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New nests of *Zethus* reveal unexpected architecture variation in the *olmecus* species group (Hymenoptera, Vespidae)

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ABSTRACT

Zethus Fabricius is the largest known genus in Vespidae, but very little is known about their nesting behavior. Belonging to the *Z. olmecus* species group, *Zethus miniatus* is widely known for its subsocial behavior, where females build together aerial nests comprised of a cluster of several cells. Nests of closely related species of the same species group, Z. *notatus*, *Z. schadei* and *Z. thoracicus*, collected in the Amazon basin, are here described and illustrated. Nests of Z. *notatus* and *Z. thoracicus* reveal architectures very distinct from those of *Z. miniatus*. Although examined nests are all aerial and comprised of at least four cells, the orientation and maceration of vegetable matter vary among these species. Finally, notes on social behavior and progressive provisioning of *Z. schadei* and *Z. thoracicus* are provided.

Introduction

Although Vespidae have probably originated from a stem-group of wasps with a fossorial nesting habit (Melo et al., 2011; Mauss et al., 2019), the more derived aerial forms of nesting stand out as they are more easily found. The nests of social vespids have intrigued naturalists for some time, with de Saussure (1853-1858) already separating nests into categories. Comprehension of nest architecture has advanced since then, with finer examination leading to the possibility of identifying genera (Wenzel, 1998) and even mapping the evolution of nest structures (Noll et al., 2021). However, the same cannot be said for the solitary vespids, whose nests are mostly subterraneous or in pre-existing cavities (Mauss et al., 2019) and therefore, only seldomly observed.

Zethus Fabricius (1804) is the genus with the highest number of species in Vespidae, reaching 299 worldwide, of which 239 occur in the New World and are, so far, divided into six subgenera (Lopes et al., 2021a). Despite its great diversity, very little is known from the nesting biology and behavior of these wasps, as only 22 species from the New World have some sort of published information on nesting (Bohart & Stange, 1965; Stange, 1969; Garcete-Barrett & Klassen Dück, 2010; Cooper, 2014, 2016; Lopes et al., 2019, 2021b; Lopes, 2023). While most of its representatives nest in pre-existing cavities, six species stand out for building aerial nests: *Z.* (*Wettsteinia*) *fabricator* Stange, 1969, with the nest described in the same study where the species was described (Stange, 1969); *Z.* (*Zethoides*) *matzicatzin* de Saussure, 1857b, with the nest described by Rau (1933); *Z.* (*Zethoides*) *binodis* (Fabricius, 1798), by Ducke (1914); *Zethus* (*Zethoides*) *schadei* Bohart & Stange, 1965, with notes of the nest by W. Weyrauch published by Bohart and Stange (1965); *Z.* (*Zethoides*) *miniatus* de Saussure (1858), also by Ducke (1914); and *Z. nodosus* Zavattari (1912), with the nest described by Lopes (2023).

Belonging to the *Z. olmecus* species group, *Z. miniatus* is perhaps the most renowned species in the genus. The depiction of communal behavior portrayed by Ducke (1914) led researchers to mistakenly believe *Zethus* displayed an intermediate stage between solitary and social behaviors (Hines et al., 2007). This has already been dismissed, as this group is derived and this social trait is clearly independent from eusociality (Lopes & Noll, 2018; Piekarski et al., 2018; Lopes et al., 2021b). Although the nest of *Z. schadei*, which also belongs to this species group, is already described (Bohart & Stange, 1965), no notes on behavior have been presented to date.

Nests assigned to *Z. notatus* Fox (1899) and *Z. thoracicus* Fox (1899), which also belong to *Z. olmecus* group, are herein examined and described. Also, notes suggesting communal social behavior of *Z. thoracicus* and *Z. schadei* are provided.

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Methodology

We studied here five nests of *Zethus* belonging to species of the *olmecus* group, all collected manually by the second author in 1991 and 1999 in different sites within the Amazon basin, in Brazil. After being collected, each nest was placed in a bag with a piece of soft paper extending from the bottom of the bag all the way through the opening. Bags were sealed through an overhand knot with the piece of soft paper entwined. The porosity of the paper connected the inside of the bag with the external environment assuring gas diffusion and avoiding moisture from accumulating inside the bag. For storage, each nest was individually preserved, wrapped in soft paper, placed within a tightly knotted plastic bag and gathered in plastic containers holding several bags. Nests and specimens are deposited in the Coleção de Entomologia "Padre J. S. Moure", Departamento de Zoologia, Universidade Federal do Paraná (DZUP). The studied nests were collected in four locations:

1. Reserva Ducke, Manaus

2. Rio Marié (left margin near the mouth at River Rio Negro): 0.4343°S, 66.4062°W, 55 m (03.vii.1999, G.A.R. Melo, ninho RN37)

3. Rio Puraquequara, Amazon Village Hotel: 2.9735°S, 59.8373°W, 30 m.

4. Plano, Rio Negro (left margin): 0.3099°S, 65.9901°W, 51 m (9.vii.1999, G. Melo)

The examination was carried out with the aid of a Leica M125 stereoscope. Pictures were taken either with a Leica DFC295 camera attached to the stereoscope through the Helicon Focus 8 software or with a Canon camera with a macro-objective.

