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NESTING BIOLOGY OF *Zethus dolosus* Bingham, 1897 (Hymenoptera: Vespidae: Eumeninae) IN TRAP NESTS FROM NORTHERN VIETNAM

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ABSTRACT

The nesting biology of *Zethus dolosus* Bingham, 1897 was investigated in northern Vietnam using trap nests. The females selected nest cavities with diameters ranging from 4 to 11 mm. Nests consisted of a linear series of one to nine brood cells, provisioned with caterpillars, probably *Biston* spp. (Lepidoptera: Geometridae). Eggs were attached to the cell ceiling by a thin thread. Nesting activity occurred from mid-May to late October, suggesting a multivoltine life cycle, likely with four generations per year, the last of which overwintered in the prepupal stage. The sex ratio is male-biased. Only 46.3% of the provisioned cells produced adult offspring; the others were either parasitized by three parasitoid species or failed during development for unknown reasons. These findings provide the first detailed account of the nesting biology and life-history traits of *Z. dolosus* in Vietnam.

Keywords: Bionomics, life history, nest structure, prey, sex ratio, symbionts, *Zethus dolosus*.

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INTRODUCTION

The genus *Zethus* (Fabricius, 1804) is the largest within Vespidae, with nearly 300 species currently recognized (Lopes & Melo, 2025). The genus is widely distributed throughout the New World, Ethiopian, and Oriental tropics (Bohart & Stange, 1965; Tan et al., 2018; Nugroho et al., 2020). A total of 26 species occur in the Oriental region, of which eight species have been recorded in Vietnam: *Zethus dolosus* Bingham; *Zethus nigerrimus* Gusenleitner; *Zethus malayanus* Gusenleitner; *Zethus trimaculatus* Cameron; *Zethus tumidus* Nguyen & Capenter; *Zethus tansoneus* Nguyen & Capenter; *Zethus angulatus* Nguyen & Capenter; and *Zethus propodeus* Nguyen & Capenter (Nguyen & Capenter, 2016).

Despite the diversity and wide distribution of *Zethus*, substantial gaps remain in our knowledge of its behaviour and biology. Bohart & Stange (1965) reviewed the available literature on the biology of 15 of the 189 New World species described at that time, and subsequent studies have provided additional bionomic data for many species in the genus (Stange, 1969; Calmbacher, 1977; Cooper, 1989; Krombein, 1991; Garcete-Barrett & Klassen Dück, 2010; Barthélémy, 2012; Cooper, 2014, 2016; Lopes et al., 2019, 2021; Lopes, 2023; Jacques et al., 2024; Lopes & Melo, 2025). Species of *Zethus* are predominantly solitary, although a few exhibit a degree of primitively social behaviour; all are predators of caterpillars.

Most *Zenthus* use pre-existing cavities for nesting, whereas some excavate burrows in soil or dead wood; all are mass provisioners. For example, females of *Z. angulatus* Nguyen & Carpenter, *Zethus pilosus* Zavattari, and *Zethus plaumanni* Bohart & Stange nest in trap nests (Barthélémy, 2012; Lopes et al., 2019, 2021). In contrast, *Zethus iheringi* Zavattari and *Zethus porteri* Stange nest into the ground (Cooper, 1989; Garcete-Barrett & Klassen Dück, 2010), whereas *Zethus otomitus* Saussure excavates burrows in dead wood (Calmbacher, 1977).

Other species construct the original nests from masticated plant material mixed with saliva. This nest type is typically found in the subgenus *Zethoides* and may be produced by cooperating females exhibiting subsocial behaviour, as reported for *Zethus miniatus* Saussure (Bohart & Stange, 1965; Jacques et al., 2024); *Zethus nodosus* Zavattari (Lopes, 2023); *Zethus notatus* Fox, *Zethus thoracicus* Fox, and *Zethus schadei* Bohart & Stange (Lopes & Melo, 2025). Females jointly construct aerial nests composed of clusters of several cells with progressive provisioning, but each female provisions only her own offspring (Bohart & Stange, 1965; Lopes & Melo, 2025).

