Antibes, France. The studies carried out at UFMG in Belo Horizonte aimed mainly at understanding *Trichogramma* species as egg parasitoids of forest insect pests.

These studies resulted in the description of the first species of *Trichogramma* collected in Brazil (Voegelé and Pointel 1980). Thus, these authors described *T. maxacalii* from eggs of *Euselasia euploea eucerus* Hewitson (Lepidoptera, Riodinidae), collected between the Jequitinhonha and Mucuri rivers in an area inhabited by the Maxacali indigenous people in Minas Gerais (MG). Also based on parasitoids collected in MG (locations not reported), Nagaraja (1983) described *T. bruni* (ex unidentified notodontid egg), *T. demoraesi* (ex egg of *Glena bipennaria* on *Eucalyptus grandis*), and *T. soaresi* (ex egg of *Euselasia euploea eucerus* on *Eucalyptus paniculata*). This last species is a junior synonym of *T. maxacalii* (see Zucchi and Monteiro 1997). Three other species, *T. manicobai*, *T. caiaposi*, and *T. acacioi*, were described by Brun et al. (1984). The first two were reared in eggs of *Erinnyis ello* (L.) (Lepidoptera, Sphingidae) collected in the municipality of Felixlândia (MG), and the latter was reared in eggs of *Psorocampa denticulata* (Lepidoptera, Notodontidae) collected in Jaboticatubas (MG). The descriptions of these species, based on specimens collected in Brazil, were based on morphological characters, mainly of the male genitalia (Nagarkatti and Nagaraja 1971).

Taxonomic studies at ESALQ

As with the studies at UFMG, Jean Voegelé also played a decisive role at the beginning of taxonomic studies at ESALQ in the 1980s, when he taught a mini-course on *Trichogramma* at the Department of Entomology. The visit of Jean Voegelé to the department sparked interest in developing a broad study on *Trichogramma*, aiming at the control

Table 1 *Trichogramma* species erroneously recorded in Brazil

Species	References	Comments
T. australicum	CIBC (1976)	Parasitized host eggs sent to Amapá State without additional information
T. bennetti	De Santis (1980)—catalog	Possible confusion with *Trichogrammatoidea bennetti* described from Brazilian specimens
T. brasiliense	De Santis (1980)—catalog	Misidentification of genus; it belongs to *Trichogrammatoidea*. Nomen dubium
T. chilotraeae	CIBC (1976)	Parasitized host eggs sent to Amapá State without additional information
T. fasciatum	De Santis (1980) – catalog	Lectotype designated in 1978; previous records do not match to *T. fasciatum*
T. japonicum	CIBC (1976)	Parasitized host eggs sent to Amapá State without additional information
T. minutum	First species recorded in Brazil (various authors), but with no taxonomic basis	Lectotype designated in 1978; not collected in recent decades in Brazil

of agricultural pests; thus, the *Trichogramma* Project was created in 1984. The various stages of the project encompassed taxonomic studies, which were crucial for the project development, as it was not known which and how many *Trichogramma* species were parasitoids of agricultural pests in Brazil. These first taxonomic studies on *Trichogramma* at ESALQ generated important information: (i) identifications of 13 species, (ii) descriptions of six new species, (iii) the first record of *T. pretiosum* in Brazil, (iv) a determination that *T. caiaposi* Brun, Moraes and Soares is a junior synonym of *T. atopovirilia* Oatman and Platner, and (*v*) questioning the record of *T. minutum* in Brazil (Zucchi 1985). The new species, all parasitoids of the sugarcane borer, *Diatraea saccharalis* (Fabricius), i.e., *T. dissimile*, *T. distinctum*, *T. galloi*, and *T. jalmirezi*, were formally described later (Zucchi 1988), as was *T. bertii*, obtained from eggs of *Glena* sp. (Querino and Zucchi 2003a). In further taxonomic studies conducted at ESALQ, in the early 1990s, the senior author RAZ examined *Trichogramma* specimens deposited at the Agricultural Research Center (USDA) in Beltsville, state of Maryland, and at the University of California in Riverside, state of California, USA, the two most important collections of *Trichogramma* in the Americas. Therefore, contrary to the comment by Parra and Coelho Jr (2021), taxonomic studies on *Trichogramma* at ESALQ were developed independently, with no collaboration or partnership with taxonomists from abroad. Possibly, if the biological control project had not been implemented at ESALQ in the 1980s, taxonomic studies of *Trichogramma* in Brazil would have advanced more slowly (Zucchi 2021).

Taxonomic studies from 2000 onward

The studies carried out at ESALQ were fundamental in the development of *Trichogramma* taxonomy in Brazil, and with the development of research, several postgraduate students became interested in taxonomic studies on *Trichogramma*. At the beginning of the twenty-first century, taxonomic knowledge of the genus *Trichogramma* continued to expand in Brazil. This phase began with a doctoral thesis on the taxonomy of species from Brazil and several other South American countries (Querino 2002).

