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New records of fern-spore feeding moths and notes on their biology from Guangdong Province, China

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Abstract

Background

Fern spore-feeding represents a specialized but understudied plant–insect interaction. Despite the growing number of taxonomic and life-history studies on spore-feeding insects, available research remains geographically biased toward East Asia, particularly Japan, South Korea, and Taiwan of China.

New information

In this study, we documented four stathmopodid moth species (Lepidoptera: Stathmopodidae: Cuprininae) associated with fern sori in Guangdong Province, southern China: *Calicotis exclamationis*, *Thylacosceles cuneiformis*, *Thylacosceloides vaginivella*, and *Trigonoda fuscimaculata*. Three of these species represent new records for mainland China, and all four were recorded on new host plants. Through field surveys and laboratory rearing, we confirmed larval host associations and documented life-history traits, including feeding behavior, shelter construction, and pupation. Larvae construct three distinct shelter types, patch-like shelters, strip-shaped shelters, and tunnels excavated within sporangia, which likely function to regulate microclimate, reduce exposure, and enhance crypsis. The relatively long activity period of these moths in subtropical Guangdong suggests that prolonged spore availability shapes their phenology. Host-use patterns varied among species, ranging from host-specific to relatively broad host ranges. These findings expand the known geographic distribution and host associations of fern spore-feeding moths and provide insights into the ecological and evolutionary constraints shaping this specialized niche.

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Keywords

fern, Fern-spore-feeder, host association, Stathmopodidae

Introduction

Ferns are the earliest-diverging lineages of vascular plants, with an evolutionary history spanning hundreds of millions of years (Testo and Sundue 2016). Despite their long evolutionary history and ecological importance, interactions between ferns and insects have historically received far less attention than those involving angiosperms (Balick et al. 1978, Cooper-Driver 1978). In recent years, however, an increasing number of studies have documented a wide range of fern-associated insects (Cenci and Horodyski 2024, Porto et al. 2025). Porto et al. compiled records of at least 1,350 insect species from 98 families associated with ferns, indicating that fern-insect interactions are more widespread than previously recognized (Porto et al. 2025). Consumptions on ferns include chewing, piercing and sucking, boring, mining, galling, and spore-feeding (Labandeira 2007, Xiao et al. 2022, Porto et al. 2025).

Among these interaction types, spore-feeding is particularly distinctive. While angiosperm seed predation has long been a central focus of plant-insect interaction research, spore-feeding in ferns has remained largely neglected. According to Porto et al. spore-feeding insects account for only 6.5% of all fern-associated phytophagous insects (Porto et al. 2025). Unlike ordinary foliar herbivory, spore-feeding targets the reproductive propagules of ferns. Spores are concentrated in sori on fertile fronds and are available only during a limited phenological window, which may impose strong temporal and spatial constraints on the insects that exploit them (Cooper-Driver 1978, Sawamura et al. 2009, Porto et al. 2025). Because spores are directly involved in fern reproduction, spore-feeding may carry more immediate fitness consequences for host than leaf herbivory, as least from the aspect of community development (Ballesteros 2011). The most common groups of spore feeders exist in Lepidoptera, Coleoptera, Hymenoptera, and Hemiptera, 5 orders, 13 families, 27 genera and about 90 species in total (Suppl. material 1). Major consuming method is feeding the whole spores as food, and partly puncturing and sucking the liquid from the spores (Pagola-Carte et al. 2004, Shen et al. 2024), of which 34 species (39.1%) belong to the subfamily Cuprinae of the family Stathmopodidae (Lepidoptera) taken up the most diverse spore feeders (Suppl. material 1). The specialized spore-feeders treated here belong to the subfamily Cuprinae of the family Stathmopodidae (Lepidoptera). Their larvae depend entirely on fern spores for development, making an understanding of their feeding habits, host preferences and life history essential for evaluating their potential impact on fern growth and reproduction.

Taxonomic and life-history studies of spore-feeding insects have increased and remain concentrated primarily in East Asia, particularly Japan, South Korea and Taiwan of China (Sawamura et al. 2009, Shen et al. 2022, Shen et al. 2024, Porto et al. 2025) (Suppl.

material 1). In mainland China, records of such insects are still scarce and are often based on isolated field observations that lack rearing confirmation, detailed life-history data, or precise host identification. Here, based on field surveys and laboratory rearing, we report three species of Stathmopodidae associated with fern spores as new records for mainland China.

