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STUDY ON THE SPECIES COMPOSITION OF SOLITARY WASPS (HYMENOPTERA: VESPIDAE: EUMENINAE) AND THE BIOLOGICAL AND ECOLOGICAL CHARACTERISTICS OF SELECTED SPECIES IN NORTHERN VIETNAM

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INTRODUCTION

1. Rationale for the dissertation

Eumeninae is the largest subfamily of the family Vespidae (Hymenoptera). These wasps play important roles in ecosystems by preying on pest larvae and contributing to plant pollination. Despite their ecological significance and potential applications in biological control, studies on the species composition, distribution, biology, and ecology of Eumeninae in Vietnam remain limited and fragmented. Northern Vietnam has diverse topography and climatic conditions that favor the differentiation and development of Eumeninae species. Therefore, investigating the species composition, distribution, biology, and ecology of these wasps is scientifically and practically important, contributing biodiversity data and providing a basis for applied research in biological control and conservation. For these reasons, the author undertook the dissertation entitled "***Study on the species composition of solitary wasps (Hymenoptera: Vespidae: Eumeninae) and the biological and ecological characteristics of selected species in Northern Vietnam***"

2. Research objectives

- Determine the species composition and distribution Eumeninae wasps in Northern Vietnam.
- Characterize selected biological and ecological traits of Eumeninae wasps in northern Vietnam.
- Initially assess the natural-enemy role of selected Eumeninae wasps in Northern Vietnam and propose directions for their use and protection.

3. Research contents

3.1. Investigate the species composition and distribution of Eumeninae wasps in Northern Vietnam.

3.2. Investigate selected biological and ecological characteristics of Eumeninae wasps in Northern Vietnam.

3.3. Conduct a preliminary investigation of the natural-enemy role of Eumeninae wasps in selected ecosystems in Northern Vietnam.

4. Scientific and practical rationale

4.1. Scientific rationale

Eumeninae is diverse, widely distributed, solitary predatory wasps that play important roles in ecosystems. However, information on their species composition, distribution, biology, and prey spectrum remains limited, particularly in Southeast Asia. In Vietnam, research on Eumeninae is fragmented, while Northern Vietnam offers diverse habitats and high potential species diversity. Accordingly, studying Eumeninae in Northern Vietnam will help expand biodiversity data and clarify their ecological roles and potential for biological control.

4.2. Practical rationale

Vietnam, particularly its northern region, has diverse natural conditions and habitats that favor high Eumeninae diversity. However, information on the species composition, distribution, biology, and ecology of these wasps remains limited. Research on Eumeninae in Northern Vietnam will contribute to the national biodiversity database, provide a scientific basis for conservation efforts, and enhance understanding of the potential of selected species as natural enemies for biological control.

5. Novel contributions of the dissertation

- ✓ The dissertation provides the most comprehensive inventory to date of Eumeninae wasps in Northern Vietnam, documenting 100 species/species-level taxa belonging to 34 genera.
- ✓ Five species new to science were discovered and described (*Antepipona crenula*, *Calligaster inflata*, *Orancistrocerus thanghen*, *Orancistrocerus thanhnhat*, and *Anterhynchium conformalum*). Two genera (*Ancistrocerus* and *Stenodynerus*) and six species were newly recorded from Vietnam.
- ✓ For the first time, nesting behavior, nest structure, pre-adult development, sex ratios, and pre-adult survival rates were documented for *Zethus dolosus*, *Orancistrocerus aterrimus*, and *Euodynerus furvus*.
- ✓ A previously undocumented host–parasitoid association was discovered, and the ichneumonid parasitoid of *Allorhynchium*

lugubrinum was described as a species new to science (*Hadrocryptus caobangensis*).

6. Dissertation structure

The dissertation comprises 150 pages, 9 tables, and 62 figures.

The dissertation is organized as follows: Introduction (5 pages); Chapter 1. Literature Review (25 pages); Chapter 2. Study Subjects and Methods (13 pages); Chapter 3. Results and Discussion (90 pages); Conclusions and Recommendations (2 pages); List of Publications Related to the Dissertation (1 page); References (14 pages); Appendices.

Chapter 1. Literature review

1.1. Studies of Eumeninae wasps on the world

1.1.1. Studies on the species composition of Eumeninae wasps on the world.

Eumeninae is the most diverse subfamily of Vespidae, with approximately 3,570 species in 210 genera recorded worldwide (Pickett and Carpenter, 2010). Species composition varies markedly among biogeographic regions. The Oriental Region is considered one of the most important centers of diversity, with approximately 782 recorded species. Other regions also exhibit high diversity, including the Palearctic (702 species) (van de Vecht and Fischer, 1972), the Neotropics (729 species) (West-Eberhard et al., 2006), Indonesia (222 species in 51 genera) (Nugroho et al., 2011, 2013), China (267 species in 51 genera) (Tan et al., 2018), and India (more than 180 species in 47 genera) (Kumar et al., 2012 - 2016).

Research on Eumeninae began in the nineteenth century and expanded substantially during the twentieth and twenty-first centuries. Numerous studies have compiled species lists, developed identification keys, described new species, and revised the taxonomy of Asian and Southeast Asian faunas. In particular, work by Giordani Soika, van der Vecht, Yamane, Gusenleitner, Kojima, Kim, Tan, Kumar, and Nugroho has made important contributions to refining the subfamily's taxonomy.

Recent studies have combined morphological characters with molecular data to reassess the taxonomic status and phylogenetic relationships of numerous taxa.

