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First Field Observation of Host Detection Behavior and a New Host Record of *Stenarella insidiator* (Smith, 1859) (Hymenoptera: Ichneumonidae: Cryptinae) in Taiwan

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ABSTRACT

Echolocation is commonly used by parasitoid wasps to detect hosts hidden under solid substrates. Female wasps produce vibrations with their modified antennal tips and receive echoes through the subgenual organ on their thickened fore tibia. This paper introduces novel biological data regarding *Stenarella insidiator* (Smith, 1859), an idiobiont ectoparasitoid wasp that parasitizes mud-nesting Aculeata. We also present the first field observation of the detection of three potter wasp species that are possible hosts, namely *Anterhynchium flavopunctatum formosicola*, *Orancistrocerus drewseni ingens*, and *Pararrhynchium ornatum sauteri*, along with a new host record of *Delta pyriforme*. Behavioral observation and morphological examination of the antennal tips and fore tibia of *S. insidiator* revealed that *S. insidiator* presumably uses echolocation for host detection, with modified antennal tips used for frequent tapping during oviposition. We also discovered that the fore tibia of female *S. insidiator* is not thickened, which is inconsistent with previous hypotheses.

Key words: host detection, echolocation, morphology, behavior, Ichneumonidae

Introduction

Osprynchotina (Hymenoptera: Ichneumonidae: Cryptinae: Cryptini) is a subtribe of Darwin wasps, which comprise a group of idiobiont ectoparasitoid wasps that attack hosts hidden under solitary substrates, particularly mud- and ground-nesting Aculeata (Kusigemati, 1987; Sawoniewicz and Wisniowski, 2007; Santos and Aguiar, 2013). Echolocation is commonly used for host detection in parasitoid wasps that parasitize hosts hidden under solitary substrates (Broad and Quicke, 2000; Vilhelmsen *et al.*, 2001). After a female wasp taps a substrate with its antennal tips, which have a modified structure called the antennal hammer, it

Fig. 1. Observation site with a bamboo scaffold on Hutou Mountain, Taoyuan City, Taiwan (approximately 25°00′37.08″ N, 121°19′57.17″ E). Photographed by the second author.

receives echoes through the subgenual organ on its thickened fore tibia, which enables it to detect potential hosts (Broad and Quicke, 2000; Vilhelmsen *et al.*, 2001; Laurenne *et al.*, 2009). According to a survey conducted by Broad and Quicke (2000), both an antennal hammer and a thickened fore tibia in female wasps significantly correlate with idiobiont lifestyle directed at hidden and immobile hosts. Laurenne *et al.* (2009) argued that the antennal hammer is a common trait in the tribe Cryptini.

Stenarella (Szépligeti, 1916) is a genus that comprises six described species that use wood-boring beetles and mud-nesting Aculeata as hosts (Meyer, 1934; Townes and Townes, 1973; Gauld, 1984). *Stenarella insidiator* (Smith, 1859) is widely distributed in oriental and eastern Palearctic regions and has been recorded in China, Taiwan, Cambodia, Indonesia, and the Philippines (Smith, 1859; Uchida, 1930; Baltazar, 1966; Momoi, 1968; Chao, 1973). *Sceliphron madraspatanum* (Fabricius, 1781) [黃柄壁泥蜂] (Hymenoptera: Sphecidae), also known as the mud dauber, is the only host recorded for *S. insidiator* (Momoi, 1968). No further biological information regarding *S. insidiator*—including its hosts, host detection behavior, and morphologies associated with host detection—is available.

In this paper, we introduce novel biological data regarding *S. insidiator* and present a new host record of the potter wasp *Delta pyriforme* (Fabricius, 1775) [黃胸錐腹蜾蠃] (Hymenoptera: Vespidae: Eumeninae). We also present the first field observation of its host detection behavior on three mud-nesting potter wasp species: *Anterhynchium flavopunctatum formosicola* (Schulthess, 1934) [黃緣前喙蜾蠃], *Orancistrocerus drewseni ingens* (Schulthess, 1934) [赭褐短腰蜾蠃], and *Pararrhynchium ornatum sauteri* (Schulthess, 1934) [赭褐旁喙蜾蠃]. The morphological characteristics hypothetically associated with the host detection of *S. insidiator*, such as their antennal tips and the thickness of their fore tibia, were examined.