Herein, the nesting biology of *Z. dolosus* Bingham is reported for the first time, based on 32 nests collected in northern Vietnam. Details of nest structure, immature development, and associated symbionts, including parasites, are described, and aspects of the life history are also discussed.

MATERIALS AND METHODS

As a part of the study on the fauna and biology of eumenine wasps in northern Vietnam, trap nests were set from 2013 to 2025 (except for 2018, 2021–2023) in the following localities (place names are given as they were before the administrative merger in July 2025): Me Linh Station for Biodiversity of the Institute of Ecology and Biological Resources (IEBR) (now the Institute of Biology), Vinh Phuc province, 21°23’N, 105°42’E, 50 m (2013–2015, 2017 and 2020); two sites of different elevations at Tam Dao, Vinh Phuc province, 21°26.5’N, 105°37’E, 400 m and 21°27.5’N, 105°38.5’E, 960 m (2013–2014); Phu Luong District, Thai Nguyen province, 21°47’N, 105°45.5’E, 73 m (2014, 2016, 2019 and 2020); Dai Tu District, Thai Nguyen province, 21°29.9’N, 105°39.9’E, 156 m (2025); Vo Nhai District, Thai Nguyen province, 21°49.2’N, 105°58.3’E, 67 m (2025); Red River Delta, Long Bien, Ha Noi City, 21°03’N 105°51’E, 10 m (2013, 2014 and 2016); Chuong My, Ha Noi City, 20°48.7’N, 105°38’E, 20 m (2019 and 2024); Luong Son, Hoa Binh province,

20°46.3'N, 105°37.3'E, 50 m (2024); Kim Boi, Hoa Binh province, 20°38.7'N, 105°32.7'E, 95 m (2019); Nghia Hung, Nam Dinh province, 20°4.9'N 106°11.8'E, 1 m (2014); and Dong Hung, Thai Binh province, 20°31.1'N 106°19.6'E, 2 m (2014). These areas have seasonally variable temperature and rainfall. The climate is cold and dry in winter (November to January). At the end of winter, there is a long period of drizzle (February to March), whereas summer is hot, humid, and rainy (April to October) (Sterling et al., 2006). Nests of *Z. dolosus* were obtained only at Me Linh (2013, 2014, and 2020), Phu Luong (2020), Dai Tu (2025), and Chuong My (2024).

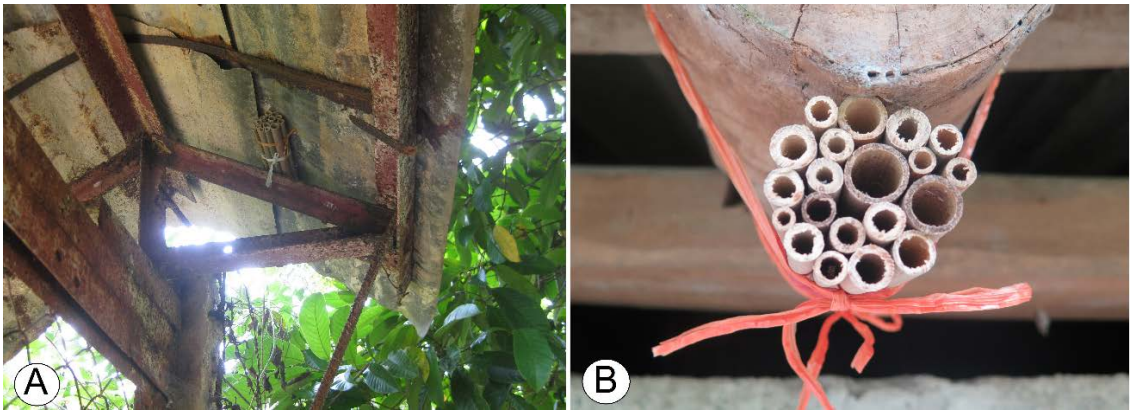

Figure 1. Trap nests placed under eaves at Me Linh in 2014 (A) and at Dai Tu in 2025 (B)

Trap nests made of stems of bamboo (*Bambusa* sp.) and reed (*Phragmites* sp.) (130–550 mm long, 3–3 with 15–35 stems. The bundles were placed nearly horizontally under eaves, in wire-mesh fences, or hung from tree branches at a height of 0.8–3.5 m (Fig. 1). They were set from late spring (early April) to mid-winter (late November) and checked once every one to four weeks.