Materials and methods

Sampling and collection

Fieldwork was conducted between May 2025 and May 2026 at four sites in Guangdong Province, southern China: Chebaling National Nature Reserve (23.09–23.11 °N, 112.32–113.04
°E) in October 2025，Nanling National Nature Reserve (24.91–24.93 °N, 113.02–113.04 °E) in June 2025 and June 2026, Dinghushan National Nature Reserve (23.16–23.18 °N, 112.54–112.55 °E) in May 2025, September 2025, and May 2026, and South China Botanical Garden (23.18 °N, 113.37 °E) in May 2026 (Fig. 1).

Fertile fern fronds bearing mature sori were inspected for the presence of spore-feeding insect larvae. When larvae were found, their feeding position, shelter structure, and associated host tissues were recorded and photographed. Each larva, together with the host frond on which it was found, was collected and transferred to an individual sealed plastic bag for transport to the laboratory.

In the laboratory, larvae were reared at room temperature. Their behavior and development were monitored regularly, and photographs were taken throughout the larval, pupal, and adult stages whenever possible.

Host plant and insect identification

Fern species were identified based on morphological characteristics such as sori, indusia, rhizomes and leaves using *Flora Reipublicae Popularis Sinicae* Volume 3 (1), Volume 6 (1), Volume 6 (2), as well as the PPG I classification (Wu 1990, Wu and Wang 1999, Lin et al. 2000, PPG I 2016)

Spore-feeding larvae were reared individually with host fern fronds in the laboratory until adult moth emergence. Moth species were identified morphologically following the classification system of Stathmopodidae (Lepidoptera) proposed by Terada (2016) and other relevant taxonomic references (Guan and Li 2016, Shen et al. 2022, Shen et al. 2024) and confirmed by DNA barcoding of the mitochondrial COI gene. Sequences of the COI gene were acquired from a leg of each adult specimen or pupa following the protocol described in Chen et al. (Chen et al. 2024). The resulting sequences were queried against the GenBank database using BLAST to verify species identity. All sequences generated in this study were deposited into GenBank. All the voucher specimens are deposited in the Insect Collection of the Guangdong Academy of Sciences (IZGAS).

Pothograph

Whole-plant images, ecological photographs and morphological detail images were captured with a Sony Alpha 7R Ⅲ digital camera. All image plates were assembled using Adobe Photoshop 2025 (Adobe Inc., USA) software during post-processing.

Data resources

A total of four species are recognized, among which three species were identified both by adult morphology and DNA barcoding and one species was identified by DNA barcoding based on a pupa. Three species are new records for mainland China: *Calicotis exclamationis* (Terada, 2016), *Thylacosceloides vaginivella* (Terada, 2016) and *Trigonoda fuscimaculata* (Terada, 2016). A new record for Guangdong province: *Thylacosceles cuneiformis* (Guan & Li, 2016), which was previously described from Yunnan Province, China (Fig. 1). All these four species were recorded on new hosts in this field survey and associated with mature fern sori and constructed distinctive silk shelters during larval feeding

Taxon treatments

Calicotis exclamationis Terada, 2016

- GenBank PZ907265
- GenBank PZ907268

Nomenclature

Calicotis exclamationis Terada, 2016: 134-137. (Type locality: Japan)

Materials

a. scientificName: ***Calicotis exclamationis*** (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Shaoguan; locality: Chebaling National Nature Reserve; verbatimLatitude: 24 43 09 N; verbatimLongitude: 114 15 20 E; samplingProtocol: Two males, three females emerged from larvae collected on 28 October 2025, reared on the sori of *Neolepisorus ovatus* (Wall. ex Bedd.) Ching (Polypodiaceae); individualCount: 5; recordedBy: Jing-Yun Wang & Hai-Dong Yang; identifiedBy: Jing-Yun Wang; identificationRemarks: These specimens represent a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: AF7ECA57-B11A-52E5-9115-FAA30DDFEC7E

b. scientificName: ***Calicotis exclamationis*** (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Shaoguan; locality: Nanling National Nature Reserve; verbatimLatitude: 24 55 32 N; verbatimLongitude: 113 01 21 E; samplingProtocol: Four males, two females emerged from larvae collected on 2 June

2026, reared on the sori of *Lepisorus fortunei* (T. Moore) Ching (Polypodiaceae); individualCount: 6; recordedBy: Jing-Yun Wang & Hai-Dong Yang; identifiedBy: Jing-Yun Wang; identificationRemarks: These specimens represent a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: BF697D02-0361-568D-A5D0-249BD7A0DF63

Distribution

China (Guangdong and Taiwan) and Japan (Shen 2021, Shen et al. 2022).