Despite considerable progress, new species continue to be discovered and described, indicating that the actual diversity of Eumeninae, particularly in tropical Asia and Southeast Asia remains incompletely documented.

1.1.2. Studies on the biology and ecology of Eumeninae wasps worldwide.

Research on biology and ecology of Eumeninae began in the early twentieth century and expanded rapidly from the 1950s onward. Studies have focused primarily on nest structure, nesting behavior, brood care, pre-adult development, prey spectrum, parasitoids, and ecological roles.

Studies have identified three main types of nests constructed by Eumeninae: (1) nests excavated in soil; (2) nests built from mud or plant materials; and (3) nests established in pre-existing cavities. Species that nest in cavities readily accept artificial trap nests and have therefore received the greatest attention in research. Krombein (1967), for example, investigated 32 species belonging to seven genera in North America, providing important insights into nest architecture, sex ratios, prey composition, and associated parasitoids.

Most Eumeninae are solitary wasps: females construct nests, provision them with food, lay eggs, and do not care for the brood after completing a provisioned cell. A small number of species exhibit presocial or subsocial behavior. Their development comprises the egg, larva, prepupa, pupa, and adult stages. Development from egg to adult generally takes 30 - 40 days, although duration varies with species and environmental conditions.

The development and survival of Eumeninae are affected by various parasitoids and predators, including members of Diptera, Hymenoptera, Coleoptera, Strepsiptera, and mites (Acari). Among the groups associated with immature Eumeninae, Chrysididae, *Melittobia* (Eulophidae), Phoridae, and Miltogramminae (Sarcophagidae) are recognized as important parasitoids or natural enemies that may cause substantial mortality during immature development.

1.1.3. Studies on prey and the natural enemy role of Eumeninae wasps worldwide.

Eumeninae is solitary wasps that play an important role in regulating populations of herbivorous insects. Their prey consists primarily of lepidopteran

larvae, although some species specialize in coleopteran larvae. Prey spectra range from broad to highly specialized, depending on wasp species, prey availability, and ecological conditions. Species such as *Ancistrocerus gazella* and *Symmorphus cristatus* have notable potential for biological control. However, effectiveness varies among species, and many Eumeninae are opportunistic predators whose prey use depends on prey abundance.

Although many studies have been conducted worldwide, knowledge of Eumeninae biology and ecology remains concentrated in Europe, North America, and East Asia. Information on tropical species, particularly in Southeast Asia, is comparatively limited and requires further study.

1.2. Studies of Eumeninae wasps in Vietnam

1.2.1. Studies on the species composition of Eumeninae wasps in Vietnam

Taxonomic studies of Eumeninae wasps in Vietnam were began relatively early by foreign researchers, but expanded substantially only after 2010. Recent studies have clarified species composition, developed identification keys, described new species, and updated the taxonomy of this group.

In 2014, a checklist of 45 Eumeninae species in 26 genera was published for Vietnam, including 13 species and six genera newly recorded for the country. Subsequent detailed studies examined genera such as *Eumenes*, *Zethus*, *Pararrhynchium*, *Anterhynchium, Discoelius, Allorhynchium, Apodynerus*, and *Euodynerus*, among others. Many species new to science have been discovered and described from Vietnamese specimens, particularly from the northern mountains and the Central Highlands. A total of 105 species in 35 genera have been recorded in Vietnam.

In addition to describing new species, researchers have documented genera and species previously unrecorded in Vietnam. Identification keys and taxonomic revisions have also helped refine the classification of Eumeninae. Local faunal surveys in Bac Giang, Bac Kan, and Cao Bang have recorded 15 - 20 species in 10 - 14 genera in each study area.

Despite these important advances, current studies have largely focused on particular genera or localities. No broad, systematic survey of Eumeninae

across Vietnam has yet been conducted. Consequently, the species composition and distribution of this group remain incompletely assessed, especially in highly biodiverse areas of Northern Vietnam.

1.2.2. Studies on the biology and ecology of Eumeninae wasps in Vietnam

Compared with taxonomy, studies on the biology and ecology of Eumeninae in Vietnam remains limited. It has focused mainly on species nesting in pre-existing cavities, while species that construct their own nests or nest in soil have received less attention.

Studies conducted in Northern Vietnam have provided information on activity periods, nesting behavior, nest architecture, life cycles, sex ratios, prey composition, and natural enemies. The findings suggest that habitat conditions, food availability, and anthropogenic disturbance can substantially influence species composition and nesting activity in Eumeninae.

Detailed studies of *Rhynchium brunneum, Pareumenes quadrispinosus*, and *Delta esuriens* have added information on nest structure, life cycles, reproduction, predation, and associations with parasitoids and predators. Notable characteristics documented include overwintering at the prepupal stage, overlapping generations, and variation in sex ratios.

Nevertheless, the number of Eumeninae species whose biology and ecology have been studied in Vietnam remains small relative to the more than 100 species recorded nationally. Significant knowledge gaps persist regarding the biology of species that construct their own nests or nest in the soil, prey spectra, the effects of environmental factors on their biology and ecology, and their potential roles in biological control. Further research is therefore needed to clarify the ecological significance of Eumeninae and assess the potential applications of selected species in biological control and conservation.

1.2.3. Studies on prey and the natural enemy role of Eumeninae wasps in Vietnam

Research on the prey spectrum and hunting behavior of Eumeninae in Vietnam remains limited. Studies of *Delta esuriens* have documented active prey hunting, paralysis, and larval provisioning with lepidopteran larvae.