Trap nests with a closing plug were taken to the IEBR (now the Institute of Biology) in Hanoi for further observation. They were kept at room temperature (14–32 °C) and opened by gently splitting longitudinally into two halves to examine nest structure and contents (immatures of *Z. dolosus*, prey, and symbionts), then reclosed by joining the halves together. Nests containing eggs were checked twice daily, whereas nests containing later immature stages were checked once daily. After completely consuming their prey, most fifth-instar larvae were transferred to a transparent glass tube (130 mm long, 12 mm inner diameter) plugged with cotton for further observation; the remaining individuals were kept in their nests.

Terms of nest structure follow Krombein (1967), with minor modifications after Dang & Fateryga (2021). Measurements of nest characters were made using Vernier calipers.

The developmental stages (eggs, larvae, prepupae, and pupae) of immatures in provisioned cells were examined under a Nikon SMZ 800N stereomicroscope. Prey items were identified and counted, and the emergence of symbionts, including parasitic wasps, was also recorded.

RESULTS AND DISCUSSION

Z. dolosus nested in trap nests placed around human dwellings adjacent to mixed forest habitats. Nests were collected from Me Linh (Vinh Phuc), Phu Luong and Dai Tu (Thai Nguyen), and Chuong My (Ha Noi), with 20, 6, and 6 nests obtained from each locality, respectively. A total of 32 nests containing 80 cells of this species were collected, with nesting activity occurring between May and

October. Of the 32 nests examined, 23 were completed, and nine were under-provisioned.

Nest structure

Females selected trap nests ranging from 63 to 423 mm in length (n = 32), and their inner diameters varied from 4 to 11 mm, with nearly 70% between 5 and 8 mm. In Hong Kong, *Z. angulatus* nested in borings of 5.5 to 13 cm in diameter (Barthélémy, 2012; Yeh & Barthélémy, 2023), whereas Lopes et al. (2021) reported that *Z. plaumanni* preferred smaller cavities: females used trap nests with entrance diameters of 0.5 and 0.7 cm but did not occupy those with diameters of 1.0 or 1.3 cm. Likewise, females of *Z. pilosus* exclusively occupied wooden blocks with entrance diameters of 7.0 and 10.0 mm (Lopes et al., 2019).

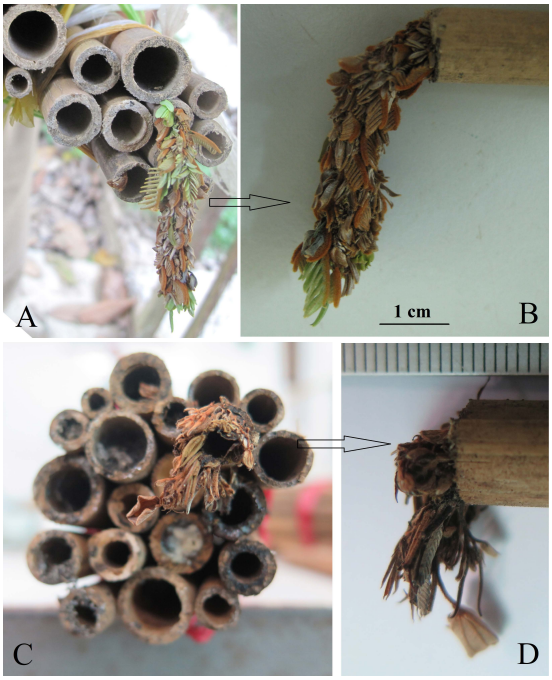

Figure 2. Nest-entrance turrets of *Zethus dolosus* were recorded at Me Linh (A, B) and Dai Tu (C, D)