Biology

Larvae are pale creamy yellow with semi-transparent cuticle, and translucent setae arise on each body segment. Larvae construct convex, irregular silk shelters alongside the host sori. The shelters are tightly woven with silk threads and mixed with empty sporangia and spore residues, generally 2-3 cm in length (Figs 2, 3). Larvae stay inside shelters and mainly feed on spores and sporangial tissues within soral patches. When local spore supplies are exhausted, larvae move to new soral patches and build new shelters. And larvae generally rapidly retracting into the nests when they get disturbed or threaten.

Mature larvae (~0.7 cm in length) abandon their feeding shelters and spin cocoons as independent pupal chambers on other parts of fronds or inside rearing-containers. Each pupal chamber consists of a double-layered silken cocoon (Figs 2, 3). Under laboratory conditions, the prepupal stage lasts 1-3 days. During this phase, larvae cease all feeding activity, their body length shrinks and segments contract tightly. Pupation stage lasts approximately 10 days (Figs 2, 3).

Notes

The COI sequences of our specimens (GenBank accession no.: PZ907265, PZ907268) show high similarity (100%) to *Calicotis exclamationis* Terada, 2016 in Genbank.

Host plants

Neolepisorus ovatus (Fig. 2) and *Lepisorus fortunei* (Fig. 3) were found as host plants, with *N. ovatus* represents a new host plant record, in this study. Previously recorded hosts include Aspleniaceae (*Asplenium scolopendrium*), Plagiogyriaceae (*Plagiogyria euphlebia*), Dryopteridaceae (*Cyrtomium fortunei*, *Polystichum polyblepharon*), Athyriaceae (*Athyrium decurrentialatum*), Pteridaceae (*Coniogramme intermedia*, *Pteris terminalis* var. f*auriei*), and Polypodiaceae (*Colysis wrightii*, *Microsorum brachylepis*, *Lepisorus fortunei* (originally recorded as (*Neolepisorus fortunei*)) (Shen et al. 2022). These records suggest that *C. exclamationis* may exploit soral resources from a relatively broad range of fern hosts (Figs 2, 3).

Thylacosceles cuneiformis (Guan & Li, 2016)

- GenBank PZ907270

Nomenclature

Thylacosceles cuneiformis Guan & Li, 2016: 218–219. (Type locality: China).

Material

a. scientificName: ***Thylacosceles cuneiformis*** (Guan & Li, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Zhaoqing; locality: Dinghushan National Nature Reserve; verbatimLatitude: 23 09 28 N; verbatimLongitude: 112 32 29 E; samplingProtocol: One male, one female emerged from larvae collected on 21 May 2026, reared on the sori of ***Tectaria harlandii*** (Hook.) C.M. Kuo (Tectariaceae); individualCount: 2; recordedBy: Jing-Yun Wang; identifiedBy: Jing-Yun Wang; identificationRemarks: These specimens represent a new record of this species for Guangdong Province, China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: 56EEFA84-9357-5FC3-93F6-C9A26E1BB669

Distribution

China (Guangdong, Yunnan and Taiwan) (Guan and Li 2016, Shen 2021).

Biology

Larvae are pale creamy yellow with semi-transparent cuticle and regularly arranged, sparse, transparent short setae. Spore particles are visible inside the larval body after feeding. Larvae construct winding tunnels and inhabit on the underside of the fern fronds. The underside of frond is densely covered with sori, then the green lower epidermis of fronds is exposed, after the larvae consuming the spores and sporangial tissues. Larvae weave silk to bind spore residues and frass, and create a tight shelter that covered the tunnel. The larvae feeding inside the shelter and continuously expanding the tunnel area (Fig. 4).