Materials and Methods

Field observations and rearing

All observations were made by the second author and recorded using a Panasonic DMC-GX85 camera (Panasonic, Osaka, Japan) equipped with an Olympus M. Zuiko Digital ED 60-mm f/2.8 macro lens (Olympus, Tokyo, Japan) while the author was on a bamboo scaffold on Hutou Mountain [虎頭山], Taoyuan City, Taiwan (approximately 25°00’ 37.08” N, 121°19’ 57.17” E; Fig. 1). On June 5, 2020; May 2 and 14, 2021; and July 3, 2021; the second author recorded videos and took field notes to determine the host detection behavior of *S. insidiator*. Species constructing mud nests were identified either

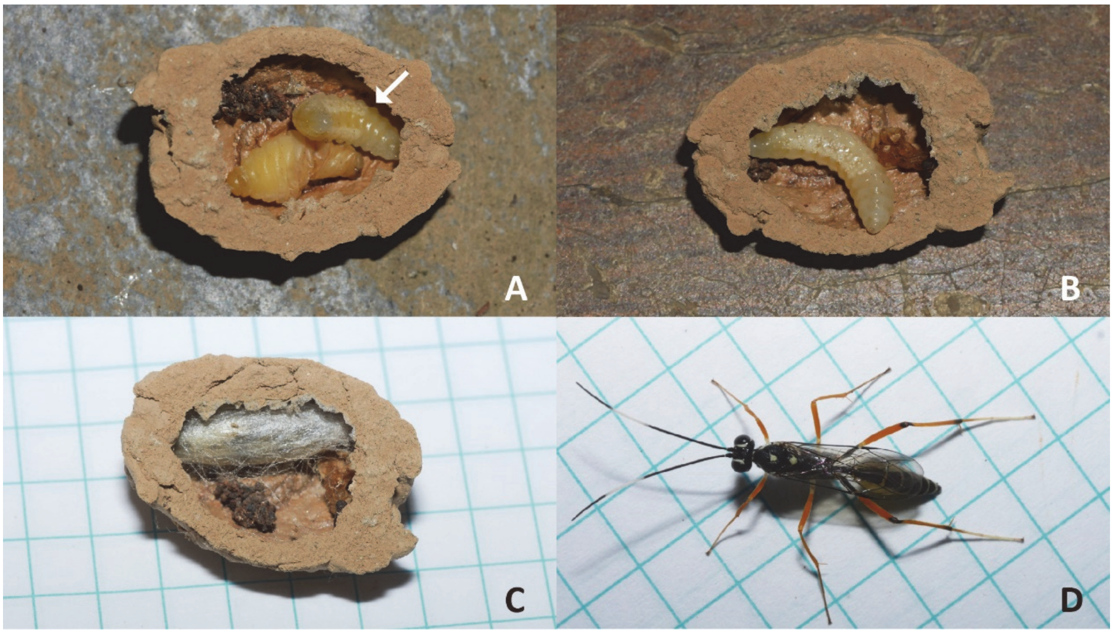

Fig. 2. (A) Final-instar larva of *Stenarella insidiator* (indicated by a white arrow) with the abnormal larva of *Delta pyriforme*; (B) *ditto*, with the dead host larva removed; (C) *ditto*, a cocoon; (D) *ditto*, the male adult. Photographed by the second author.

through their nest morphology (e.g., *O. drewseni ingens*) or through recent observations of adult wasps building or occupying nests. On November 5, 2020, the second author collected one mud nest of *D. pyriforme* for observation.

Morphological examination and analysis

Both newly collected specimens and older specimens of *S. insidiator* deposited at the Taiwan Agricultural Research Institute (TARI), Taichung, Taiwan, were examined. These newly collected specimens were deposited at the National Museum of Natural Science (NMNS), Taichung, Taiwan.