A distinctive feature of *Z. dolosus* nests, compared with those of other Eumeninae species, is the presence of a long entrance turret with the opening directed towards the ground. The female constructed the entrance turret using young leaves of two undetermined plant species (Figs. 2A, D). The leaves were attached to one another with plant resin (or gum). The entrance turrets were 3.5 to 4.0 mm in diameter (n = 32), and their length reached up to 4.2 cm. The leaves forming the turret dried after a few days. Females crawled through the dried turrets to enter the nest, which sometimes resulted in breakage. Remnants of broken turrets were observed in eight of the 32 collected nests.

Similar entrance turrets have been reported in the nests of some other *Zethus* species. For example, in *Z. angulatus* and *Z. ceylonicus*, the turrets are constructed from plant stems bearing small leaves (Krombein, 1991; Barthélémy, 2012), whereas in *Z. iheringhi* the turret is made of mud (Garcete-Barrett & Klassen Dück, 2010). Each completed nest comprised one to nine provisioned cells (3.04 ± 0.40 mm; n = 23), with 17.4%, 30.4%, 21.7%, 17.4%, 8.7%, and 4.3% of all nests having one, two, three, four, six, and nine cells, respectively (Fig. 3).

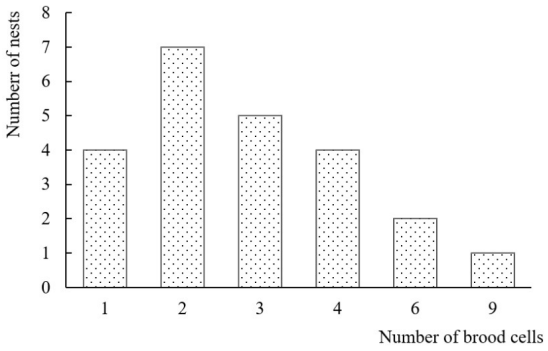

Figure 3. Frequency distribution of numbers of brood cells in *Zethus dolosus* nests

The length of a provisioned cell varied from 12 to 58 mm (24 ± 1.2 mm; n = 73). However, nearly 70% of examined cells (48/73) were from 15 to 24 mm long, with a median of 20 mm. There was no significant difference in the length between male and female cells (Mann–Whitney U = 198; P = 0.2). Female cells were from 15 to 58 mm long (28.1 ± 3.5 mm, n = 15), whereas male cells

were from 13 to 37 mm long (22.0 ± 1.3 mm, n = 21) (Fig. 4).

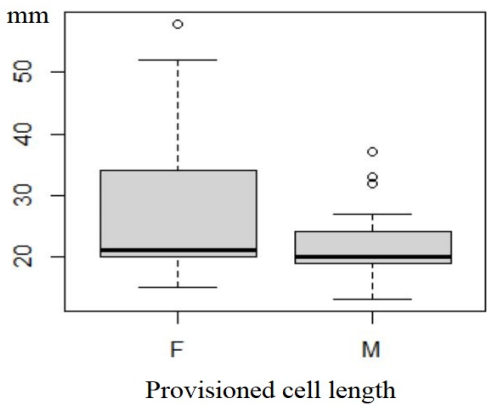

Figure 4. Frequency distribution of provisioned cells of *Zethus dolosus* by length

In 28 nests, the first provisioned cell was constructed directly in the inner-most part of the trap nest, without a preliminary plug (Fig. 5A). In the remaining four nests, a preliminary plug was present, and the length of the empty space varied from 0 to 53 mm. Notably, all four of these nests had small holes at the end of the trap nest (Fig. 5D). This suggests that females carefully inspected the trap nest and selected a nesting strategy that improved offspring protection from natural enemies. All 23 completed nests had a vestibular cell, the length of which was highly variable, ranging from 24 to 390 mm (115.3 ± 21.7 mm, n = 23), and five of the 23 contained intercalary cells. These intercalary cells occurred between provisioned cells and ranged from 7 to 48 mm in length (13.1 ± 3.9 mm, n = 10).