Mature larvae (~0.5 cm in length) abandon their original shelters and construct independent pupal chambers at new sites. The pupal chamber is composed of a double-layered silken cocoon (Fig. 4). Under laboratory conditions, the prepupal stage lasts 3-5 days, during which larvae cease feeding, shrink in body length, and contract their body segments. After prepupation, adults eclose within 8-12 days (Fig. 4).

Notes

The COI gene sequence of the specimen from this study (GenBank accession number: PZ907270) shares a 96.1% sequence similarity with the sequence of *Thylacosceles cuneiformis* Guan & Li, 2016 in GenBank.

Host plants

Tectaria harlandii (Tectariaceae) (Fig. 4) found here represents a new host record. Previously recorded host was *Tectaria decurrens* (Tectariaceae) (Shen 2021). These two records in same genera might indicate that *Thylacosceles cuneiformis* exhibits specialism host specificity, albeit more host records could be found in the future.

Thylacosceloides vaginivella (Terada, 2016)

- GenBank PZ907266

Nomenclature

Pachyrhabda vaginivella Terada, 2016: 117–120. (Type locality: Japan). Transferred to *Thylacosceloides* by Shen et al. 2024: 20.

Material

a. scientificName: *Thylacosceloides vaginivella* (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Shaoguan; locality: Chebaling National Nature Reserve; verbatimLatitude: 24 41 59 N; verbatimLongitude: 114 11 31 E; samplingProtocol: One pupa obtained from larva collected on 29 October 2025, reared on the sori of *Pteris fauriei* Hieron. (Pteridaceae); individualCount: 1; recordedBy: Jing-Yun Wang; identifiedBy: Jing-Yun Wang; identificationRemarks: This specimen represents a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: 1ABEF2C1-4D8F-55C2-8F57-ADD79F651D38

Distribution

China (Guangdong and Taiwan) and Japan (Terada 2016, Shen 2021).

Biology

Larvae are pale yellow with semi-transparent cuticle and regularly arranged, sparse, transparent short setae. The shelters constructed by larvae is along the sporangia which distributed at the edge of each pinnule, weaved by sporangial tissues and frass. The larvae stay within shelters and enlarge the consuming area. When disturbed, the larvae retreat rapidly into the shelter (Fig. 5).

Mature larvae (~0.7 cm in length) abandon their shelters and select new locations to build pupal chambers. Each pupal chamber consists of a double-layered silken cocoon (Fig. 5). Under laboratory conditions, the prepupal stage lasts 2-4 days, during which the larvae stop feeding, reduce their body length and contract their body segments (Fig. 5). No adults have been successfully reared so far, and hence no complete record of the pupal stage can be provided.

Notes

The COI sequence of a pupa (GenBank accession no.: PZ907266) show high similarity (99.4%) to *Pachyrhabda vaginivella* Terada, 2016 (=*Thylacosceloides vaginivella* (Terada, 2016)) in Genbank.

Host plants

Previously recorded hosts include Thelypteridaceae (*Christella acuminata* and *Cyclosorus parasiticus*) (Shen 2021). *Pteris fauriei* found in this study represents a new host plant record, which expands the known fern host range of this species from Thelypteridaceae to Pteridaceae (Fig. 5).

Trigonoda fuscimaculata (Terada, 2016)

- GenBank PZ907264
- GenBank PZ907267
- GenBank PZ907269

Nomenclature

Pachyrhabda fuscimaculata Terada, 2016: 109–111. *Trigonoda* fuscimaculata (Terada, 2016) Shen et al. 2024: 17.

Materials

a. scientificName: ***Trigonoda fuscimaculata*** (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Shaoguan; locality: Nanling National Nature Reserve; verbatimLatitude: 24 54 49 N; verbatimLongitude: 113 02 25 E; samplingProtocol: One female emerged from larva collected on 2 June 2026, reared on the sori of ***Pteris ensiformis*** Burm. (Pteridaceae); individualCount: 1; recordedBy: Jing-Yun Wang; identifiedBy: Jing-Yun Wang; identificationRemarks: This specimen represents a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: 15BE4AA0-CA29-5CB3-9EE9-0C63CB429BFE

b. scientificName: ***Trigonoda fuscimaculata*** (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Guangzhou; locality: South China National Botanical Garden; verbatimLatitude: 23 10 54 N; verbatimLongitude: 113 22 01 E; samplingProtocol: Two males, one female emerged from larvae collected on 28