The left terminal flagellomeres and fore legs of two *S. insidiator* specimens (one female and one male) were preserved in 75% ethyl alcohol for ultrastructural examination. The morphological terminology of the antennal sensilla follows Snodgrass (1926). After the samples had been treated with sequential dehydration using 70% to 100% acetone, critical point drying was conducted using a Polaron Z-3100 critical point dryer (Quorum Technologies, East Sussex, UK) to replace 100% acetone with CO_2. Subsequently, the dried samples were coated with gold using an SPI Module Sputter Coater (SPI, West Chester, PA, USA). Finally, the ultrastructure of the samples was observed using a JEOL JSM-5600 scanning electron microscope (JEOL, Tokyo, Japan). All images were edited using Adobe Photoshop and Illustrator CC (Adobe, San Jose, CA, USA).

The length and width of the fore tibia were measured using Fiji (Schindelin *et al.*, 2012) and expressed as a ratio of length to width to represent the thickness of the fore tibia. Descriptive statistical analysis was conducted using R software version 4.2.1 (R Foundation for Statistical Computing, Vienna, Austria) to compare the thicknesses of the fore tibia in male and female *S. insidiator*.

Results

New host record of *S. insidiator*

The collected mud nest (collected on November 5, 2020) contained two late-instar wasp larvae: an abnormal larva and a live larva (Fig. 2A). The abnormal larva, which was found dead and had turned black, was subsequently removed on November 7, 2020. The live larva formed a white silk cocoon 1 day later (Fig. 2B). The pupa in the cocoon darkened after 147 days, that is, on April 4, 2021 (Fig. 2C). One male *S. insidiator* eclosed after 5 days (Fig. 2D). The total recorded pupal stage of *S. insidiator* was approximately 153 days.