In *Rhynchium brunneum*, 12 prey morphotypes have been recorded, with 2–25 prey individuals per nest cell, indicating a relatively broad prey spectrum. In contrast, *Pareumenes quadrispinosus* utilizes only two prey morphotypes, one accounting for 90% of recorded prey, suggesting a narrower prey spectrum. Each nest cell contains 2–6 prey items.

These findings highlight the potential of Eumeninae as natural enemies of insect pests. However, few species have been investigated, and quantitative assessments of their effectiveness in suppressing pest populations under field conditions remain lacking. Further research on prey spectra, prey specialization, and ecological roles is needed to evaluate their potential in biological control and sustainable agriculture.

*** General assessment of research on Eumninae in Vietnam**

Research on Eumeninae in Vietnam has advanced in taxonomy and distribution, but remains fragmented, with several genera insufficiently studied.

Biological and ecological research is limited and focuses primarily on a few common species. Important knowledge gaps persist regarding pre-adult development, adult longevity, brood care, parasitism, and predation. Furthermore, the biology and ecology of species newly described from Vietnam remain largely unexplored.

Chapter 2. STUDY SUBJECTS AND METHODS

2.1. Study sites and period

The study was conducted from 2022 to 2025 at sites in Northern Vietnam, as listed below:

No.	Study site before 1 July 2025	Study site after 1 July 2025	Study period
1	Ha Giang (Bat Dai Son and Thanh Van Communes, Quan Ba District)	Tuyen Quang	16 - 19/6/2023

2	Cao Bang (Luong Can, Thong Luong, and Truong Ha Communes, Ha Quang District; Thanh Cong and Phan Thanh Communes, Nguyen Binh District; Thanh Hen Lake, Tra Linh District)	Cao Bang	12 - 15/6/2023 13 - 15/7/2025
3	Lao Cai (Y Ty Commune, Bat Xat District)	Lao Cai	28 - 30/5/2022 08 - 12/4/2023
4	Tuyen Quang (Thuong Lam Commune, Lam Binh District)	Tuyen Quang	24 - 27/6/2024
5	Lang Son (Huu Lien Commune, Huu Lung District)	Lang Son	06 - 08/8/2024
6	Thai Nguyen (Thuong Nung and Than Sa Communes, Vo Nhai District; Quan Chu Commune, Dai Tu District)	Thai Nguyen	May–September 2025
7	Phu Tho (Xuan Son National Park)	Phu Tho	20 - 24/3/2024 16 - 20/12/2024
8	Lai Chau (Sa De Phin Commune, Sin Ho District; Ta Tong Commune, Muong Te District)	Lai Chau	31/5 - 2/6/2022 06 - 09/3/2023
9	Dien Bien (Xa Nhe Commune, Tua Chua District; Pa Ham Commune, Muong Cha District; Pa Thom and He Muong Communes, Dien Bien District)	Dien Bien	11 - 16/4/2022 28/2 - 5/3/2023
10	Hoa Binh (Lien Son Commune, Luong Son District)	Phu Tho	May–October 2024
11	Hai Phong City (Cat Ba National Park)	Hai Phong City	14 - 18/3/2024
12	Hanoi City (Tran Phu Commune, Chuong My District; Nghia Do Ward, Cau Giay District)	Hanoi City	May–September 2024 26/8 - 05/9/2024

The study also incorporated specimens and data previously collected by the doctoral candidate and colleagues.

2.2. Study subjects and equipment

2.2.1. Study subjects

The study subjects comprised Eumeninae wasps, their nests, the larvae serving as prey, and associated parasitoids and predators.

2.2.2. Equipment

Equipment was used for field surveys, specimen collection and preservation, morphological examination, photography, and laboratory identification.

2.3. Research methods

2.3.1. Field methods

2.3.1.1. Collection of adult wasps in the field

Adult wasps were collected using insect nets and Malaise traps in different habitats across the study area. Malaise traps were fixed at locations suitable for insect flight paths and checked periodically throughout the study.

2.3.1.2. Collection of nests in the field

Wasp nests were collected directly from natural sites, including trees, earthen banks, rock cavities, buildings, and other nesting locations. Artificial trap nests made from bamboo tubes of varying diameters and lengths were also used to attract cavity-nesting species. At each study site, 200–300 trap tubes were installed and inspected periodically to collect newly established nests.

2.3.1.3. Observation of nesting behavior

Nesting behavior was observed directly in natural settings and at trap nests. Recorded information included nest-site selection, nest construction, oviposition, prey capture and transport, collection of nesting materials, the time required for each activity, and total nest-completion time. Activities were recorded in notes and photographs and monitored continuously throughout the study.

2.3.2. Laboratory methods

2.3.2.1. Examination of nest structure

Nests collected in the field were measured and their structures analyzed. For natural nests, the number and dimensions of nest cells and the thickness of partitions were determined. For trap nests, observations included nest structure, cell length and diameter, partitions, nest plugs, and empty cavities within the nest.

2.3.2.2. Monitoring pre-adult development

Nest cells were opened to determine the developmental stage of the individual inside, and development was monitored from egg through larva, prepupa, and pupa to adult. Individuals were reared under laboratory conditions at ambient temperature to determine developmental duration, survival and mortality rates, and adult emergence behavior.

2.3.2.3. Study of prey

Nest cells containing eggs or young larvae were examined to determine prey number and composition. Prey specimens were characterized morphologically, grouped into categories, and tallied to determine their frequency in each wasp species studied.

2.3.2.4. Study of parasitoids and predators

Parasitoids and predators associated with wasp nests were observed in the field and monitored in the laboratory. They were reared to adulthood for identification and determination of their relationships with host species.