May 2026, reared on the sori of *Pteris semipinnata* L. (Pteridaceae); individualCount: 3; recordedBy: Jing-Yun Wang; identifiedBy: Jing-Yun Wang; identificationRemarks: These specimens represent a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: ACACF8CE-EC3B-57D5-8C70-B3276FF8232F

c. scientificName: *Trigonoda fuscimaculata* (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Zhaoqing; locality: Dinghushan National Nature Reserve; verbatimLatitude: 23 10 37 N; verbatimLongitude: 112 32 32 E; samplingProtocol: Two males, one female emerged from larvae collected on 20 May 2026, reared on the sori of *Pteris ensiformis* Burm. (Pteridaceae); individualCount: 3; recordedBy: Jing-Yun Wang; identifiedBy: Jing-Yun Wang; identificationRemarks: These specimens represent a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: C6458650-B22C-5875-97B7-331BED9DBFF3

d. scientificName: *Trigonoda fuscimaculata* (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Zhaoqing; locality: Dinghushan National Nature Reserve; verbatimLatitude: 23 10 37 N; verbatimLongitude: 112 32 32 E; samplingProtocol: One male, one female emerged from larvae collected on 20 May 2026, reared on the sori of *Pteris semipinnata* L. (Pteridaceae); individualCount: 2 ; recordedBy: Jing-Yun Wang; identifiedBy: Jing-Yun Wang; identificationRemarks: These specimens represent a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: C7728A9F-2782-5806-8F38-BFFAA3D98093

e. scientificName: *Trigonoda fuscimaculata* (Terada, 2016); higherClassification: Insecta; Lepidoptera; Stathmopodidae; Stathmopodinae; continent: East Asia; country: China; countryCode: CN; stateProvince: Guangdong; county: Shaoguan; locality: Chebaling National Nature Reserve; verbatimLatitude: 24 43 22 N; verbatimLongitude: 114 15 48 E; samplingProtocol: One male, two females emerged from larvae collected on 28 October 2025, reared on the sori of *Pteris semipinnata* L. (Pteridaceae); individualCount: 3 ; recordedBy: Jing-Yun Wang; identifiedBy: Jing-Yun Wang; identificationRemarks: These specimens represent a new record of this species for mainland China.; type: PhysicalObject; language: en; institutionCode: IZGAS; basisOfRecord: PreservedSpecimen; occurrenceID: D9AD3D5D-9880-57ED-B32D-4DDD053D3775

Distribution

China (Guangdong and Taiwan) and Japan (Honshu) (Terada 2016, Shen 2021).

Biology

Larvae are pale yellow with semi-transparent cuticle, bearing sparse, neatly arranged transparent setae on the body surface. Larvae construct shelters tightly attached to the sori which distributing at the margins of fertile fronds. The shelters are composed of sporangial fragments mixed with frass. Larvae dwell inside shelters and

continuously expand the structures outward as they feed, rapidly retracting into the nests when disturbed (Figs 6, 7).

Some mature larvae (~0.8 cm in length) abandon their original feeding shelters to build separate pupal chambers elsewhere, while most pupate directly hang on in their shelters. Each pupal chamber consists of a double-layered silken cocoon (Figs 6 , 7). Laboratory observations show the prepupal stage lasts 2-4 days: larvae cease feeding, shrink in body length and contract their segments during this period. Adults eclose 7-13 days after pupation (Figs 6, 7).

Notes

The COI sequences of our specimens (GenBank accession no.: PZ907264, PZ907267, PZ907269) show high similarity（100%）to *Pachyrhabda fuscimaculata Terada*, 2016 (=*Trigonoda fuscimaculata* (Terada, 2016)) in Genbank.

Host plants

Previously recorded hosts include Pteridaceae (*Pteris longipinna*, *Pteris excelsa*) (Shen 2021). *Pteris semipinnata* and *Pteris ensiformis* found as new host plant records in this study (Figs 6, 7).