Measurements were taken with a digital caliper, except for cell diameter and leaf fragment sizes, for which the eyepiece ruler of the stereoscope was used. Cell depth of the nests of *Z. schadei* and *Z. thoracicus* was measured by inserting a pin in the cell until it hit the bottom, marking the depth in the pin and finally measuring with the pachymeter. Leaf fragments were measured from material that detached from the nest, using those that had little or no warping, being as straight as possible for accurate measuring. Brood cell and leaf fragment measurements are presented by average and standard deviation values and individual measurements are provided in the Supplementary Material.

Specimens collected from the nests were identified following the identification key from Lopes and Noll (2024).

Results

Three of the collected nests belong to three species in the *Zethus olmecus* species-group: *Z. notatus* Fox, 1899, *Z. schadei* Bohart & Stange, 1965 and *Z. thoracicus* Fox, 1899. The other two nests were abandoned and are tentatively assigned to *Z. notatus* and *Z. thoracicus* based on similarities in nest architecture. The nests of *Z. notatus* and *Z. thoracicus* were hereto unknow, while as for the nest of *Z. schadei* it was known in the literature only from drawings in Bohart and Stange (1965). The nests are described and illustrated below.

Zethus (Zethoides) notatus Fox, 1899

Nest 1

Collecting data: Translated from field notes of the second author: "RN37 – *Zethus*, nest constructed around filamentous fungus (same set of fibers that RN36 [belonging to a species of *Trypoxylon*] was hanging). No adult present. Four cells, three open and one closed. Marié River, 03.vii.1999. In 15.vii.1999, there was a dead adult in the plastic bag. Nest was probably being provisioned at the time of collecting, because there is a live larva in one of the cells. I was able to extract the larva and it is relatively small. Species most likely of progressive provisioning. The larva was placed in fixative with the adult".

Overall aspect (Fig. 1C): the nest is composed of four exposed cells that close a circle, following a counter-clockwise direction (when observed from above), around the fungus. A very long "ornament" (a lower prolongation) made of vegetable matter extends downwards following the fungus filament.

Fixation: the nest is firstly attached through long strips of cut foliage and resinous matter that wrap around three filaments of a *Marasmius* fungus in a downward spiral (Fig. 1D) that is then fixed in the basolateral side of what probably is the first cell. The following cells are fixed adjacently on the underside of the previous cell.

Brood cells: The set of four cells were disposed in a circular pattern. Each cell spirals upward, with the fungus filament as a central axis. Each cell makes an approximate 160° turn, leaving the opening facing almost in the opposite direction of the bottom, giving a J-shape to the cell. The cells are more robust at the bottom, narrowing along the curvature and becoming cylindrical on the apical straight half. The cells are built in a manner that the bottom of each cell begins at approximately the same height in lateral view. The heights of the openings are also at the same level. Each cell is built adjacently on the underside of the previous one, where there is contact until about half of the cell length. Although very close, the fourth cell closes the circle but does not touch the first cell. The cells are made of long strips of cut leaves, tightly glued together, that spiral towards the opening (Fig. 1E). While it is possible to discern each layer, it is difficult to stablish the end and beginning of each strip. The space between each strip is coated with a blackish resinous matter, leaving the light-brown apical margin of the strip free.

Ornament (Fig. 1F): projecting from the underside of each cell, a series of long leaf strips converge centrally towards the fungus filament, with six strips originating from under the first cell, seven from the second, two from the third and two from the fourth. These cuttings, once converged, lie parallel to the axis of the fungus filament, fixed to it. The spaces between leaf strips are also coated in dark resinous material, with the light uncoated margin outwards oriented. Other cuttings are placed along the ornament but only four form at the apical end. One fragment was broken off.

Measurements: Length of fungus filament above nest = 85,75 mm. Nest: height = 12.16 mm; width = 19.75 mm. Ornament = 29.39 mm. Cells: length = 8.43 mm ± 0.38mm; distance between bottom of adjacent cells = 4.27 mm ± 0.35 mm; distance between bottom of cell and opening of previous cell = 11.24 mm ± 0.50 mm; opening diameter = 3.80 mm± 0.10 mm.