2.3.3. Specimen preparation, preservation, and identification

2.3.3.1. Specimen mounting and preservation

Adult wasp specimens were prepared as pinned specimens or preserved in alcohol. Each specimen was labeled with complete information on collection locality, collection date, and collector. Mounted specimens are deposited in the Entomology Laboratory, Institute of Biology.

Collected nests were preserved after structural examination or developmental monitoring for reference and long-term storage. Some specimens were preserved in high-concentration alcohol for future molecular studies.

2.3.3.2. Specimen identification

Identification was based primarily on external morphological characteristics of adults. Specimens were examined under a stereomicroscope and photographed using a digital microscope/camera system; image-stacking software was used to combine images. Identification references included Yamane (1990), Tan et al. (2018), publications by Nguyen Thi Phuong Lien from 2014 onward, Disney (1994), Ta Huy Thinh (2001), Lee and Han (2017), Dahms (1984), Kimsey and Bohart (1991), and Pham et al. (2024).

Chapter 3. RESULTS AND DISCUSSION

3.1. Species composition and distribution of Eumeninae wasps in Northern Vietnam

3.1.1. Species composition of Eumeninae wasps in Northern Vietnam

Northern Vietnam has high Eumeninae diversity because it lies at a biogeographic transition zone and contains diverse topography, climates, and habitats. This study recorded 53 species in 24 genera and added substantial new information, increasing the number of Eumeninae known from Northern Vietnam from 82 to 100 species and from 31 to 34 genera. The number of species/species-level taxa recorded for each genus in the study area is presented in the following table.

No.	Genus	Species/species-level taxa recorded		
		In this study	Previously recorded	Total to date
1	*Allorhynchium*	2	5	5
2	*Ancistrocerus*	2	0	2
3	*Antepipona*	6	1	6
4	*Anterhynchium*	4	3	4
5	*Antodynerus*	1	1	1
6	*Apodynerus*	3	6	6
7	*Calligaster*	2	1	2
8	*Coeleumenes*	1	2	3

9	*Delta*	2	2	2
10	*Discoelius*	0	2	2
11	*Ectopioglossa*	0	4	4
12	*Eumenes*	5	8	8
13	*Euodynerus*	4	4	4
14	*Gribodia*	0	1	1
15	*Indodynerus*	0	1	1
16	*Labus*	0	3	3
17	*Lissodynerus*	0	1	1
18	*Malayepipona*	1	4	4
19	*Okinawepipona*	1	2	2
20	*Orancistrocerus*	4	2	4
21	*Orientalicesa*	0	1	1
22	*Paraleptomenes*	1	0	1
23	*Parancistrocerus*	1	1	2
24	*Pararrhynchium*	5	4	7
25	*Pareumenes*	1	2	2
26	*Phimenes*	1	2	2
27	*Pseudonortonia*	0	2	2
28	*Pseudozumia*	0	2	2
29	*Pseumenes*	0	2	2
30	*Rhynchium*	1	1	1
31	*Stenodyneriellus*	2	4	4
32	*Stenodynerus*	1	0	1
33	*Symmorphus*	1	1	1
34	*Zethus*	1	7	7
	Total genera	**24**	**31**	**34**
	Total species	**53**	**82**	**100**

Notably, six species were recorded from Vietnam for the first time: *Antepipona bipustulata, Antepipona ceylonica, Antepipona rufescens, Antepipona tytides, Pararrhynchium impunctatum*, and *Pararrhynchium obsoletum*. In addition, *Paraleptomenes communis* was recorded for the first time in Northern Vietnam. In addition, the genera *Ancistrocerus* Wesmael, 1836 and *Stenodynerus* de Saussure, 1863 were recorded from Vietnam for the first time.

One of the dissertation's major findings is the discovery and description of five species new to science: *Antepipona crenula, Anterhynchium conformalum, Calligaster inflata, Orancistrocerus thanghen,* and *Orancistrocerus thanhnhat.* This indicates considerable untapped taxonomic diversity in the Eumeninae fauna of Northern Vietnam. Further surveys in high mountains, natural forests, and border areas are therefore needed to discover and document additional, previously unknown taxa.

3.1.2. Morphological characteristics of new species in Northern Vietnam

The dissertation provides detailed descriptions of five species new to science based on body coloration and the morphology of the head, thorax, abdomen, wings, and male genitalia. Each new species was compared with morphologically related species, and key diagnostic characters were identified.

Calligaster inflata, Orancistrocerus thanghen, Orancistrocerus thanhnhat, Antepipona crenula, and *Anterhynchium conformalum* each possess distinctive morphological features that do not match any previously described species. Their discovery and description substantially expand knowledge of Eumeninae diversity in the Oriental Region and provide important baseline data for future taxonomic, phylogenetic, and biodiversity-conservation research.

3.1.3. Distribution of Eumeninae wasps in Northern Vietnam

By synthesizing published records and field results, this study documented 100 Eumeninae species and species-level taxa in Northern Vietnam, providing the most comprehensive distribution dataset for the region to date. Numerous new locality records were added, particularly in northern

mountainous provinces, and distribution data were provided for newly described and newly recorded species. A distribution map of the 100 species/species-level taxa in Northern Vietnam was produced.

Species' geographic ranges differed markedly. Some, including Eumenes inconspicuous, Orancistrocerus aterrimus, and Rhynchium brunneum, were widely distributed, whereas many were recorded from only one or two localities, potentially reflecting endemism, specialized ecological requirements, or insufficient survey effort.

The findings indicate substantial potential for discovering and adding Eumeninae species in Northern Vietnam, particularly in areas that have not been adequately surveyed.