The main studies in this phase encompassed the descriptions of ten new *Trichogramma* species, lepidopteran egg parasitoids (Querino and Zucchi 2003a, 2003b), collected in suction traps in a forest reserve (Querino and Zucchi 2004a). Study of the holotype confirmed that *T. demoraesi* Nagaraja 1983 was mistakenly considered a parasitoid of *E. ello* in Brazil (Vieira et al. 2014). Two new species as well as the redescription of *T. marandobai* and new records of distributions and hosts were published (Vieira et al. 2015; Querino et al. 2017).

In this stage, studies have used not only morphological characters (classical taxonomy), but also other methods for accurate definition of the species, discussed below.

Morphometric analyses

The first taxonomic studies of *Trichogramma* that used reliable characters were based exclusively on morphological characters. Once this taxonomic base was constructed, morphometric analyses were used to better characterize the species. Some articles on this topic have been published in Brazil.

Querino and Zucchi (2002, 2004b) conducted morphometric analyses for six *Trichogramma* species: *T. acacioi* Brun, Moraes & Soares; *T. atopovirilia* Oatman & Platner; *T. demoraesi* Nagaraja; *T. distinctum* Zucchi; *T. galloi* Zucchi; and *T. bruni* Nagaraja. These analyses detected differences between these species and also intra- and interspecific morphological variations, which are important for identification of *Trichogramma* species.

Querino et al. (2002) carried out the first study on geometric morphometric analysis in Brazil, in order to detect morphological differences in the genital capsules of male *T. pretiosum* reared on ten hosts. Subsequently, Querino and Zucchi (2004b), in a morphometric analysis involving six species, detected differences between species and also intra- and interspecific morphological variations.

Molecular analyses

The first analyses of *Trichogramma* species in Brazil were carried out in early 2000. The separation between *T. rojasi* and *T. lasallei*, two related species, was performed with the sequencing of the ITS2 region of the rDNA (Ciociola et al. 2001a). Next, Ciociola et al. (2001b) created a molecular key, using sequences from the ITS2 region and the restriction analysis to identify seven species recorded in Brazil.

Querino and Zucchi (2003b), in the first study of this nature in Brazil, used molecular data to *T. esalqueanum* (AY182763.1) and *T. iracildae* (AY182760.1), which were originally described based on morphological characters.

Molecular analyses were also useful to define and characterize several South American species, including from Brazil, and to construct an identification key (Almeida and Stouthamer 2015). The morphological separation among *T. exiguum* Pinto (Alegre, Espírito Santo State), *T. galloi* (Dourados, Mato Grosso do Sul State), and *T. pretiosum* Riley (Primavera do Leste, Mato Grosso State) was also confirmed through sequencing the ITS2 region of ribosomal DNA (Santos et al. 2015). Vieira et al. (2015) also used molecular data to clarify the identity of *T. marandobai*. Viana et al. (2021) then used an ITS2 rDNA sequence analysis to confirm the morphological identification of *T. galloi*

(Teresina, Piauí State), *T. manicobai* (Rio Largo, Alagoas State), *T. marandobai* (Rio Largo, Alagoas State; Belém, Pará State), and *T. pretiosum* (Teresina, Piauí) as well as for an analysis of genetic diversity. The molecular markers cytochrome *c* oxidase I (COI) and the internal transcribed space region 2 (ITS2) were also useful in clarifying the identity of *Trichogramma foersteri* Takahashi, used in the control of *Palpita forficifera* (Lepidoptera: Crambidae) in olive trees (Villalba et al. 2022, 2023) and *Anticarsia gemmatalis* Hübner (Lepidoptera: Erebidae) in soybean (Takahashi et al. 2021). The sequences (ITS2 and CO1) of 13 species recorded in Brazil are now deposited in GenBank.

Integrative taxonomy

Studies on integrative taxonomy are still little used to define *Trichogramma* species. In Brazil, integrative taxonomy has been used in only three studies.

In the first such approach to *Trichogramma* identification in Brazil, Querino and Zucchi (2002) clarified the identity of *T. bruni* Nagaraja, using morphological and biological analyses to evaluate the intraspecific variations of the parasitoid in different hosts. The genital capsule of *T. bruni*, mainly the dorsal lamina, shows variations; however, morphological, morphometric, and biological analyses confirmed that the variations observed in *T. bruni* are intraspecific. Due to these variations, a combination of diagnostic characters must be considered when identifying *T. bruni*.

Vieira et al. (2014, 2015) also used an integrative taxonomy approach to clarify the identity of *T. marandobai*, a parasitoid of *E. ello* eggs, due to variations in the male genitalia. Those aucthors redescribed the species through integration of biological, morphometric, and molecular data, elucidating the complex of species associated with *Erinnyis ello*. This complex was clarified by Vieira et al. (2014, 2015), whose data correspond to the first studies involving integrative taxonomy in the genus *Trichogamma.*

Recently, for the first time in Brazil, Takahashi et al. (2021) described a species of *Trichogramma* based on an integrative approach. Their description of *T. foersteri* Takahashi, a parasitoid of *A. gemmatalis* eggs in soybean, used both morphological and molecular analyses.