Nest 2

Collecting data: unknown. Stored with another nest collected in 1991 in the Reserva Ducke, so it is probably from this site or from nearby areas north of Manaus.

Overall aspect (Figs. 2A, 2B): similar to the first nest, also with four cells and it is also built using a *Marasmius* fungus as substrate. Most other traits are similar, except for orientation of cells and formation of the ornament. The cells follow a similar pattern spiraling upwards with a curvature around the fungus, however in a clockwise manner. Also, the cells are not leveled, with each subsequent cell lower than the previous, with the bottom built below the bottom of the previous cell. A small circular orifice on the bottom of the first cell suggests emergence of a parasitoid. There is also an orifice of irregular shape on the side of the third cell but does not remind those left behind by parasitoids. The ornament is also similar but seems to originate from a single spot, rather than the bottom of each cell like in the previously described nest. Also, its strips are all dark without any lighter colored margins. Measurements: Nest: height = 15.72 mm; width = 14.32. Ornament = 28.65 mm.



Figure 1 Nest of *Zethus notatus*. A) Nest in collecting site. B) Lateral view of nest. C) Overhead view of nest. D) Area of fixation of the nest, revealing the leaf threads wrapping around the fungus. E) Closeup on the arrangement of strips used to build cells. F) Detailed view of the ornament.

Zethus (Zethoides) schadei Bohart & Stange, 1965

Collecting data: Translated from field notes of the second author: "RN126 – *Zethus miniatus* (?). Nest built on a piece of straw on the margin of straw roof. Four adults present. 14 cells: 3 open (all with larvae; one of them still without the collar and with its walls still green). Amazon Village Hotel, Rio Puraquequara, 31.vi.1999: (nest recorded in 05.viii.1999: another cell had the cap partially open and has an apparently dead adult inside; I finished opening it and found out that it contained a female, which was alive; it was removed and sacrificed)".

Overall aspect (Figs. 3A, 3B): The nest was fixed hanging on a fine piece of straw and is comprised of a cluster of fourteen adjacent exposed cells that are perpendicular to the substrate.

Fixation: a single piece of straw runs adjacent to the lateral walls of the first cells of rows one, two and four and is partially englobed by a mixture of vegetable and resinous matter.

Brood cells: there are fourteen cells, all barrel-shaped of similar height, aligned and arranged in five rows: four rows of three cells each and one row of two cells. The left lowermost cell is incomplete, empty and its color is now brownish instead of green like described in the journal. The first cell of rows three to five are completely open and empty (Fig. 3C). The first cell of rows one and two and the second cell of rows two and three are completely sealed (Fig. 3D). The remaining cells present different degrees of incomplete opening of the cap, each one with a developed adult inside (Fig. 3D). External cell walls are comprised by irregular-shaped cuttings of leaves intercalated by dark resinous substance, giving it a scale-like appearance (Figs. 3B, 3D). Internal walls and the border of the openings are made of finely macerated vegetable matter, giving a more regular appearance.

Measurements: Nest: length = 20.40 mm; width = 15.54 mm; height = 12.30. Cell opening diameter = 2.89 mm ± 0.22 mm.

Zethus (Zethoides) thoracicus Fox, 1899

Nest 1

Collecting data: collected in 24.viii.1991 in the Reserva Ducke, Manaus. The nest was found suspended by a fine root in a small earth