3.2. Biology and ecology of Eumeninae wasps in Northern Vietnam

3.2.1. Biology and ecology of four species of the genus Euodynerus Dalla Torre, 1904 in Northern Vietnam

A total of 73 nests containing 271 cells were recorded for four *Euodynerus* species. *E. nipanicus* was the most common, with 43 nests and 177 cells; nesting activity lasted from April to October, with peaks in June and August. *E. dantici* and *E. trilobus* were recorded only on the Red River mid-channel bars from May to July, whereas *E. furvus* occurred mainly in the natural forests of Tam Dao and Me Linh, and new nests were collected only in May and June.

All species nested in pre-existing cavities and used mud to construct partitions and closing plugs. Each nest contained 1 - 9 provisioned cells and commonly featured three types of empty cavities: an innermost, an intermediate, and an outermost cavity. Nest structures were broadly similar among species but differed in cell number and dimensions. Provisioned cell length varied considerably, ranging from 7 to 48 mm in *E. nipanicus*.

All species passed through five developmental stages: egg, larva, prepupa, pupa, and adult. Eggs developed in approximately two days; the larval stage of *E. nipanicus* lasted 7 - 8 days. The prepupal stage usually lasted 3 - 7 days, whereas *E. furvus* overwintered as a prepupa for as long as 10 - 11 months. The pupal stage lasted 6 - 14 days, depending on species.

Sex ratios differed among species: *E. nipanicus* was male-biased (1 female:1.2 males), whereas *E. trilobus* (2.1 females:1 male) and *E. furvus* (2.75 females:1 male) were female-biased. In most nests, females occupied inner cells and males occupied outer cells.

Adult emergence rates ranged from 50% to 64.4%, depending on species. Major mortality agents included *Megaselia* sp. (Phoridae), *Melittobia* sp. (Eulophidae), *Chrysis* sp. (Chrysididae), *Bombylella* sp., and ants. *Megaselia* sp. was the most frequently encountered parasitoid.

3.2.2. Biology and ecology of Orancistrocerus aterrimus (Bingham, 1897) in Northern Vietnam

Nesting activity of *Orancistrocerus aterrimus* continued from May to November, with peaks in July and September.

This is one of the few Eumeninae species in Northern Vietnam reported to use two distinct nesting strategies: constructing mud nests and nesting in pre-existing cavities (trap nests). The species exhibited both mass provisioning and progressive provisioning. Communal nesting, with multiple females constructing nests on the same substrate, was also observed.

Twenty-two self-constructed tubular mud nests were collected; each had a distinctive chimney-like entrance and contained 3 - 5 provisioned cells. Trap nests yielded 50 nests with 152 cells. Females selected bamboo tubes 8 - 16.5 mm in diameter and 100 - 478 mm long. Completed nests contained 1 - 9 provisioned cells, most commonly 2 - 5. Cells were arranged sequentially, always with an outer empty cavity, and separated by thin earthen partitions.

Development comprised five stages: egg, larva, prepupa, pupa, and adult. Eggs developed in 2 - 3 days, larvae in 7 - 9 days, and prepupae in 5 - 7 days. Individuals emerging in September - October overwintered as prepupae for approximately 20 - 27 weeks before pupating the following spring. In individuals that did not overwinter as prepupae, the pupal stage lasted 9 - 15 days (mean 12.5 ± 0.4 days, n = 29); in overwintering individuals, it lasted 13 - 21 days.

Sexing 102 individuals indicated a nearly balanced sex ratio (approximately 1 female:1.05 - 1.3 males). Female-containing cells were consistently located toward the inner end of the nest, while male-containing cells were toward the outside.

Of the 152 trap-nest cells, 74 individuals (48.7%) successfully reached adulthood and 78 (51.3%) died during development. Six groups of parasitoids and natural enemies were recorded; *Melittobia* sp. (Eulophidae) and *Chrysis* sp. (Chrysididae) were the most common.

The 22 self-constructed nests contained 66 cells, of which 28 individuals (42.4%) reached adulthood. Individuals in 37 cells died for unknown reasons, and only one cell was found to have been killed by *Macrosiagon* sp. (Ripiphoridae, Coleoptera).

This study provides the first data from Vietnam on the nesting behavior, nest structure, life cycle, and parasitoid associations of *Orancistrocerus aterrimus*.

3.2.3. Biology and ecology of Zethus dolosus Bingham, 1890 in Northern Vietnam

Thirty-two nests containing 80 provisioned cells of *Zethus dolosus* were collected in Vinh Phuc, Thai Nguyen, and Hanoi; nesting occurred from May to October. The species used bamboo tubes 4 - 11 mm in diameter and 63 - 423 mm long. A notable feature was the construction of a “chimney” at the nest entrance from young leaves bound with plant resin; the chimney reached 4.2 cm in length. The female built it immediately after selecting a nest site, then laid an egg before collecting prey for the larva. Each completed nest contained 1 - 9 provisioned cells (mean 3.04 cells per nest), with partitions also made from finely processed plant material.

Pre-adult development comprised five stages: egg, larva, prepupa, pupa, and adult. Eggs developed in approximately 2 - 3 days, and the larval stage lasted an average of 8.4 days. Individuals from the final generation overwintered as prepupae for 22 - 28 weeks and pupated the following spring.

In individuals that did not overwinter, development from egg to adult took approximately one month. Nesting activity from May to October suggests that the species has at least four generations per year in Northern Vietnam.