Checklists

Checklists are important tools in the study of a taxon, as they bring together much information (valid names, hosts, distribution, etc.) about the species, facilitating the search for taxon data.

The increase in the number of *Trichogramma* species in Brazil required the preparation of checklists. In the first checklist published in Brazil, Zucchi and Monteiro (1997) compiled information on hosts and associated plants for 24 *Trichogramma* species from South America, 14 of which occurred in Brazil. More than a decade later, Zucchi et al. (2010) listed 41 South American species, 26 of which were recorded in Brazil. A checklist for South America included 40 species; *T. koehleri*, described from Argentina, was considered *species inquirenda* (Querino and Zucchi 2019). With the description of *T. foersteri* Takahashi in 2021, 41 species are currently known in South America, 30 of which occur in Brazil (Querino 2024) (Table 2).

Databases available for *Trichogramma* species in South America are "Species of *Trichogramma* from South America" (Querino et al. 2021) and "Taxonomic Catalog of the Brazilian Fauna (TCBF)" (Querino 2024).

Table 2 List of *Trichogramma* species recorded in Brazil (*exclusively)

Species	Habitats
1. *Trichogramma acacioi* Brun, Moraes & Soares, 1984*	Both
2. *Trichogramma acuminatum* Querino and Zucchi, 2003*	Forest
3. *Trichogramma alloeovirilia* Querino and Zucchi, 2003*	Forest
4. *Trichogramma atopovirilia* Oatman and Platner, 1983	Crops
5. *Trichogramma atropos* Pinto, 1992	Forest
6. *Trichogramma bertii* Zucchi and Querino, 2003*	Forest
7. *Trichogramma bruni* Nagaraja, 1983	Both
8. *Trichogramma clotho* Pinto, 1992	Forest
9. *Trichogramma demoraesi* Nagaraja, 1983	Forest
10. *Trichogramma dissimile* Zucchi, 1988*	Crops
11. *Trichogramma distinctum* Zucchi, 1988*	Crops
12. *Trichogramma esalqueanum* Querino and Zucchi, 2003*	Forest
13. *Trichogramma exiguum* Pinto and Platner, 1978	Crops
14. *Trichogramma foersteri* Takahashi, 2021*	Crops
15. *Trichogramma galloi* Zucchi, 1988	Crops
16. *Trichogramma iracildae* Querino and Zucchi, 2003*	Forest
17. *Trichogramma jalmirezi* Zucchi, 1988	Crops
18. *Trichogramma lasallei* Pinto, 1999	Crops
19. *Trichogramma manicobai* Brun, Moraes & Soares,1984*	Crops
20. *Trichogramma marandobai* Brun, Moraes & Soares, 1986	Crops
21. *Trichogramma maxacalii* Voegelé and Pointel, 1980*	Forest
22. *Trichogramma parrai* Querino and Zucchi, 2003*	Forest
23. *Trichogramma pratissolii* Querino and Zucchi, 2003*	Crops
24. *Trichogramma pretiosum* Riley, 1879	Crops
25. *Trichogramma piracicabense* Querino and Zucchi, 2017*	Crops
26. *Trichogramma pussilum* Querino and Zucchi, 2003*	Forest
27. *Trichogramma rojasi* Nagaraja and Nagarkatti, 1973	Crops
28. *Trichogramma tupiense* Querino and Zucchi, 2003*	Forest
29. *Trichogramma valmiri* Querino and Zucchi, 2017*	Forest
30. *Trichogramma zucchii* Querino, 2003*	Forest

Illustrated keys

Knowledge of the species recorded in Brazil allowed the creation of the first illustrated key to *Trichogramma* species, which included 26 species (Querino and Zucchi 2005). Then, aiming to assist researchers and technicians in *Trichogramma* studies, Querino and Zucchi (2011) prepared the "Guide for *Trichogramma* Identification for Brazil," with basic information (preparation and assembly of specimens, morphological structures, and terminology) to introduce interested parties to taxonomic studies of *Trichogramma*, in addition to presenting data on each species (diagnosis, host insects, and associated plants) and an illustrated key. As taxonomic studies advanced in Brazil, species from several South American countries were also identified. Thus, Querino and Zucchi (2019) created a checklist for 43 South American species, including information for each species (diagnosis, comments, type repository, type locality, distribution, and hosts), in addition to an illustrated key.

Collection

In the 1980s, a reference collection of *Trichogramma* was organized at the Luiz de Queiroz Entomology Museum (MELQ) at ESALQ. This collection contains preparations of *Trichogramma* species from several countries in the Americas, in addition to the type material of 17 species from Brazil (Querino et al. 2021). The organization of this collection was a historic milestone in supporting *Trichogramma* studies, as it is the only collection of these egg parasitoids in Brazil.