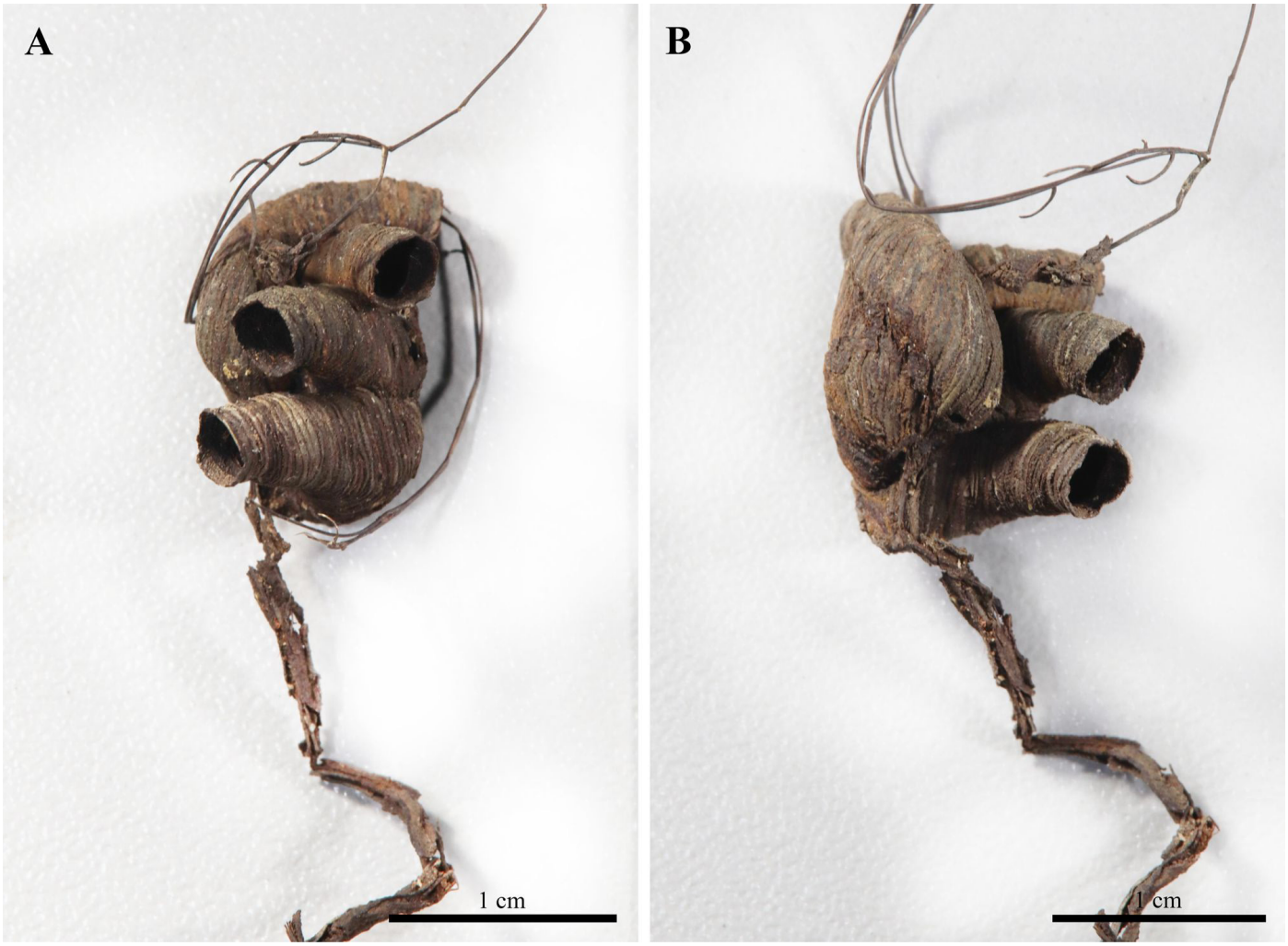


Figure 2. Abandoned nest tentatively assigned to *Z. notatus*. A) View exposing openings. B) View exposing bottom of brood cells.