In the laboratory, 37 individuals reached adulthood, comprising 22 males and 15 females. The sex ratio was male-biased among individuals whose prepupae underwent diapause, whereas it was nearly balanced among individuals whose prepupae developed without diapause. In four nests for which the sex of every cell was determined, females occupied the innermost cells and males the outer cells.

Of the 80 provisioned cells in the 32 nests, 37 individuals (46.3%) successfully reached adulthood and 43 (53.7%) died during development. Three parasitoid groups were recorded: Phoridae (*Megaselia* sp.), Eulophidae (*Melittobia* sp.), and Chrysididae (*Chrysis* sp.). This is the first report of the biology, ecology, and parasitoid associations of *Zethus dolosus* in Vietnam.

The first record of the biology and ecology of *Zethus dolosus* in Vietnam adds to the still limited knowledge of nesting behavior in the genus *Zethus*.

3.2.4. Overview of nest morphotypes of Eumeninae wasps in Northern Vietnam

Nests of 29 Eumeninae species were recorded in Northern Vietnam, revealing considerable diversity in nesting sites, construction materials, and nest architecture. Three main nest types were identified: nests excavated in soil, nests constructed from mud or plant materials, and nests built in pre-existing cavities.

** Nests excavated in soil*

This nest type was uncommon and recorded only in *Antepipona biguttata* and *Allorhynchium punctatum*. Four nests containing 16 provisioned cells of *A. biguttata* were collected in Ha Giang and Phu Tho. Nests were built beneath rock cavities or at tree bases and had an external chimney-like tube 0.5 - 1.2 cm long and 0.3 - 0.4 cm in diameter. The cells were located in soil and measured 0.9 - 1.1 cm long and 0.3 - 0.4 cm in diameter. Only two nests

of *Allorhynchium punctatum* were collected; the limited sample was insufficient to fully characterize their structure.

** Nests constructed from mud or plant material*

Eleven species that construct their own nests were recorded. Their composition, nest-building materials, and number of cells per nest in the study area are presented in the following table:

No.	Species	Nest-building material	Cells per nest (number of nests collected)
1	*Calligaster himalayensis*	Leaves and plant resin	4 - 10 (17)
2	*Calligaster inflata*	Leaves and plant resin	4 (1)
3	*Delta esuriense*	Mud	2 - 33 (30)
4	*Delta pyriforme*	Mud	1 - 8 (4)
5	*Eumenes inconspicuous*	Mud	1 - 5 (9)
6	*Eumenes labiatus*	Mud	1 (2)
7	*Eumenes quadratus*	Mud	17 (1)
8	*Orancistrocerus altus*	Mud	1 (1)
9	*Orancistrocerus aterrimus*	Mud	2 - 5 (22)
10	*Paraleptomenes communis*	Mud	3 - 4 (2)
11	*Phimenes flavopictus*	Mud	3-11 (8)

Calligaster himalayensis and *C. inflata* used leaves combined with plant resin to construct nest cells; the remaining species primarily used mud.

Nests of *Delta* species comprised multiple sequential cells and were often covered with a thin layer of soil after completion. *Delta esuriens* had 2 - 33 provisioned cells per nest, whereas *D. pyriforme* had 1 - 8. *Eumenes* species constructed characteristic pot-shaped mud cells, with 1 - 5 cells per nest. *Orancistrocerus aterrimus* built elongated tubular nests with chimney-shaped entrances, each containing 2 - 5 cells; communal nest clusters could also

form. *Phimenes flavopictus* nested on walls, with 3 - 11 cells arranged in several layers and covered externally by a thin layer of soil.

** Nests in pre-existing cavities*

This was the most common nest type, recorded in 17 species. Species composition and nest measurements are presented in the following table:

No.	Species	Provisioned cells per nest (number of nests)	Nest diameter (mm)
1	*Allorhynchium argentatum*	1 - 4 (88)	4,5 - 10
2	*Allorhynchium lugubrinum*	1 - 2 (3)	8 - 9
3	*Ancistrocerus* sp1.	2 (1)	8
4	*Anterhynchium conformalum*	1 - 8 (133)	8 - 19,5
5	*Apodynerus troglodytes*	1 - 5 (13)	4 - 9
6	*Coeleumenes* sp.	1 (1)	3
7	*Euodynerus dantici*	1 - 2 (6)	5,5 - 9
8	*Euodynerus furvus*	1 - 6 (14)	4 - 11,5
9	*Euodynerus nipanicus*	1 - 9 (43)	3,5 - 14
10	*Euodynerus trilobus*	4 - 7 (8)	3 - 10,5
11	*Orancistrocerus aterimus*	2 - 9 (50)	8 - 16,5
12	*Parancistrocerus* sp2.	3 (1)	3
13	*Pararrhynchium striatum*	1 - 7 (46)	5 - 10
14	*Pareumenes quadrispinosus*	1 - 4 (876)	5 - 18
15	*Rhynchium brunneum*	1 - 11 (510)	5,5 - 17
16	*Symmorphus laoticus*	1 - 2 (10)	3,5 - 4
17	*Zethus dolosus*	1 - 9 (32)	5 - 11

Among these 17 species, 10 nested only in bamboo tubes or trap nests; four nested in both trap nests and old nests of other species; two used only old nests; and one nested in pre-drilled holes in bamboo or wood.

Cavity-nesting species used various materials to construct partitions. Two species belonging to *Allorhynchium* genus and *Zethus dolosus* used plant

resin and leaves, whereas most of the other species used mud. Nest structures differed in cell size, partition thickness, and number of cells per nest. Some species, such as *Euodynerus* spp. and *Apodynerus formosensis*, preferred cavities of small diameter, whereas others used larger cavities.