Biological control

The use of *Trichogramma* in the biological control of agricultural pests has led to major advances in knowledge of the species in Brazil, with the description and characterization of several species, associations with insect hosts, and geographic distributions. This taxonomic basis has improved the reliability of species identified in studies with these parasitoids. However, paradoxically, *Trichogramma* studies in Brazil have shown that only two species—*T. galloi* and *T. pretiosum*—have been used successfully in the biological control of lepidopteran pests. Interestingly, these species were collected and identified in the initial phase of the implementation of *Trichogramma* studies in the 1980s. Both species have been reared on a large scale in the laboratory with similar methodology and are marketed by several companies. However, *T. galloi* and *T. pretiosum* differ markedly in host preference, as *T. galloi* is host-specific and *T. pretiosum* is a generalist.

Trichogramma galloi was described based on males from eggs of the sugarcane borer, *D. saccharalis*, and, to date, it has been found only in this host, of which *T. galloi* is the most efficient parasitoid. In a comparative study between *T. galloi* and *T. atopovirilia* Oatman & Platner (easier to rear in the laboratory), *T. galloi* was more effective (Camarozano et al. 2022). For this reason, *T. galloi* has been used in the biological control of the sugarcane borer (Parra and Coelho 2021). The name of this parasitoid is a tribute to Prof. Domingos Gallo (ESALQ/USP), who conducted pioneering studies in Brazil on the biological control of the sugarcane borer (Zucchi 1988). Currently, nine commercial products with *T. galloi* are registered for control of *D. saccharalis* in Brazil (AGROFIT 2023) (Fig. 3).

Trichogramma pretiosum, similar to *T. minutum*, was accurately identified only after establishment of the neotype (Pinto et al. 1978). Previous identifications were confusing due to the lack of reliable morphological characters. Therefore, records of *T. pretiosum* prior to the 1970s have no scientific value, as it is not known which species was (or were) actually studied or released. *T. pretiosum* is the most widely distributed species in the Neotropics and the most commonly collected in agricultural environments. Throughout its distribution, *T. pretiosum* shows reproductive incompatibility, indicating the occurrence of cryptic species (Pinto 1999). The species was recorded in Brazil in the 1980s (Zucchi 1985). Under laboratory conditions, *T. pretiosum* is aggressive and often contaminates and eliminates other species from the rearing colony. In the early 1980s, laboratory rearings of *T. galloi* was contaminated and replaced by *T. pretiosum*, displacing the parasitoid intended for rearing (Zucchi 2002). This behavior of *T. pretiosum* was also observed on massal production in the United States (Pinto 1999). *Trichogramma pretiosum* has been used in Brazil in the biological control of *Chrysodeixis includens* (Walker) and *Phtorimaea absoluta* (Meyrick) in protected tomato crops (Parra and Coelho 2021). Currently in Brazil, 13 commercial products with *T. pretiosum* are registered for eight biological targets (AGROFIT 2023) (Fig. 3).

Validation of *Trichogramma* taxonomic data is a basic milestone for the successful use of these egg parasitoids in biological pest control (see Shimbori et al. 2023).

Species diversity in Brazil

Trichogramma species from around the world are available online (Noyes 2019); however, some records of Brazilian species in this database are incorrect (see item "Taxonomic studies in Brazil"). Species recorded in Brazil and their distribution in the Brazilian states are available online (Querino 2024). The *Trichogramma* species from South American countries and the type material of the species described in Brazil, deposited in the MELQ collection, are also available online (Querino and Zucchi 2019; Querino et al. 2021).

Taxonomic studies over the last four decades have been significant, considering that 30 species have been recorded