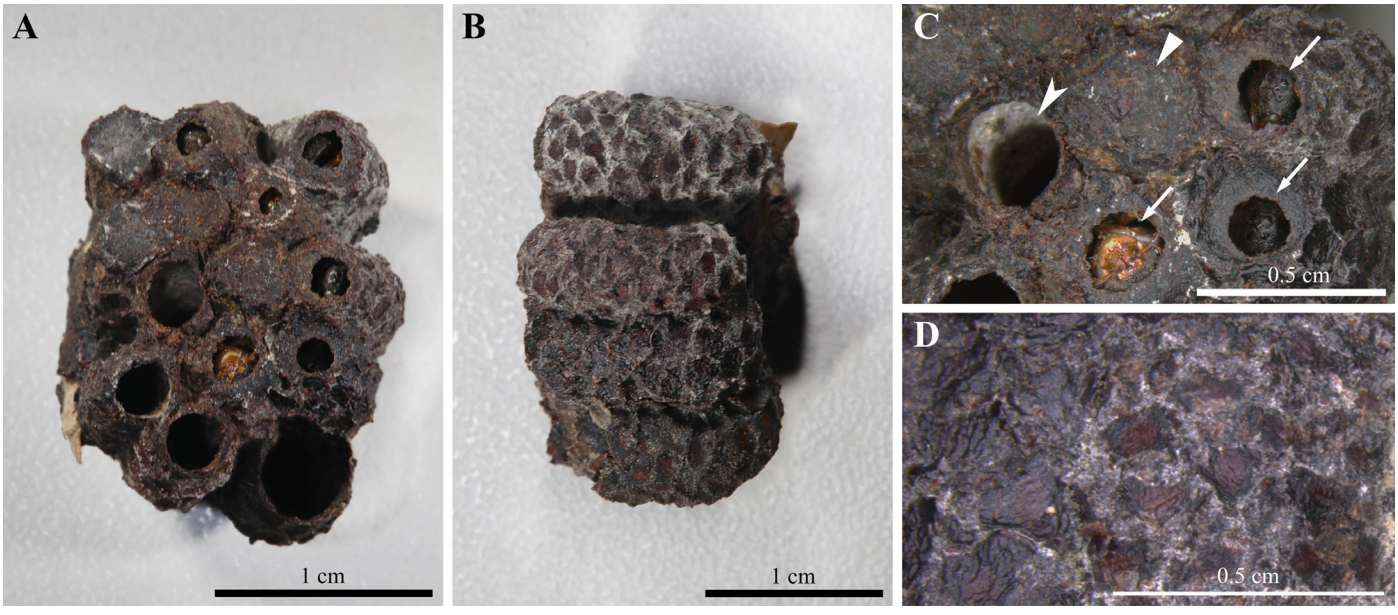


Figure 3. Nest of *Z. schadei*. A) View of the openings. B) Lateral view. C) Closeup showing examples of nest entrances: completely closed (triangle); completely open (arrowhead); and partially open (arrow). D) Close up of leaf fragments on external surface of cells.

bank. There were six females in the nest at the time of collecting. Cell content was not examined.

Overall aspect (Figs. 4A-4C): The nest consisted of an approximate spherical structure, bearing a dome made of cut leaves on the upper part. Unfortunately, no details about the dome were taken at the time of collecting and desiccation of the leaves led to its rapid fragmentation. The lower portion of the nest remained mostly intact and comprised a group of vertically oriented and adjacent brood cells, all aligned parallel to the root, with their opening directed upwards. Laterally and in the bottom, the cell set was surrounded by layers of leaf fragments, similar to those making up the dome.

Fixation: the nest used a ramified root as substrate, with two more robust segments and several thin, more delicate segments which were broken, but previously continued into the nest. The more robust portions appear to be the main support of the nest, one in each side of an outermost cell of the cluster (third cell of the second row). The root reemerged from the nest below, making a loop under it.

Brood cells: total of 25 cells, arranged in six rows with 3, 3, 7, 5, 4 and 3 cells. This arrangement in rows is indicated here simply for mapping purpose and does not imply the order in which they were built. The second row presents a cavity that superficially resembles a cell, but closer examination reveals it is not, as it does not possess the typical concentric walls and it is much shallower than the cells. Cell openings are circular to ellipsoid. Cell walls are built with a finely macerated material (Fig. 4D), which is impossible to determine foliar structure beyond some sparse trichomes. Borders of some openings may present small leaf fragments.

Cover: we refer here basically to the layers covering the lower portion of the nest around the cell set. It comprised of cuttings of foliage arranged in several layers. Leaf fragments were majorly strips with few fragments presenting short and/or irregularly shapes (Fig. 4E). The material presents leaves of different morphology regarding trichomes, which when present can be restricted to veins or along the whole fragment. Also, coloration and vein pattern of leaves vary. Most fragments present one serrated margin, usually along the length of the fragment, that indicates where the leaves were cut by the wasp. The "teeth" of these serrations are curved. Leaf fragments appear to be randomly arranged, glued together only at some points, rather than the entire extent and so leaving wide spaces between each strip.

Measurements: Root: length above nest = 9 cm; ramification until nest attachment = 4.43 cm; length inside nest = 2.61 cm. Nest: greatest length = 47.53 mm; greatest height = 37.49 mm. Cell area: greatest length = 51.94 mm; greatest width = 29.43 mm. Cell depth = 18.16 mm ± 2.16 mm; cell opening diameter = 3.92 mm ± 0.27 mm. Leaf cover of variable width: greatest width = 18.07 mm; smallest width = 3.36 mm. Leaf fragments: greatest length 9.1mm; smallest length = 3.3 mm; greatest width = 2.9 mm; smallest width = 0.8 mm. Length/width ratio of leaf fragments: greatest = 9.1; smallest = 2.5.

Nest 2

Collecting data: Translated from field notes of the second author: "RN58 – *Zethus*(?) Nest built with pieces of cut leaves fixed to a thin root on a bank formed by a fallen tree. (Terra firme forest). No adult present. Nest will not be dissected (no signs of wasps exiting from the nest; also, cannot know if there are built cells). Plano, 09.vii.1999."