Nest reuse was also relatively common. *Anterhynchium conformalum, Pararrhynchium striatum, Rhynchium brunneum, Euodynerus furvus, Pareumenes quadrispinosus, Coeleumenes* sp., and *Parancistrocerus* sp. 2 were recorded nesting in old cavities or nests of Vespidae, Sphecidae, or honey bees. This demonstrates that many Eumeninae can exploit pre-existing nesting resources in nature.

These findings provide the first relatively comprehensive evidence of nest-morphology diversity among Eumeninae in Northern Vietnam and help clarify their reproductive strategies and ecological adaptations.

3.2.5. Parasitoids and predators affecting the development of Eumeninae wasps in Northern Vietnam

Analysis of 3,450 nest cells from 19 Eumeninae species recorded parasitoids and natural enemies belonging to 11 families in four insect orders: Diptera, Hymenoptera, Coleoptera, and Strepsiptera. Hymenoptera was the most diverse order, with six families.

** Order Diptera*

Megaselia spp. (Diptera: Phoridae) were the most common and serious mortality agents, affecting 422 nest cells, mainly those of *Pareumenes quadrispinosus* and *Rhynchium brunneum*. Female flies entered nests when adult wasps left, killed eggs, and laid eggs in the nest or on prey. The maggots consumed stored provisions and soft prey tissues, then pupated; adult flies emerged by boring through nest partitions.

Miltogrammatinae (Diptera: Sarcophagidae) were recorded as kleptoparasites that entered nests when the host wasp left and deposited larvae in nest cells. The fly larvae consumed prey and/or host larvae, causing the wasp larvae to die. This group damaged 49 nest cells belonging to four Eumeninae species, primarily *Rhynchium brunneum*.

Bombylella spp. (Diptera: Bombyliidae) were also recorded in 13 cells belonging to five Eumeninae species. Their larvae fed on host body fluids and then pupated. Under laboratory conditions, development to the pupal stage took 9 - 11 days, and the pupal stage lasted 15 - 17 days.

** Order Hymenoptera*

Among hymenopteran natural enemies, *Melittobia* sp. (Eulophidae) caused the greatest mortality, occurring in 127 cells of 11 Eumeninae species. These parasitoids entered nests before the host sealed the cell and parasitized hosts at the prepupal or pupal stage; hundreds of *Melittobia* individuals could develop on a single host.

Five morphospecies of *Chrysis* (Chrysididae) were recorded, causing mortality in 73 cells of 10 Eumeninae species. Females often waited at nest entrances and entered to lay eggs when the host was away. *Chrysis* larvae then attacked host larvae and consumed the stored prey as well.

Other recorded groups included Formicidae, Chalcididae, Ichneumonidae, and Trigonalidae, but their impacts were lower. Notably, *Hadrocryptus caobangensis*, a species new to science, was discovered parasitizing *Allorhynchium lugubrinum*. Trigonalidae were recorded in six cells; the larval stage lasted 5 - 6 days and the pupal stage 6 - 7 days.

** Order Coleoptera*

Only the family Ripiphoridae was recorded among Coleoptera, represented by two morphospecies of *Macrosiagon* parasitizing two cells of *Orancistrocerus aterrimus* and *Paraleptomenes communis*.

The parasitoid larvae appeared when the host was at the prepupal stage and primarily fed on host body fluids. The larval stage lasted 11 - 12 days, followed by a pupal stage of 9 - 11 days.

** Order Strepsiptera*

The family Xenidae (Strepsiptera) was recorded parasitizing 19 cells of three Eumeninae species: *Anterhynchium conformalum*, *Pareumenes quadrispinosus*, and *Rhynchium brunneum*. Xenidae are primarily

endoparasites of adult wasps: females remain attached within the host body, whereas adult males are free-living and seek mates. Although parasitism does not usually kill the host, it may alter physiology, behavior, and reproductive capacity, and severe infections may cause “physiological castration.”

3.3. Natural enemy roles of Eumeninae wasps in ecosystems of Northern Vietnam

3.3.1. Prey spectrum of Eumeninae wasps in Northern Vietnam

The prey of all 14 Eumeninae species examined consisted of lepidopteran larvae. The number of prey items per nest cell ranged from 2 to 34, depending on wasp species and prey size. Most species used 2 - 4 distinct larval morphotypes to provision their brood cells.

Among the species studied, *Rhynchium brunneum* exhibited the broadest prey spectrum, comprising 14 larval morphotypes. Each nest cell contained 2 - 26 caterpillars, and a female was estimated to kill up to approximately 650 pest larvae during its lifetime. This species also preyed on important crop pests, including the soybean leaf-folder (*Omiodes indicus*), bean pod borer (*Maruca vitrata*), and black-headed leafroller (*Archips asiaticus*).

Euodynerus nipanicus utilized at least six prey types, mainly leaf-rollers and pod borers that damage legumes, suggesting its potential contribution to agricultural pest suppression. Other species, including *Delta esuriens*, *D. pyriforme*, *Eumenes inconspicuus*, *Orancistrocerus aterrimus*, and *Phimenes flavopictus*, also exhibited relatively broad prey spectra.

Pareumenes quadrispinosus provisioned each nest cell with an average of 2.7 caterpillars. Based on an estimated lifetime fecundity of 20 - 30 eggs, a female could potentially kill approximately 180 pest larvae during its lifetime. This species is widely distributed in Northern Vietnam and may contribute to natural pest suppression.