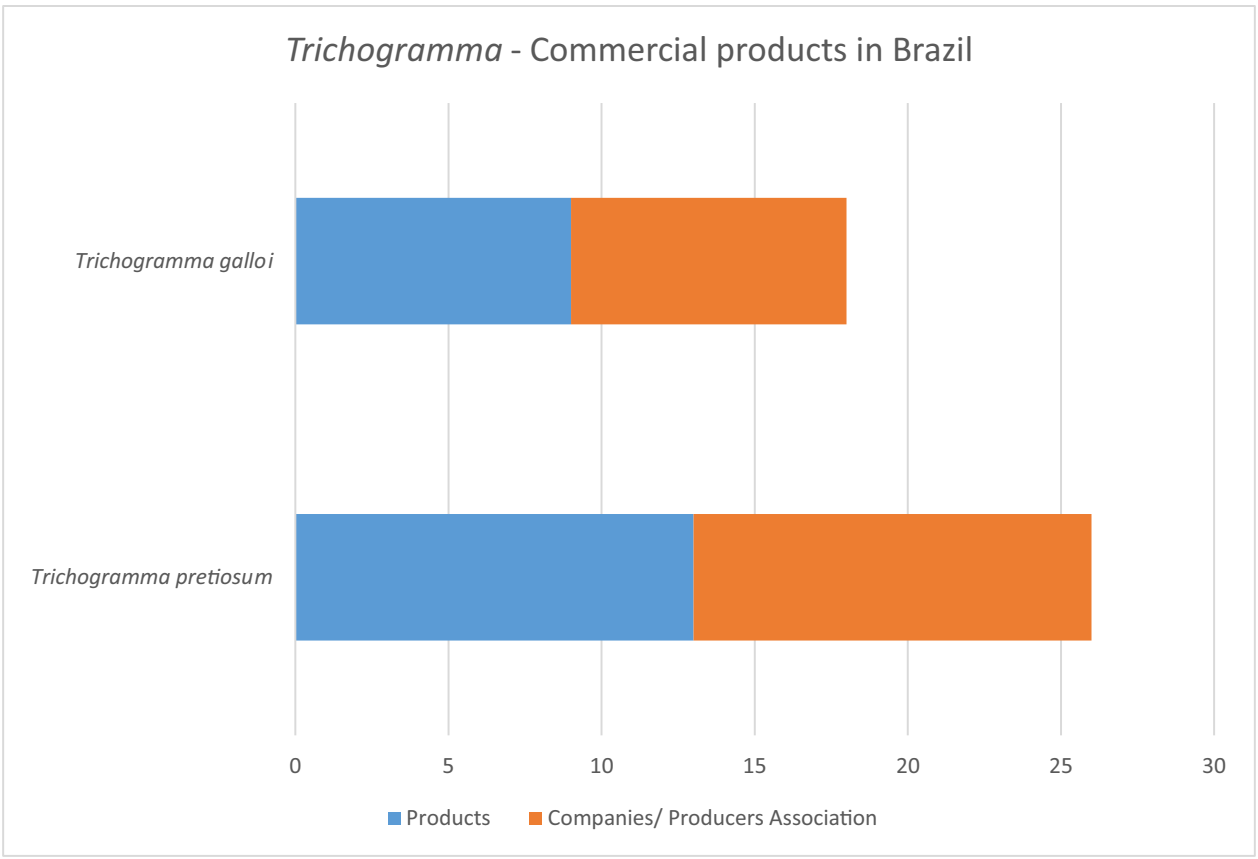

Fig. 3 Commercial products of *Trichogramma galloi* and *Trichogramma pretiosum* registered in Brazil

in Brazil (Querino et al. 2021), 20 of which are not recorded in another South American country (Table 2). Compared with data from other South American countries, Brazil has the highest diversity of *Trichogramma* species (Fig. 4). In the Americas, only the United States has a higher diversity of *Trichogramma* species than Brazil (Zucchi et al. 2010). Considering that approximately 240 species are known worldwide, the species recorded in Brazil account for approximately 13% of the total.

Studies on *Trichogramma* diversity were leveraged by the economic importance of these parasitoids, which can be mass-reared in the laboratory and marketed for the control of lepidopteran pests. Therefore, collections have been carried out almost exclusively in agricultural areas. In undisturbed environments, surveys have been few (Querino and Zucchi 2003a, 2003b, 2004a). The diversity of egg parasitoids in these environments needs to be explored, since new species have been discovered beside those that occur in agroecosystems (Querino and Zucchi 2004a). Undisturbed environments may hold high potential for the discovery of egg parasitoids for future studies on biological control.

The genus *Trichogramma* is divided into the subgenera *Trichogramma*, *Vanlisus*, and *Trichogrammanza*. Most species recorded in Brazil are classified in the subgenus *Trichogramma* (28) and only two, *T. atropos* Pinto and *T. clotho* Pinto, in the subgenus *Vanlisus*. No species from South America falls into the subgenus *Trichogrammanza*. Among the species of *Trichogramma* recorded in Brazil, 14 (approximately 46%) occur exclusively in agricultural environments, another 14 are present in native and forest areas, and only two, *T. acacioi* and *T. bruni*, originally from forest areas, transit to agricultural sites (Table 2).

Associations between *Trichogramma* and lepidopteran hosts in Brazil

As mentioned, surveys of *Trichogramma* species have been carried out mainly in agricultural environments. Therefore, the associations of *Trichogramma* species with pest species are more commonly known. Consequently, *Trichogramma* relationships with non-economically important species or in undisturbed environments are only occasionally or little known (Querino and Zucchi 2019).

Trichogramma pretiosum parasitizes the largest number of hosts (24 species) in Brazil, most of which are pests of various agricultural crops. The number of host species