Overall aspect (Fig. 5A): this abandoned nest showed great similarity with the one described above. It was smaller in size and presented an intact dome. The dome is of a rough cone shape. The complex arrangement of leaf fragments seems to be more loosely mounted on the dome and a circular opening directed upwards can be seen near

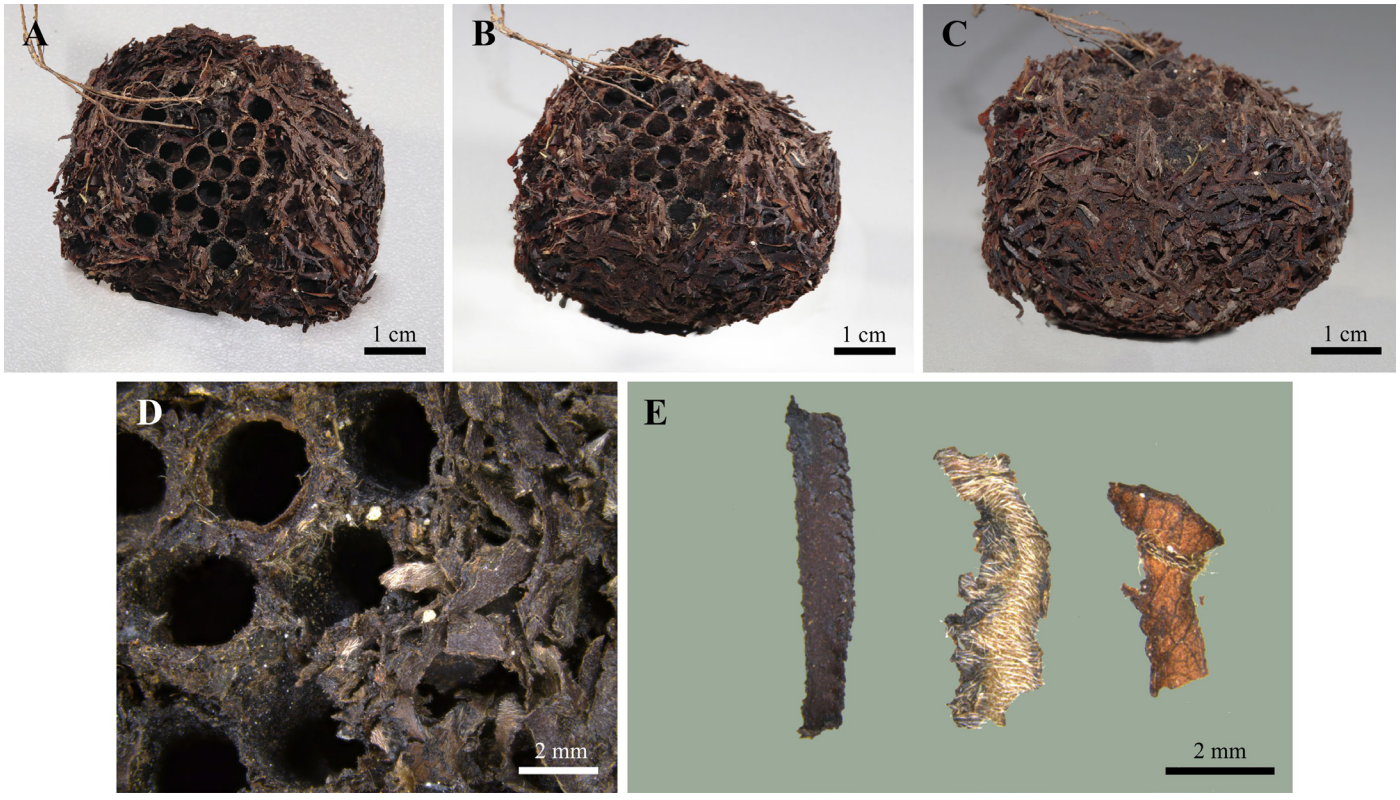


Figure 4. Nest of *Zethus thorcacicus*. A) Overhead view. B) Oblique view. C) Lateral view. D) Closeup of nest, showing finely macerated matter comprisinf cells (left) and larger leaf fragments comprising the cover (right). E) Examples of leaf fragments detached from the nest: without trichomes (left); completely covered in trichomes (middle); trichomes only on midrib (right).