Discussion

The present study documents four stathmopodid moth species, namely *Calicotis exclamationis* (Terada, 2016), *Trigonoda fuscimaculata* (Terada, 2016), *Thylacosceles cuneiformis* (Guan & Li, 2016), and *Thylacosceloides vaginivella* (Terada, 2016), three of which are new records for mainland China. By integrating field observations with laboratory rearing, we confirm larval host plant associations and provide supplementary life-history information, including feeding behaviour, shelter-building habits, and larval and pupal characteristics.

The larvae we found in this study construct shelters while feeding on sori, producing three distinct forms: patch-like shelters, strip-shaped shelters, and tunnels excavated within sporangia. These forms may reflect the spatial arrangement of the sporangia. Larvae abandon a shelter once surrounding food resources are depleted and construct a new shelter at the next feeding site. At pupation, larvae incorporate sporangia or sporangial fragments into the cocoon surface. These shelter-building behaviors likely serve multiple adaptive functions. In other fern-feeding lepidopteran larvae, analogous structures can buffer microclimatic variation, reduce exposure, and lower the risk of attack by natural enemies (Ruehlmann et al. 1988).For the species examined in this study, shelters on the abaxial leaf surface may help maintain local humidity, reduce the time larvae spend crawling on exposed leaf surfaces, and limit contact with epiphytic microbes and natural enemies. In contrast, the incorporation of sporangia into cocoon surfaces

probably functions primarily in crypsis, matching pupae to the surrounding background (Baer and Marquis 2020).

Most ferns occur in understory environments, and their spore resources are patchy and strongly limited in both time and space (Sawamura et al. 2009). Spore maturation is seasonal, and many ferns produce distinct sterile trophophylls and fertile sporophylls, with sori typically concentrated in specific regions of the abaxial frond surface. Spore-feeding therefore represents a specialized ecological niche shaped by spore phenology, abaxial leaf-surface microhabitats, and the spatial distribution of host ferns (Srivastava et al. 1997). Because spore availability is tightly coupled to host phenology, female moths must select suitable fronds for oviposition so that newly hatched larvae can feed on spores without delay. Compared with temperate Japanese forests, where spore-feeding moths are active from June to October, our subtropical study sites in Guangdong recorded four stathmopodid species with an extended activity period from May to October, beginning approximately one month earlier. We attribute this latitudinal difference to the prolonged availability of spore resources in subtropical ecosystems: warmer temperatures and longer growing seasons accelerate sporangial development and maturation, thereby extending the resource window and allowing earlier population emergence and broader temporal niches for fern-spore-feeding larvae. Additionally, phenological asynchrony in spore production among host fern species likely further extends the overall activity period of the stathmopodid community.

Host-use patterns among spore-feeding moths vary considerably: some taxa are highly host-specific, whereas others exploit multiple fern species or families (Terada 2016, Shen et al. 2024). In this study, *Trigonoda fuscimaculata* feed exclusively on *Pteris* ferns, whereas *Calicotis exclamationis* used multiple fern families as hosts. Host adaption can strongly influence larval developmental performance. Fuentes-Jacques et al. found found that larvae transferred to hosts with greater phylogenetic distance from their original host experienced reduced fitness (Fuentes-Jacques et al. 2022), suggesting that spore nutritional composition and secondary metabolites differ among fern species (Raghavan 1980) and may affect larval digestion, detoxification, and overall performance. Insect gut microbiota are known to participate in the degradation of plant secondary metabolites and to modulate host detoxification enzyme systems (Shao et al. 2024, Zhang et al. 2024). Larvae of spore-feeding moths collected from different fern hosts may therefore harbor distinct gut microbial communities. Future research should compare gut microbiota across larvae with different host-use patterns to clarify the detoxification mechanisms mediated by gut microbes.