Figure 5. Overall nest architecture of *Zethus dolosus* (A, D). PP: Preliminary plug; Pa: Partition; PC: Provisioned cell; IC: Intercalary cell; VC: Vestibular cell; PCl: Partition closing (scale bar = 1 cm)

The cell partitions were constructed from the same material as the entrance turret. Females used chewed young leaves mixed with resin to build the cell partitions. The partitions had a smooth, concave outer surface and a rough inner surface; in some cases, fragments of larger, less macerated leaves adhered to the inner faces (Fig. 5A), or the partitions consisted of two to three distinct layers (Fig. 5C). The female also constructed a closing partition at the nest entrance, with a small central orifice sufficient for passage.

This partition was composed of the same material as the cell partitions and remained open after nest construction was completed.

Similar construction materials have been reported in other *Zethus* species. Barthélémy (2012) and Lopes et al. (2021) recorded that the cell partitions of *Z. angulatus* and *Z. plaumanni* were made of plant fibers mixed with a small amount of resin, whereas in *Z. pilosus* the partitions were composed of macerated vegetable fibers mixed with resin, mud, grains of sand, and fragments of other insects (Lopes et al., 2019). A closing partition with a small central orifice has also been documented in the nests of *Z. pilosus* and *Z. plaumanni* (Lopes et al., 2019, 2021).

Prey

Z. dolosus can be considered an effective predator of pests in northern Vietnam, similar to *Rhynchium brunneum* (Dang & Nguyen, 2019) and *Delta esuriens* (Pham et al., 2024). The provisioned cells were mass-provisioned with 7–19 lepidopteran larvae (11.7 ± 0.5 mm, n = 24). The number of caterpillars per cell appeared to depend on prey size or prey type. The caterpillars were lightly paralysed and able to defecate. All prey belonged to the family Geometridae, probably *Biston* spp. (Fig. 6).

Previous studies have also shown that *Zethus* species prey on lepidopteran larvae. Caterpillars found in the nests of *Z. angulatus* in Hong Kong were mainly from Geometridae, with a single prey item from Noctuidae, probably *Spodoptera* sp. (Barthélémy, 2012). Larvae of the superfamily Gelechioidea have been recorded in the cells of *Z. nigricornis*, *Z. dicomboda*, and *Z. hilarianus* and lepidopteran larvae of the family Pyraustidae were found in the cells of *Zethus laevinodus* (Bohart & Stange, 1965).

Figure 6. Prey of *Zethus dolosus*

Life history and sex ratio

The eggs were creamy, slightly arched, and suspended from the upper wall near the inner end of the cell by a short thread. Eggs were observed in two cells collected at Me Linh in May 2013 (ML-13-034 and ML-13-071). One provisioned cell contained 19 caterpillars; the egg measured 2.7 mm in length and 0.8 mm in diameter, and hatched one day after collection. Another egg was found in a newly constructed cell without prey; this egg measured 2.8 mm in length and 0.8 mm in diameter and hatched on the third day after collection. These observations indicate that the egg stage lasted approximately two to three days.

During the first to fourth larval instars, larvae fed by sucking fluids from caterpillar prey after biting a hole in the prey's body (Figs. 7A, B). Only in the fifth instar, the larvae consumed the solid parts of the prey, including the head capsules and the egg shell (Fig. 7C). The larva first produced a varnish-like secretion that coated the inner surface of the partition and cell walls, then spun a cream-colored cocoon. Cocoon thickness varied among cells (Fig. 5A). The cocoon usually had

a width equal to the inner diameter of the cell (Fig. 5B). It was always positioned at the base of the provisioned cell, and the pre-pupal larva consistently oriented its head toward the open end of the nest (Fig. 5). Prey feces and prey remains were always located outside the cocoon. The larval stage lasted six to ten days (8.38 ± 0.50 days, n = 8).