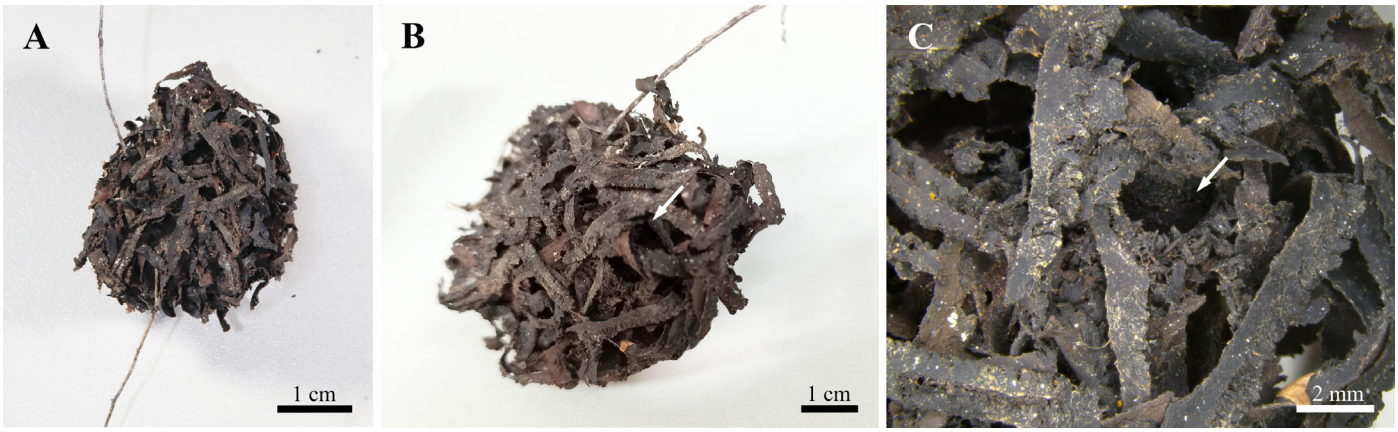


Figure 5. Abandoned nest tentatively assigned to *Zethus thoracicus*. A) Lateral view. B) Oblique view showing probable main entrance (arrow). C) Closeup showing cell amidst fragments of leaves.

the top (Fig. 5B). This is speculated to be the nest entrance, but it is uncertain since the loose arrangement of the dome may leave other spaces that the wasps apparently can crawl through. Among the spaces between the leaves of the dome, two cells can be observed (Fig. 5C), but there may be more since these cells are far from the fixation to the root. There is no clear external definition between the dome and the inferior portion containing the cells. Height = 33.34 mm; length = 29.25 mm; width = 19.26 mm.

Discussion

Nesting behavior in New World *Zethus* is still poorly known. The aerial nests, although probably convergent between different species groups, seem to be frequent among species groups of *Z.* (*Zethoides*) Fox, 1899, specifically the *Z. binodis* and *Z. olmecus* species groups. This makes the subgenus the one with, proportionally, the highest number of species with information of nesting behavior.

Curiously, Lopes and Noll (2024) report examining specimens of *Z. luederwaldti* (von Ihering, 1911), *Z. toltecus segmentalis* (von Ihering, 1911) and *Z. utingensis* Lopes, 2024 collected from trap nests, indicating that not all species in the *olmecus* species group build aerial nests. Bohart and Stange (1965) briefly describe a cell of *Z. luederwaldti*, but no other traits of the nest are given, leaving us without knowing whether the nest is aerial or in a cavity.

The use of fungal rhizomorphs of the genus *Marasmius* for nest construction is widely reported among birds (Elliott et al., 2019). These rhizomorphs have also been previously reported in Vespidae as substrate for nest fixation. Starr (1988) translates Jacobson's (1935) "Aanteekeningen over Stenogastrinae" where it is stated that *Parischnogaster mellyi* (de Saussure, 1852) uses *Marasmius equicrinus* or another species of *Marasmius* as a petiole for the comb of the nest. In a similar manner, Turillazzi (1990) also reports the use of *Marasmius* for the suspension of *Metischnogaster drewseni* (de Saussure, 1857a) nests.

A convergence of such distantly related organisms using the same material for nesting should have its benefits. Recently, Oliveira and Ishikawa (2019) described *M. yanomami*, that was being used for basket manufacturing by the indigenous Yanomami people from Brazil. The mechanical resistance of the rhizomorph is considerable and although considered as reason for selection, studies of bird nests indicate occurrence of more resistant alternative materials in the area. Therefore, a hypothesis that justifies its selection based on strength alone could be dismissed (Rana et al., 2021). Another fact that helps dismiss this criterion for wasp nests is that their nests are usually very light, not requiring a very resistant material. Other studies indicate that there are antibiotic and antiteratogenic properties in *Marasmius* fungi (Rosa et al., 2009; Ramesh & Pattar, 2010), from which the animals that use it as building material could benefit from, as the fungi become both a resource for nest support and biochemical combatant of pathogens (Aubrecht et al., 2013).