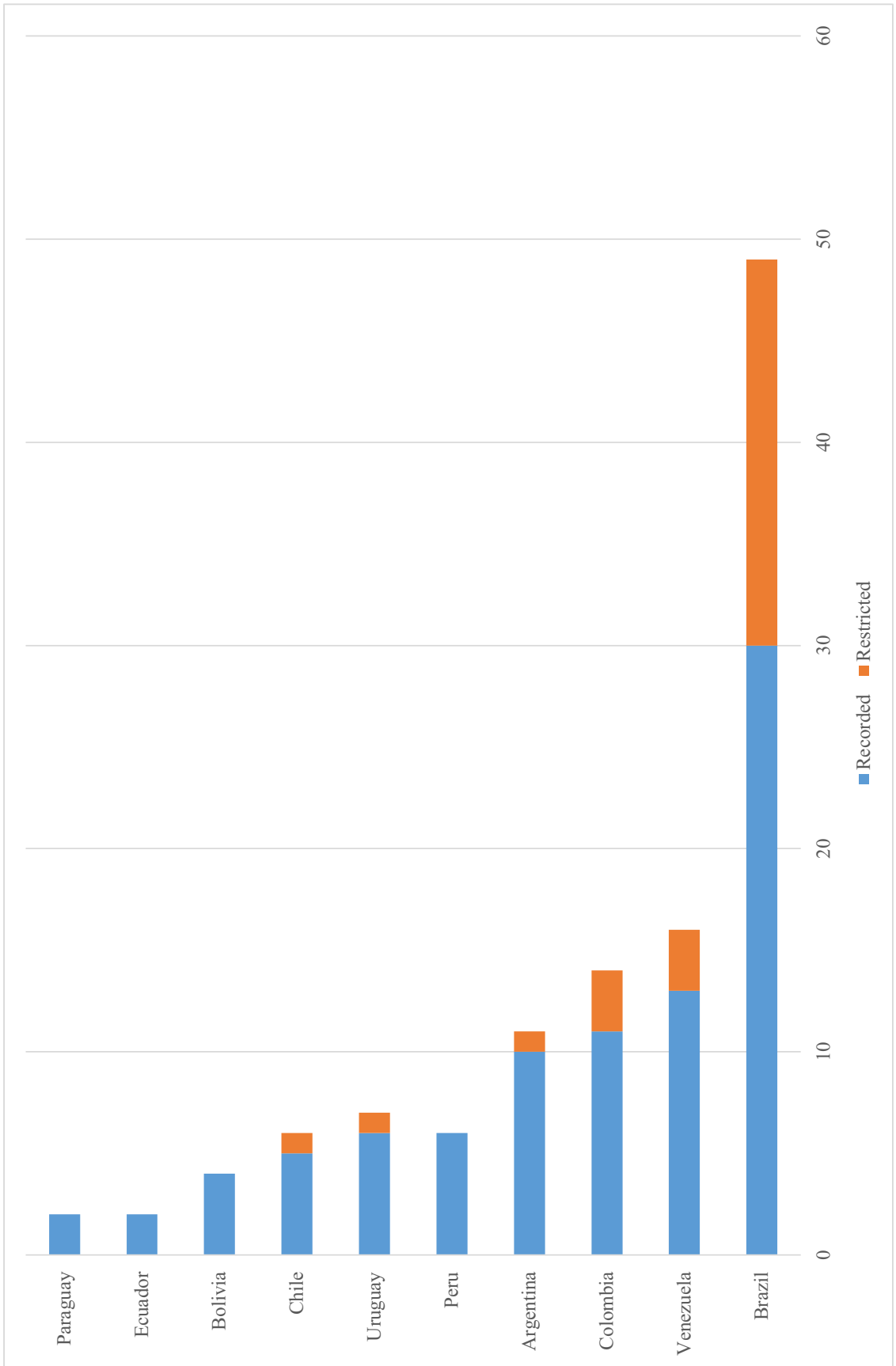

Fig. 4 Number of *Trichogramma* species in South American countries (Adapted from Querino and Zucchi 2019)

varies considerably among other *Trichogramma* species. For instance, for 13 species of *Trichogramma* (*T. chloto*, *T. dissimile*, *T. distinctum*, *T. galloi*, *T. iracildae*, *T. jalmirezi*, *T. lasallei*, *T. manicobai*, *T. marandobai*, *T. piracicabense*, *T. rojasi*, *T. valmiri*, and *T. zucchii*) only one host is known, while seven hosts are known for only two species (*T. acacioi* and *T. bruni*). Species with intermediate numbers of hosts are *T. atopovirilia* with four, *T. maxacalii* with three, and *T. bertii*, *T. demoraesi*, and *T. foersteri* with two hosts each (Fig. 5).

No natural insect host is yet known for nine species (*T. acuminatum*, *T. alloeovirilia*, *T. atropos*, *T. esalqueanum*, *T. parrai*¸ *T. pratisolii*, *T. pusillum*, *T. tupinense*, and *T. zucchii*).

The lepidopteran host species parasitized by most *Trichogramma* species in Brazil are *A. gemmatalis*, associated with six *Trichogramma* species, and *D. saccharalis*, with five species (Fig. 6). Of lepidopteran families, Noctuidae has the most species parasitized by *Trichogramma* in Brazil, followed by Crambidae and Sphingidae (Fig. 7).