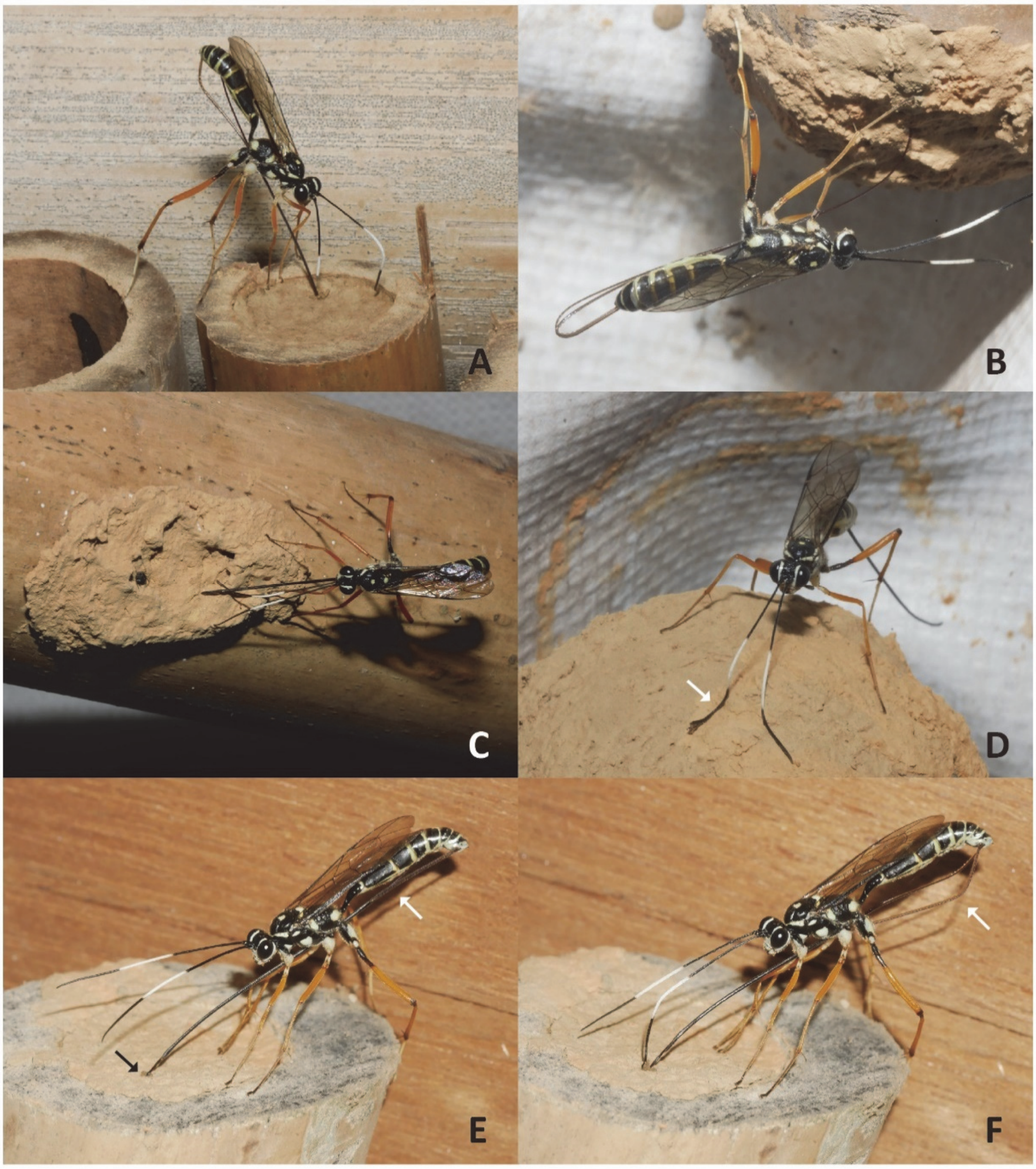

Fig. 3. Observations of the host detection behavior of *Stenarella insidiator* on mud nests of (A) *Anterhynchium flavopunctatum formosicola* (July 3, 2021); (B) *Orancistrocerus drewseni ingens* (June 5, 2020); and (C) *Pararrhynchium ornatum sauteri* (May 2, 2021). (D) Tapping behavior with a downward-curved apical flagellum (indicated by a white arrow). (E) Initial phase of oviposition with a straight ovipositor sheath (indicated by a white arrow). The mud nest wall was moistened around the ovipositor (indicated by a black arrow). (F) As the wasp drilled deeper, the ovipositor sheath bent lengthwise, supporting the ovipositor (indicated by a white arrow). Photographed by the second author.

Field observations of the host detection behavior of *S. insidiator*

During our observations, we discovered that female *S. insidiator* detected and oviposited on the mud nests of three eumenine species: *A. flavopunctatum formosicola* (Fig. 3A), *O. drewseni ingens* (Fig. 3B), and *P. ornatum sauteri* (Fig. 3C). Table 1 presents detailed information of all observations.

The host detection process of the female *S. insidiator* spanned 7–11 minutes. The female wasp landed on the mud nest of potential hosts and started its search process by tapping the nest surface with its antenna while walking over it. The wasp's antenna was typically curved downward during the search process, with the apical black part slightly turned upward. The wasp used both its apical black part and antennal tips to tap the nest surface (Fig. 3D). Once the oviposition process had started, the antenna became less curved, and the wasp primarily used its antennal tips for tapping (Fig.

Table 1. Details on the host detection behavior of *S. insidiator*.

Date	Target	Description
June 5, 2020	Mud nest of *O. drewseni ingens*	A female wasp detected and oviposited on a mud nest of *O. drewseni ingens* in a bamboo tube. The process of oviposition lasted approximately 7 minutes.
May 2, 2021	Mud nest of *P. ornatum sauteri*	A female wasp detected and oviposited on a mud nest of *P. ornatum sauteri* in a bamboo tube. The process of oviposition lasted approximately 7 minutes.
May 14, 2021	Mud nest of *O. drewseni ingens*	A female wasp detected and oviposited on a mud nest of *O. drewseni ingens* in a bamboo tube. The process of oviposition was interrupted and lasted approximately 8 minutes.
July 3, 2021	Mud nest of *A. flavopunctatum formosicola*	No detailed information was provided by the second author.