Ferns are an ancient lineage of vascular plants with an evolutionary history spanning hundreds of millions of years (Testo and Sundue 2016). The six fern species exploited by stathmopodid moths in this study belong to the genera *Lepisorus* (Polypodiaceae), *Tectaria* (Tectariaceae), and *Pteris* (Pteridaceae). Published molecular dating estimates place the crown-group age of Polypodiaceae at approximately 40 Ma and the initial diversification of *Lepisorus* at approximately 17 Ma (Nitta et al. 2022, Porto et al. 2025). For Tectariaceae, the crown age is estimated at about 77.29 Ma, whereas the diversification of *Tectaria* began around 31.9 Ma (Wan et al. 2023). Pteridaceae, one of

the early-diverging lineages within Polypodiales, has a stem age of approximately 164 Ma, and *Pteris* began diversifying around 47 Ma (Chao et al. 2014). In comparison, Cuprininae, the stathmopodid moth subfamily specialized on fern spores, is estimated to have diversified between the Late Oligocene and Early Miocene (35–25 Ma) (Shen et al. 2024). This chronological disparity indicates that the specialized utilization of fern spores by Cuprininae did not arise from synchronous coevolution with their fern hosts. Rather, this trophic specialization likely resulted from subsequent host shifts, ecological adaptation, or the tracking of an evolutionarily conserved spore resource. Thus, despite the early emergence of fern spore resources, insects may have needed to overcome considerable adaptive hurdles before stably colonizing this ecological niche.

Conclusions

In conclusion, this study expands the known distribution and host associations of spore-feeding Stathmopodidae in subtropical China and documents their shelter-building behavior and life history. Specialized shelters likely mitigate desiccation, predation, and microbial exposure. Extended phenology relative to temperate populations highlights climate-mediated resource availability, while variable host breadth suggests differential physiological adaptations among sympatric species. The evolutionary lag between fern antiquity and recent stathmopodid diversification indicates that colonizing this niche required overcoming substantial ecological and physiological barriers.

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Author contributions

HYL, LFX and YJW conceived and designed this study; JYW, HDY, LFX, collected the samples and observe the biology information; JYW, HDY, HYL, LFX and YJW wrote and revised the manuscript. All authors read and approved the final manuscript.

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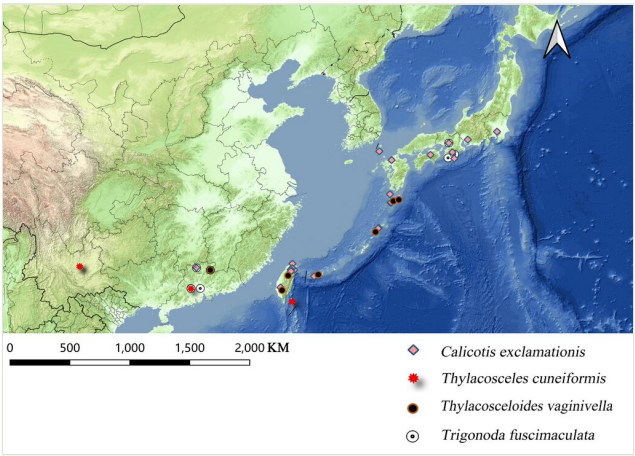

Figure 1.

Species distribution map.

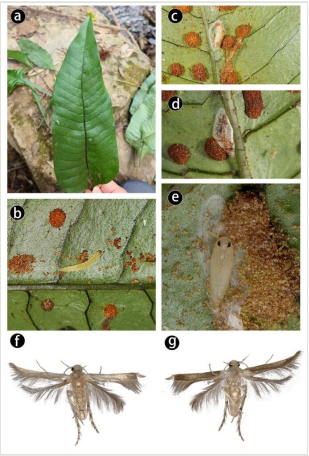

Figure 2.

a Field photograph of *Neolepisorus ovatus*; **b** Larva of *Calicotis exclamationis*; **c** Shelter constructed by larva of *Calicotis exclamationis*; **d** Cocoon of *Calicotis exclamationis*; **e** Pupa of *Calicotis exclamationis*; **f, g** Adult moth

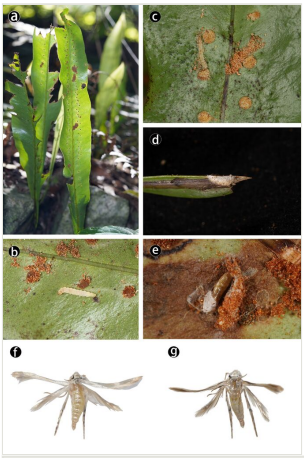

Figure 3.

a Field photograph of *Lepisorus fortunei*; **b** Larva of *Calicotis exclamationis*; **c** Shelter built by the larva of *Calicotis exclamationis*; **d** Cocoon of *Calicotis exclamationis*; **e** Pupa of *Calicotis exclamationis*; **f, g** Adult moth