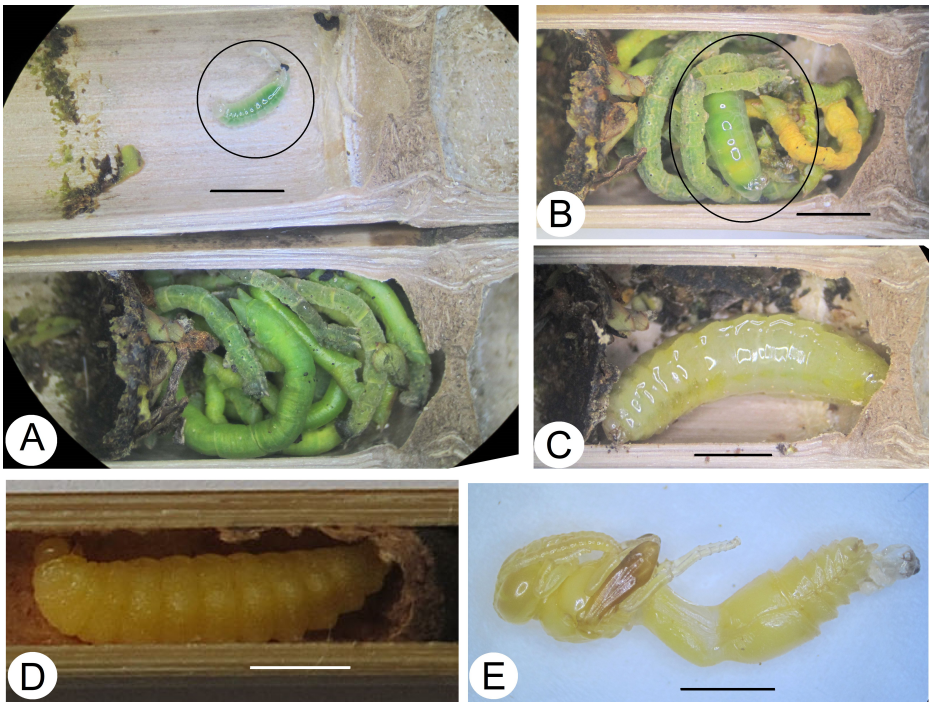

Figure 7. Nest of *Zethus dolosus*: second instar larva (A), fourth instar larva sucking prey (B); fifth instar larva (C); overwintering prepupa (D); pupa (E) (scale bar = 0.5 cm)

Prepupae observed in mid-September 2013 (at Me Linh) and mid-October 2020 (at Me Linh and Phu Luong) overwintered and pupated the following spring (mid-April 2014 and early April 2021, respectively). The prepupal period, therefore ranged from 22 to 28 weeks.

The pupal stage lasted from seven to 17 days. In non-dormant prepupae, their pupal periods varied from nine to 14 days (11.78 ± 0.46 days, n = 9) in females and from 8 to 12 days (10.38 ± 0.5 days, n = 8) in males. In dormant prepupae, the pupal period was from 14 to 17 days (15.33 ± 0.88 days, n = 3) in females and from seven to 15 days (12.1 ± 0.81 days, n = 10) in males.

Teneral adults remained in their cells for two to three days, during which the wings lost their callow appearance. The developmental period from eggs to adults in non-dormant individuals was approximately one month. Nesting activity was observed from mid-May to late October, suggesting at least four generations per year in northern Vietnam, with the last generation overwintering in the prepupal stage. The same pattern has been reported for *Rhynchium brunneum* in northern Vietnam (Dang & Nguyen, 2019). Overwintering at the prepupal stage has also been reported in *Z. angulatus* (Barthélémy, 2012), whereas *Z. pilosus* and *Z. plaumanni* overwinter at the adult stage (Lopes et al., 2019, 2021).

Adult females sheltered in their nests at night and during rainy days, as also observed for Neotropical *Zethus* species (Bohart & Stange, 1965) and in Hong Kong (Barthélémy, 2012). In one nest collected on 27 October 2020 at Phu Luong (TN-20-109), a dying

female was found sheltering inside her nest (Fig. 4B).