Final remarks

The knowledge of *Trichogramma* taxonomy in Brazil is directly related to the use of these egg parasitoids in biological pest control. Possibly, if there was no interest in the use of *Trichogramma* in biological control, knowledge of the taxonomy, species diversity, and associations with host lepidopterans would still be incipient in this country. Initially, it was necessary to clarify the identity of the *Trichogramma* species involved in biological control studies in Brazil; therefore, training of taxonomists was stimulated by the need to accurately recognize *Trichogramma* species. Taxonomic studies in Brazil were initially developed without partnerships with taxonomists from abroad and the studies occurred during a period of great global effervescence in the use of egg parasitoids, stimulated mainly by international events, which constituted the various editions of the "International Symposium of *Trichogramma* and other Egg Parasitoids," with publication of the respective proceedings.

In the history of *Trichogramma* taxonomy in Brazil, in addition to the urgency of species identification in biological

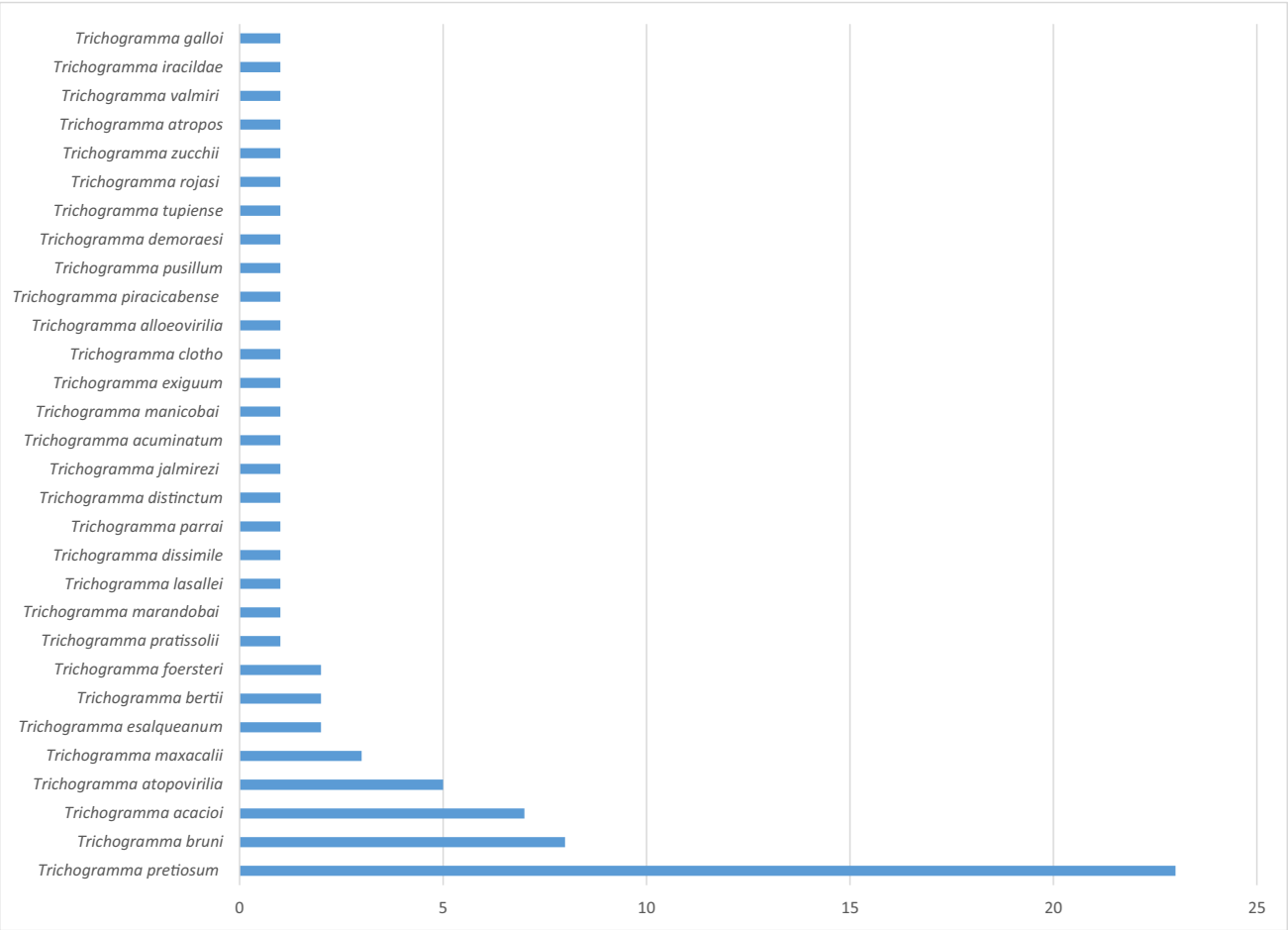

Fig. 5 Number of lepidopteran pests parasitized by *Trichogramma* species in Brazil