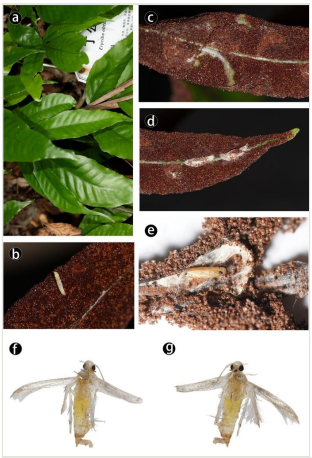

Figure 4.

a Field photograph of *Tectaria harlandii*; **b** Larva of *Thylacosceles cuneiformis*; **c** Shelter built by the larva of *Thylacosceles cuneiformis*; **d** Cocoon of *Thylacosceles cuneiformis*; **e** Pupa of *Thylacosceles cuneiformis*; **f, g** Adult moth

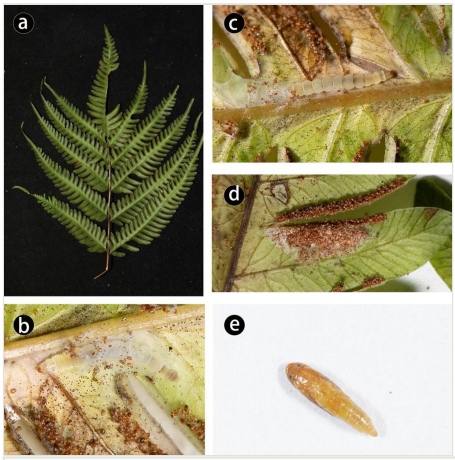

Figure 5.

a Field photograph of *Pteris fauriei*; **b** Larva of *Thylacosceloides vaginivella*; **c** Shelter built by the larva of *Thylacosceloides vaginivella*; **d** Cocoon of *Thylacosceloides vaginivella*; **e** Pupa of *Thylacosceloides vaginivella*

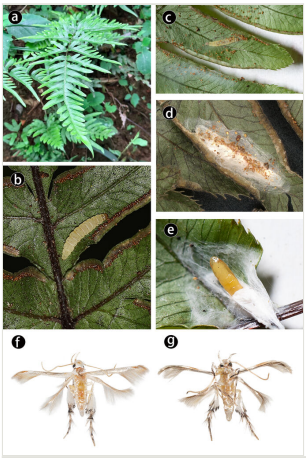

Figure 6.

a Field photograph of *Pteris semipinnata*; **b** Larva of *Trigonoda fuscimaculata*; **c** Shelter built by the larva of *Trigonoda fuscimaculata*; **d** Cocoon of *Trigonoda fuscimaculata*; **e** Pupa of *Trigonoda fuscimaculata;* **f, g** Adult moth

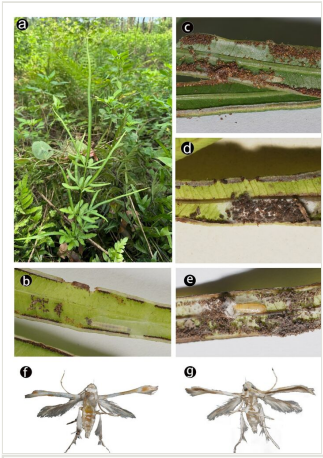

Figure 7.

a Field photograph of *Pteris ensiformis*; **b** Larva of *Trigonoda fuscimaculata*; **c** Shelter built by the larva of *Trigonoda fuscimaculata*; **d** Cocoon of *Trigonoda fuscimaculata*; **e** Pupa of *Trigonoda fuscimaculata;* **f, g** Adult moth

Supplementary material

Suppl. material 1: New records of fern-spore feeding moths and notes on their biology from Guangdong Province, China

Authors: Jingyun Wang, Haidong Yang, Yongjie Wang, Haoyu Liu, Lifang Xiao
Data type: occurrences
Brief description: The appendix S1 provides the global records (No. 259) of fern spore feeding insects, which including about 5 orders, 13 families, 27 genera, 87 species. The host fern including 16 families, 102 species, and 42 unidentified species.
Download file (29.60 kb)