3A, C). Once a suitable position had been detected, the wasp moved its metasoma upward and inserted its ovipositor into the hard mud nest wall. During the initial drilling phase, the wasp moistened the nest wall around the ovipositor with certain secretions (Fig. 3E, F). The ovipositor sheath remained straight (Fig. 3E). As the ovipositor drilled deeper, the sheath bent lengthwise, providing support for the ovipositor (Fig. 3F). Throughout the oviposition process, the wasp continued tapping the nest with its antennal tips.

Morphologies associated with host detection for *S. insidiator*

This study examined six female and two male specimens, including five newly collected specimens and three from museum collections. The following is a list of these specimens.

TAIWAN. TAOYUAN: Taoyuan Dist., Hutou Mountain [虎頭山], approx. 25°00’ 37.08” N, 121°19’ 57.17” E, 1♂, 5. XI. 2020, Mei-Ling Lo leg., reared from the mud nest of *D. pyriforme*, eclosed on 9-IV-2021. (NMNS); Taoyuan Dist., Hutou Mountain [虎頭山], approx. 25°00’ 37.08” N, 121°19’ 57.17” E, 1♀, 2. V. 2021, Mei-Ling Lo leg. (NMNS); Fuxing Dist., Dongyanshan National Forest Recreation Area [東眼山森林遊樂區], 1♀, 9. VIII. 2020, Po-Cheng Huang leg. (NMNS); TAIPEI: Da'an Dist., National Taiwan University, Agricultural Insect Building [國立臺灣大學農業昆蟲館], 1♀, 1. XII. 2021, Hung-Ju Huang leg. (NMNS); Wenshan Dist., Mt. Maokong [貓空山], 1♂, 18. V. 2023, Sheng-Jie Hu leg. (NMNS); Wulai [烏來], 1♀, 7-8. XI. 1953, S. C. Chiu leg. (TARI); YILAN: Hatonozawa, Taiheizan [鳩之澤, 太平山], 1♀, 15. VII. 1938, J. Sonan leg. (TARI); Shonan-o (Rato) [羅東], 1♀, 11. XII. 1930, Y. Yamazaki leg. (TARI).

The last flagellomere of female *S. insidiator* was laterally depressed, with a cluster of thickened, apically truncated, and spoon-shaped *sensilla trichodea* at its apex (Fig. 4A). Although the male and female wasps were highly similar, the male wasps had lesser modified apical sensilla than did the female wasps (Fig. 4B). These results indicated that both male and female *S. insidiator* had modified antennal tip structures.

The mean length-to-width ratio of the fore tibia was 8.04 (SD= 0.19, n= 6) for the female and 6.74 (SD= 0.28, n= 2) for the male. Because the mean length-to-width ratio of the fore tibia of the male wasps was smaller than that of the female wasps and was outside the 95% confidence interval of the female wasps' ratio ([7.841007, 8.22566]), it suggests that the fore tibia of the male may be relatively thicker than that of the female (Fig. 4E, F).

Discussion

Only one mud dauber species, *Sceliphron madraspatanum* (Fabricius 1781), has been