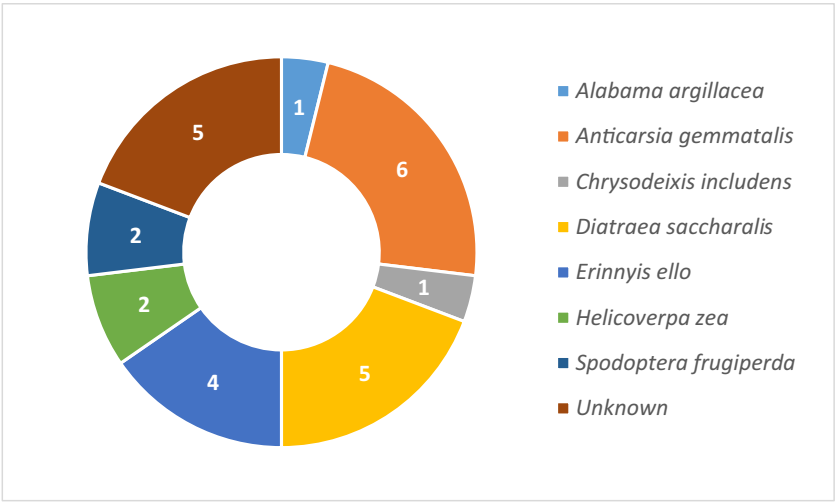

Fig. 6 Number of *Trichogramma* species associated with lepidopteran pests

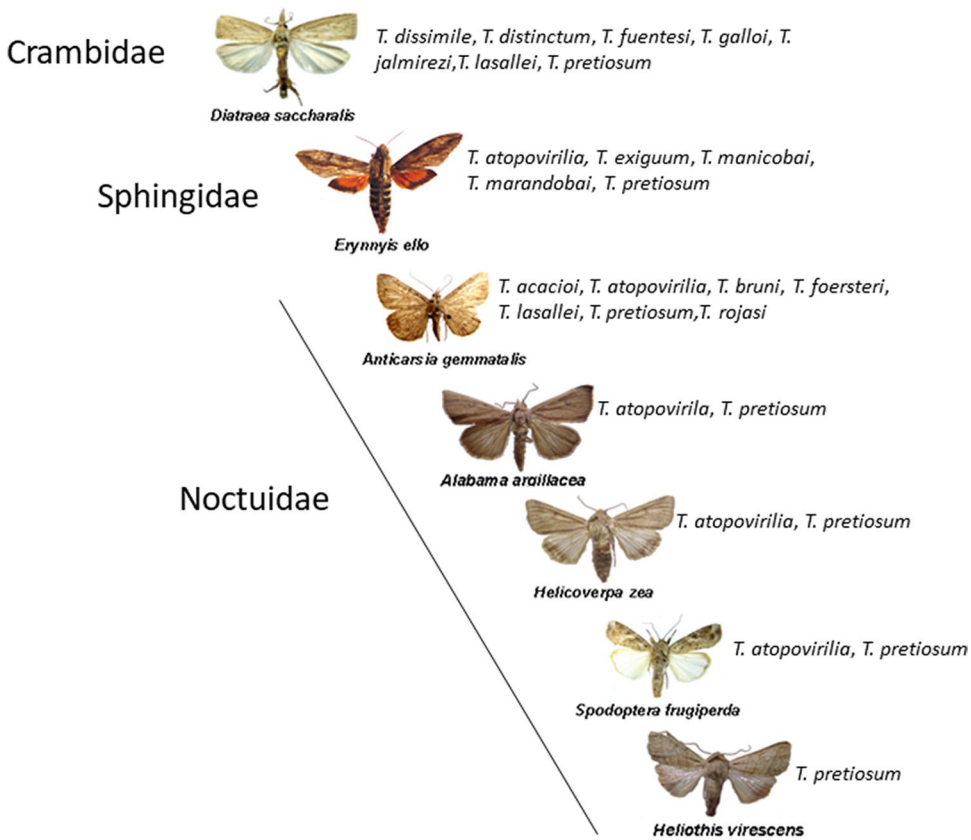

Fig. 7 Families with some lepidopteran pests parasitized by *Trichogramma* species in Brazil (adapted from Querino and Zucchi 2016)

control programs, another important factor was the continuity of research in graduate programs with the participation of students dedicated to taxonomic studies through the production of theses and dissertations. As usual, when the taxonomy of a group is developed, the level of understanding passes beyond an applied level, as new hosts and environments are explored with the experience gained, expanding knowledge of species diversity, regardless of the economic aspect. *Trichogramma* studies are an excellent example, as a broader knowledge of the genus was obtained that transcended the exclusive interest in economically important species.

Taxonomic studies of *Trichogramma* in Brazil form a narrative of advancement in taxonomic understanding of the genus in recent decades, starting with traditional morphological identification, passing through biology (crosses), morphometry, and finally integrative taxonomy. Brazil is one of the few countries where research on *Trichogramma*, in the

most diverse areas of biological control, was based from its beginning on the concomitant development of taxonomy. This history provided a firm basis for the results obtained in the use of these egg parasitoids, marking a successful trajectory. Currently, the knowledge gained in Brazil forms a valuable reference base in *Trichogramma* taxonomy.

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Declarations

Conflict of interest The authors declare no competing interests.

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