The nest of *Z. thoracicus* is remarkable in size, with 25 cells and at least six adult females (more could be away from the nest at the time of collecting). However, brood cell inspection revealed them to be empty without any larvae or pupae. Hence, there is reason to believe the nest would be in the end of its cycle and that the captured females were probably newly emerged and/or would soon leave the nest.

The nest of *Z. schadei* here observed agrees with the description brought by Bohart and Stange (1965), although with a smaller number of cells and different cell arrangement. Nevertheless, this nest was apparently in a moment of sharp growth, evidenced by the large number of closed cells at the time of collecting (many recorded as partially open at present examination) and cells that were still being built. Furthermore, this nest is very similar to the nest of *Z. nodosus* and the more widely known nest of *Z. miniatus*, from which it differs mainly in cell orientation. Nevertheless, the architecture of the newly described nests of *Z. notatus* and *Z. thoracicus* greatly vary from each other and from *Z. miniatus*, *Z. nodosus* and *Z. schadei*, revealing great difference of nest architecture in this species group.

If looking into similarity between these aerial nests, we can form three groups: one composed of *Z. miniatus*, *Z. nodosus* and *Z. schadei*; one by *Z. thoracicus*; and the last by *Z. notatus*. The *miniatus*-type nests will have cells fixed transversely to the substrate, cell walls made of finely macerated material and covered by tightly glued leaf fragments. The *thoracicus*-type group shares with the latter the cell walls of finely processed material, but its cells are parallel to the substrate and the leaf fragments covering are loosely fixed. Although loosely fixed, the leaf-dome and cover may act as a barrier against predators and parasitoids, serving as a maze to hinder attempts to approach brood through the opening or cell walls. Finally, the *notatus*-type nests share no common traits other than being aerial and made of foliage. Their cells are made from tightly glued leaf strips without any cover layer and follow a circumcentric orientation regarding the substrate. The nests from trap nests will probably form a fourth group. These similarities and differences require deeper exploration but are plausible characters to be explored in the advent of phylogenetic analysis.

Although no ethological observations on nest building were made, collecting four and six adult females inside the nests of, respectively, *Z.*

schadei and *Z. thoracicus* indicate communal nesting. This classification of subsocial behavior, where two or more females nest together, but each tends to its own brood, has been reported previously for *Z. miniatus* by Ducke (1914), who mistakenly identified as *Z. lobulatus*. Observing this trait for species with so distinct nest architectures raises the question of where communal nesting originated in the *Z. olmecus* species group. However, this question can only be answered through a proper phylogenetic study.

Conclusion

The yet unknown nests of *Z. notatus* and *Z. thoracicus* were described along with reports of several females nesting together in *Z. schadei* and *Z. thoracicus.* These are valuable additions to the large gap in the knowledge of nesting in *Zethus*. The notorious diversity of architecture and the alternation of solitary and subsocial behavior within very closely related species is intriguing and deserves a phylogenetic study (Lopes et al., in prep.) to better understand the evolution of this group.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

RBL and GARM ideated the study, took pictures and wrote and revised the manuscript. RBL described and measured the nests, made line drawings and mounted the plates. GARM collected the material.

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Supplementary Material

The following online material is available for this article:

Table S1 - Depth and diameter of the cells of the examined Zethus schadei nest. SD – Standard deviation.

Figure S1 - Nest of Zethus schadei, lateral view (below), and mapping of its cells (above). Gray – cell walls. Closed gray circles – closed cells. White circles – open cells. Double-margined circles – partially open cells. Unmargined white circle – incomplete cell. Dark gray – straw piece used for fixation. Numbers – cell identification.

Figure S2 - Nest of Zethus notatus (below) and respective mapping of its cells (above) viewed from above (left) and laterally (right). Gray – cell walls. White circles – cell openings. Dark gray – leaf strips participating on fixation. Asterisk – point of fixation. Numbers – cell identification. dbb – distance between bottom of adjacent cells. dbo - distance between bottom of present cell and opening of previous cell.

Table S2 - Diameter and length of the cells of the examined Zethus notatus nest and distance between bottom of adjacent cells (dbb) and distance between bottom of present cell and opening of previous cell dbo. SD – Standard deviation.

Table S3 - Depth and diameter of the cells of the examined Zethus thoracicus nest. SD – Standard deviation.

Figure S3 - Nest of Zethus thoracicus, overhead view (below), and mapping of its cells (above). Gray – leaf cover. Circles – cell openings. Asterisks – point of fixation. Numbers – cell identification.

Table S4 - Measurements of 20 leaf fragments from the cover of a nest of Zethus thoracicus.