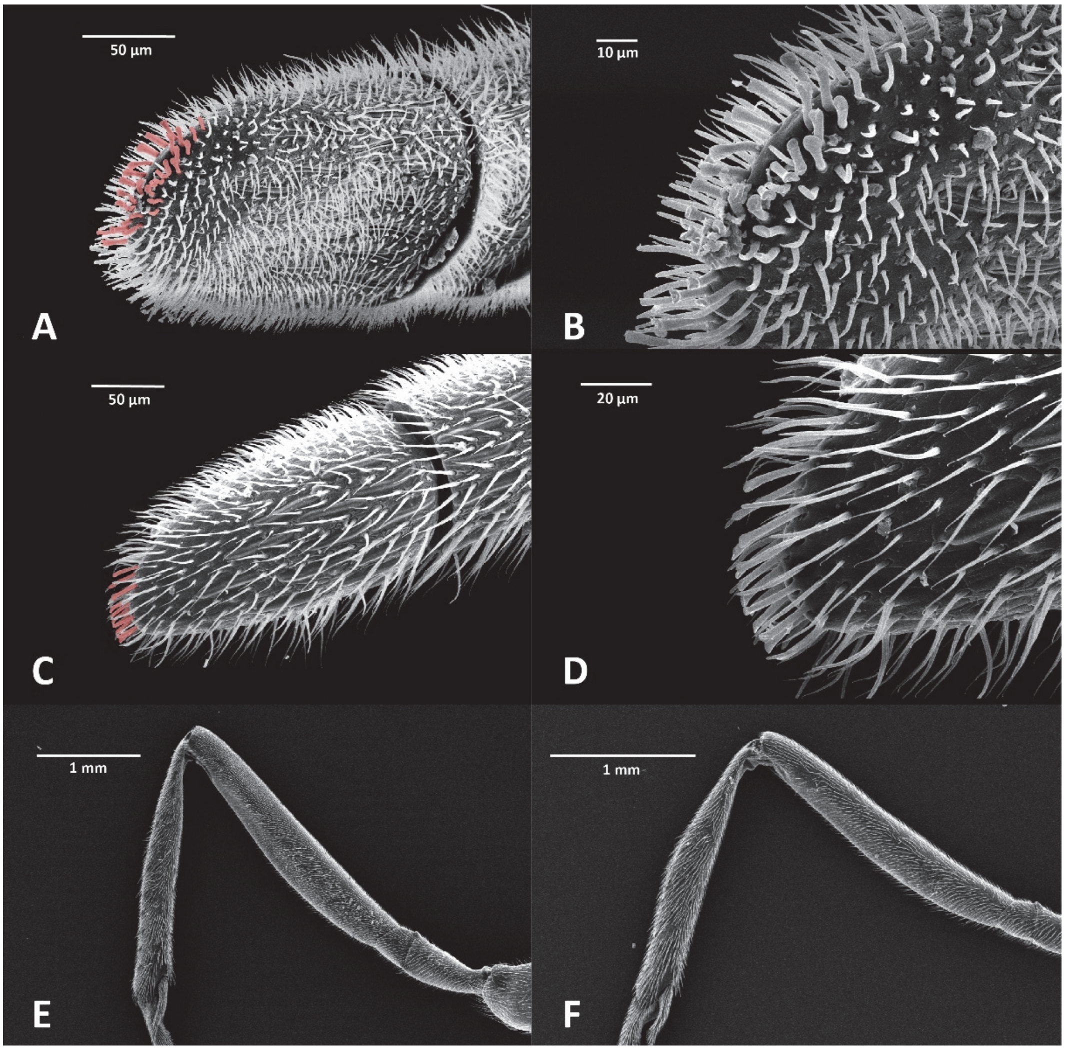

Fig. 4. Antennal hammer and fore tibia of *Stenarella insidiator*. (A) Antennal tip of a female wasp (the red marking indicates the modified sensilla), with a cluster of thickened, apically truncated, and spoon-shaped *sensilla trichodea*. (B) Close-up view of the antennal tip of a female wasp. (C) Antennal tip of a male wasp (the red marking indicates the modified sensilla). (D) Close-up view of the antennal tip of a male wasp. (E) Fore tibia of a female wasp. (F) Fore tibia of a male wasp. Photographed by Wei-Chun Chien.

reported as being the host of *S. insidiator*; this finding was based on only one specimen reared from the mud nest of *Sc. madraspatanum* and was not obtained through direct observation (Momoi, 1968). In this study, we obtained new information regarding the host record of *D. pyriforme*, expanding the host range of *S. insidiator* from Sphecidae to Vespidae. We discovered that the larvae of *S. insidiator* consume those of *D. pyriforme*, as evidenced by an unusually soft *D. pyriforme* larva (Fig. 1A), presumably killed by the larva of *S. insidiator*. According to our observations of host detection behavior in *A. flavopunctatum formosicola*, *O. drewseni ingens*, and *P. ornatum sauteri*, *S. insidiator* may have a wider host range and may be able to use any mud-nesting Aculeata as a host. Nevertheless, we were unable to confirm whether the three species mentioned above serve as hosts for *S. insidiator* because of the lack of direct evidence of *S. insidiator* consuming these potter wasps. Given that the currently available information does not accurately indicate the true host range of *S. insidiator*, additional intensive sampling, and collaboration with citizen scientists are required to reveal the complex biology of *S. insidiator*.