A total of 37 broods successfully developed at least to the pupal stage under laboratory conditions and were sexed (22 males and 15 females). Brood sex ratios were male-biased in broods with dormant prepupae, whereas they were approximately equal in broods with non-dormant prepupae.

In four nests in which the sex of all brood cells was known, the innermost cells were female and the outer cells were male. This pattern has also been reported for *Z. angulatus* in Hong Kong (Barthélémy, 2012).

Symbionts and brood mortality

Among the 80 provisioned cells from 32 examined nests, 37 individuals (46.3%) developed to maturity, whereas 43 (53.7%) died during development. Among the 43 failed cells, mortality occurred at the egg, larval, and prepupal stages in 21 (48.8%), 8 (18.6%), and 14 (32.6%) cells, respectively. Of the 43 failed cells, nine were attacked by three parasitoid species, while the remaining 34 died from unknown causes.

Megaselia sp. (Diptera: Phoridae) (Fig. 8A) was recorded attacking three cells. One prepupa was parasitized by an unidentified eulophid species (Hymenoptera: Eulophidae), and five cells were attacked by *Chrysis* sp. (Hymenoptera: Chrysisdae) (Fig. 8C). A total of 34 immatures died for unknown causes, 18 eggs had shrunk at the time of nest collection (Fig. 8B), while eight larvae and eight prepupae died during development.

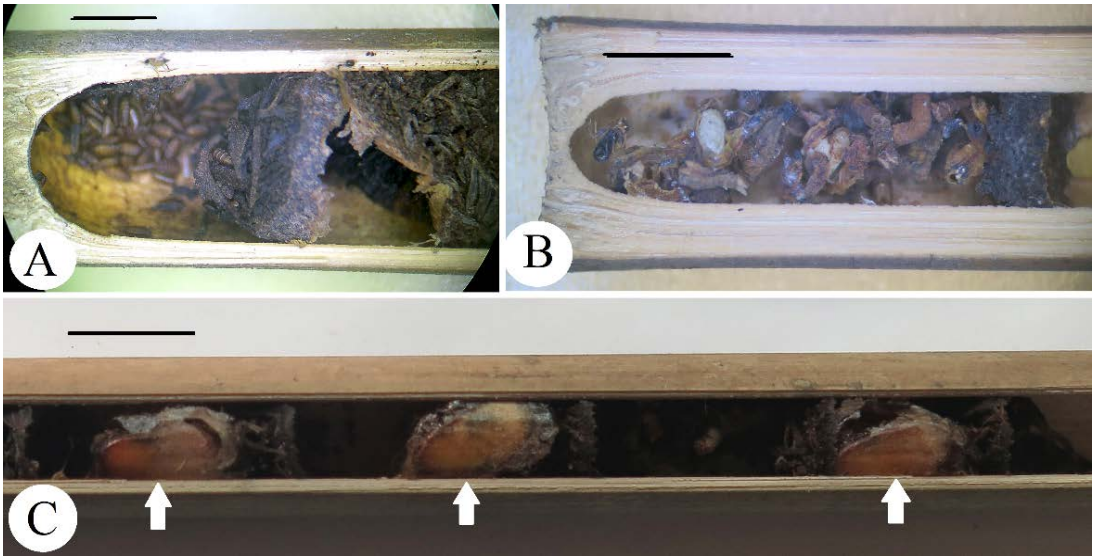

Figure 8. Cells with dead progeny found in *Zethus dolosus* nests: died phorid females and their pupae (A); provisioned cell with dry caterpillars (B); three cocoons of *Chrysis* sp. (C)

CONCLUSSION

The biology, nesting behavior, and parasitism of *Z. dolosus* are recorded for the first time in Vietnam. This study provides an additional contribution to the still limited knowledge of nesting behavior in *Zethus*. The nesting biology of *Z. dolosus* appears to be more similar to that of *Z. angulatus* (Barthélémy, 2012) than to that of other described congeners. Both species construct comparable leaf-based entrance turrets and overwinter in the prepupal stage.

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