Overall, these findings highlight the ecological importance of Eumeninae as predators of lepidopteran larvae and their potential contribution to natural pest regulation and biological control in agricultural and forest ecosystems.

3.3.2. Proposed directions for the use and conservation of wasps important in biological control

The findings indicate that Eumeninae species play a role in limiting pest species. Such as, *Rhynchium brunneum, Euodynerus nipanicus, Delta esuriens*, and *Phimenes flavopictus* have considerable potential for biological control because of their broad prey spectra and ability to kill large numbers of pest larvae.

The following measures are recommended to conserve this group and enhance its role:

- ✓ Conservation of nesting habitats: Maintain semi-natural habitats such as field margins, hedgerows, orchards, and patches of secondary forest, and minimize destruction of natural nesting sites to provide suitable conditions for wasp occupancy and reproduction.
- ✓ Maintaining food resources and reducing agricultural impacts: Conserve or plant flowering vegetation to provide food for adult wasps. Implement integrated pest management (IPM) and use plant-protection products judiciously to minimize adverse effects on wasp populations.
- ✓ Research on artificial nesting substrates: Test suitable substrates, such as hollow bamboo or structures containing nesting cavities, and monitor nest occupancy, reproduction, and population persistence before wider implementation.

Combining these measures will help conserve Eumeninae predatory-wasp populations and make effective use of their natural-enemy roles in pest control, thereby supporting sustainable agriculture.

CONCLUSIONS AND RECOMMENDATIONS

CONCLUSIONS

1. A total of 100 Eumeninae species and species-level taxa belonging to 34 genera were recorded in Northern Vietnam, and a distribution map was compiled. Five species new to science were described, and six species and two genera were newly recorded from Vietnam.
2. Three nest types were documented for 29 species. Nesting behavior, nest structure, pre-adult development, sex ratios, and pre-adult survival were investigated in four *Euodynerus* species and in *Zethus dolosus* and *Orancistrocerus aterrimus*.
3. Parasitoids and predators associated with Eumeninae were identified, representing 11 families in four insect orders. In particular, the parasitoid *Hadrocryptus caobangensis* was recorded from the predatory wasp *Allorhynchium lugubrinum*; this parasitoid species was described as new to science.
4. The prey spectra of 14 Eumeninae species in Northern Vietnam were determined. All species studied provisioned their larvae with lepidopteran larvae, with 2–34 prey individuals per nest cell.

RECOMMENDATIONS

1. Continue surveying Eumeninae species composition and distribution in poorly studied areas of Vietnam.
2. Expand research on biology, ecology, prey spectra, and associations with parasitoids and predators.
3. Assess the biological-control potential of promising species and investigate habitat-conservation measures and approaches to maintaining their populations.

LIST OF PUBLICATIONS RELATED TO THE DISSERTATION

A. Monograph

1. Nguyen Thi Phuong Lien and Dang Thi Hoa, 2023. Biodiversity of stinging wasps (Hymenoptera: Aculeata) at the Me Linh Biodiversity Station, Vinh Phuc. Vietnam Academy of Science and Technology Publishing House, 281 pp.

B. International articles indexed in ISI-listed journals

2. Lien Thi Phuong Nguyen, Anh D. Nguyen, **Hoa T. Dang**, 2024. The solitary wasp genus *Orancistrocerus* from Vietnam, with descriptions of two new species (Hymenoptera, Vespidae, Eumeninae). ZooKeys 1193: 95 - 110 (2024).
3. Cuong Quang Nguyen, **Hoa Thi Dang**, Lien Thi Phuong Nguyen, 2024. A new species of the presocial potter wasp genus *Calligaster* de Saussure, 1852 (Hymenoptera, Vespidae, Eumeninae) from Vietnam. Journal of Hymenoptera Research 97: 241 - 254.
4. Lien Thi Phuong Nguyen, Anh D. Nguyen, **Hoa T. Dang**, Seiki Yamane & Michael S. Engel, 2024. Taxonomic review of the potter wasp genus *Antepipona* de Saussure, 1855 (Hymenoptera, Vespidae, Eumeninae) from Vietnam, with descriptions of two new species and keys to the Oriental fauna. *Zoosystema* 46 (27): 697-722.
5. Nhi Thi Pham, **Hoa Thi Dang**, Duong Dinh Tran, 2025. First record of the genus *Hadrocryptus* Cameron (Ichneumonidae: Cryptinae) from Vietnam, with description of two new species. Raffles Bulletin of Zoology 73: 504-513.
6. **Hoa Thi Dang**, Duong Dinh Tran, Anh Duc Nguyen & Lien Thi Phuong Nguyen, 2025. Review of the genus *Anterhynchium* de Saussure (Hymenoptera: Vespidae: Eumeninae) from Vietnam, with the description of a new species and a key to the Oriental species. Zootaxa 5716 (4): 541 - 557.

C. Domestic journal

7. **Dang Thi Hoa,** Nguyen Thi Phuong Lien, Tran Dinh Duong, Truong Xuan Lam, 2025. Nesting biology of Zethus dolosus Bingham, 1897 (Hymenoptera: Vespidae: Eumeninae) in trap nests from Northern Vietnam. Academia Journal of Biology 2026, 48(2): 43-52.

D. Conference proceedings

8. **Dang Thi Hoa**, Nguyen Thi Phuong Lien, Truong Xuan Lam, Vu Quang Con, 2026. Nesting activity in trap nests by predatory wasps of the family Vespidae (Hymenoptera: Vespidae: Eumeninae) in Chuong My, Hanoi. Proceedings of the 9th National Entomology Conference, Agriculture Publishing House, pp. 271–276.