Laurenne *et al.* (2009) classified the antennal tip morphology of Cryptini into six classes in accordance with the degree of modification. According to their classification, the antennal tip of *S. insidiator* is defined as type 2, which refers to a cluster of apically modified structures. Although the antennal tip morphology of *S. insidiator* is less modified than that of other ichneumonids using similar types of host (e.g., Broad and Quick, 2000: 2404, Fig. 1), this species still has certain structures defined as antennal hammers. As Laurenne *et al*. (2009) reported in another unidentified *Stenarella* species, these results indicate that the morphology of the antennal tip may be conserved within the genus. Compared with female *S. insidiator*, male *S. insidiator* have less strongly modified antennal tip morphology. Because modified structures are also observed in certain members of Cryptini, the modified structures observed in male wasps may be somehow controlled by homologous genes and not directly related to the hammer-like structures observed in female wasps (Laurenne *et al.*, 2006; Laurenne *et al.*, 2009).

Although we were unable to conduct a statistical test because of the limited number of male samples, we discovered that the length-to-width ratio of the fore tibia in the male wasps was lower than that in the female wasps and was outside the 95% confidence interval of the female wasps' ratio, which may account for the relatively thicker fore tibia in male wasps. These findings are inconsistent with a previous hypothesis indicating that the fore tibia of female wasps is typically enlarged as a result of the presence of a more developed subgenual organ (Broad and Quicke, 2000; Vilhelmsen *et al.*, 2001; Laurenne *et al.*, 2009). Therefore, the thickness of the foretibia may not be a reliable indicator of subgenual organ development. To support the hypothesis mentioned above, the subgenual organ of female *S. insidiator* should be further developed as those of other ichneumonids that use similar host types.

The host detection behavior of Cryptini ichneumonids that parasitize hosts hidden under solid substrates has rarely been reported in *Acroricnus seductor* (Scopoli, 1786), *Buathra tarsoleuca* (Schrank, 1781), and *Gabunia* sp. aff. *togoensis* (Casiraghi *et al.*, 2001; Quicke *et al.*, 2003; Polidori *et al.*, 2011). Our observations regarding the behavior of *S. insidiator* are similar to those of previous studies; this behavior comprised frequent tapping and reciprocation, followed by oviposition after the detection of suitable sites. Frequent tapping, an essential component of host detection that produces vibrational sound, occurs in almost the entire process of host detection and oviposition in *S. insidiator*. Although the subgenual organ may not be well developed in this species, the combination of antennal hammer utilization and frequent tapping during host detection suggests that *S. insidiator* is capable of using echolocation for host detection.

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中華窄姬蜂（膜翅目：姬蜂科：秘姬蜂亞科）寄主偵測行為之首次野外觀察暨一新寄主紀錄

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摘　　要

回聲定位是寄生蜂在偵測隱蔽於固體介質下寄主時常用的策略。這類寄生蜂的雌蜂利用特化之觸角末端來敲擊介質產生振動，再由位於膨大的前足脛節之膝下器接收回聲以定位寄主。中華窄姬蜂 (*Stenarella insidiator* (Smith, 1859)) 是一種以築泥巢的有螫蜂為寄主的抑性外擬寄生蜂。本研究提供中華窄姬蜂生物學之新資訊，包含其於黃緣前喙蜾蠃、赭褐短腰蜾蠃、及赭褐旁喙蜾蠃之泥巢外進行寄主偵測行為的野外觀察紀錄，及黃胸錐腹蜾蠃的新寄主紀錄。藉由對中華窄姬蜂與寄主偵測相關之形態構造—觸角末端及前足脛節的形態檢視以及行為觀察，我們根據其雌蜂在產卵時對寄主泥巢的頻繁觸角碰觸，且其觸角末端的特化構造，推測中華窄姬蜂可能使用回聲定位作為寄主偵測的策略。此外，我們亦發現中華窄姬蜂雌蟲前足脛節並未膨大於雄蟲，可能並不吻合過往的假說。

關鍵詞：寄主偵測、回聲定位、形態學、行為、姬蜂科