

Nesting Biology of *Xylocopa xinjiangensis* (Hymenoptera: Apidae: Xylocopinae)

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Subject Editor: Sandra Rehan

Received 13 February 2018; Editorial decision 22 May 2018

Abstract

Xylocopa, an important genus in Hymenoptera: Apidae, is of great significance in research on the early stages of insect social evolution. Most species in this genus burrow into wooden structures. Only the *Proxylocopa* subgenus nests in the soil. Here, we report the nesting behavior of *Xylocopa xinjiangensis* (Hymenoptera: Apidae: Xylocopinae), which is distributed only in Western China. During July 2013 and August 2016, we observed the nest architecture and nest building process of *X. xinjiangensis*. *X. xinjiangensis* is solitary and nests in the soil walls of gullies, mounds, and cliffs in the Manas area, Xinjiang, multiplying at the rate of one generation a year. Newly emerged females eclose in the fall and build wintering nests first. The next spring, outbound wintering females build breeding nests, although a few wintering females may use the breeding nests built by their mothers. The location and structure of *X. xinjiangensis* wintering nests are different from those of the breeding nests. The wintering nest is simple in structure, consisting of a tunnel leading perpendicularly from the surface to the interior. The structure of the breeding nest may be either a branching tunnel or a straight-chain tunnel. The first cell that *X. xinjiangensis* builds in the breeding nest is closest to the entrance, which is a significant difference from the behavior of carpenter bees that construct nests in wood structures. The results of this study lay the foundation for the utilization and protection of *X. xinjiangensis* resources and facilitate a better understanding of the evolution of the *Xylocopa* population.

Key words: *Proxylocopa*, *Xylocopa xinjiangensis*, breeding nest, wintering nest, cell structure

Bees construct nests for colony protection, food storage, and reproduction (Michener 2007). The nest type, cell structure, bee breed type, and brood behavior not only are crucial for the survival of bees but also can provide an ecological basis for understanding the phylogeny of bees, leading to a theoretical basis for artificial breeding and commercial production (Wu 2000, Michener 2007).

The subfamily Xylocopinae has been recognized as the most basal lineage within the family Apidae and comprises four tribes: Allodapini, Ceratinini, Xylocopini, and Manueliini (Michener 2007, Flores-Prado et al. 2010, Rehan et al. 2012). Phylogenetic studies indicate that Xylocopini contains only one genus, *Xylocopa*, which includes 31 subgenera containing approximately 470 species (Minckley 1998, Leys et al. 2000, 2002; Michener 2007, Ascher and Pickering 2017). The species within *Xylocopa* are distributed throughout the world except for Antarctica, mainly in tropical and subtropical regions, with a few in temperate regions (Hurd and Moure 1963). Fourteen subgenera of Xylocopinae containing approximately 40 species are already known in China (Wu 2000). Most Xylocopinae nest in dead wood, hollow stems, and bamboo

(Hurd 1978, Camillo and Garófalo 1989, He et al. 2009, Prager and Hunter 2011, Hannan et al. 2012). The nest structures in wood materials mainly consist of the branching type and the nonbranching type, also called the straight-chain type (Gerling et al. 1989, Steen and Schwarz 2000, Bernardino and Gaglianone 2008, Prager 2008, Prager and Hunter 2011, Rahman and Deka 2011, Hannan et al. 2012). Different species of Xylocopinae build different nest structures. Relationships exist between the nest architecture and the distribution of cells within the nest, the cell size, the efficiency of bee bread storage, and the sensitivity to parasitism (Steen and Schwarz 2000, Prager and Hunter 2011).

Proxylocopa is the only subgenus in *Xylocopa* that nests in the soil. *Proxylocopa* is reported to contain 16 species, mainly distributed in Albania, Greece, East Israel, and the desert areas of Western China. Sporadic reports have been published on the morphology, the distribution, and certain biological behaviors of *Xylocopa olivieri* (Lepelletier) and *Xylocopa rufa* Friese, two species within *Proxylocopa* (Wu 2000, Gottlieb et al. 2005, Özbek 2013, Ascher and Pickering 2017). *X. olivieri* nests on slopes with a thick soil layer. The daily activity pattern of *X. olivieri* on *Antirrhinum majus*

is clearly bimodal; the peak flower visiting time periods are the early morning before sunrise and dusk after sunset (Gottlieb et al. 2005). *Xylocopa (Proxylocopa) xinjiangensis* (Hymenoptera: Apidae: Xylocopinae) is mainly distributed in Xinjiang, China. Wu (1983, 2000) observed the morphological characteristics of its females. To the best of our knowledge, little literature has been published on the characteristics of the nesting biology of *X. (Proxylocopa) xinjiangensis* (Wu 1983, 2000).

In this study, we studied and described the nesting biology of *X. xinjiangensis*. We observed in detail the nest location, nest architecture, and cell characteristics of *X. xinjiangensis* as well as the correlation between different nest architectures and nest structures.

Materials and Methods

Research Sites and Field Methods

From July 2013 to August 2016, we studied the nesting biology of *X. xinjiangensis* in Qingshuihe Kazakh Ethnic Township (43° 52' N, 86° 01' E) and Hankazitan Kazakh Ethnic Township (43° 51' N, 86° 12' E) in southern Manas County, Xinjiang, China. We observed and collected samples of breeding nests constructed by wintering females from July 4 to 22 in 2013 ($n = 18$), from May 14 to 26 ($n = 10$) and from July 16 to 27 in 2015 ($n = 8$), and from July 17 to 23 in 2016 ($n = 9$). On the afternoon prior to collecting the breeding nest, we marked the nest entrance of the homing female. Between 9:00 and 10:00 the next morning, when the female had not left the nest, we blocked the entrance with tissue paper. A large chunk of soil was cut around the entrance, and the nest was brought back to the laboratory. The nests were dissected, and the structure of the breeding nests was observed. From July 26 to 29 in 2016, nine nests were dissected at the research site to observe the development of offspring bees and the number of males and females.

We observed and collected samples of wintering nests constructed by newly emerged females from August 18 to 26 in 2014 and from July 23 to August 8 in 2016. The study time was from 14:00 to 20:00 when the weather was not rainy. The nesting locations of the newly emerged females were observed, and wintering nests at the research site were then dug out. Ten wintering nest samples were dissected at the research site from August 1 to 8 in 2016 to observe their structure.

Nest Dissections

The breeding nest and cell structure of *X. xinjiangensis* was observed as follows: A knife was used for dissection along the tunnel direction at the entrance of the *X. xinjiangensis* breeding nest (35 breeding

nests). A Vernier caliper was used to measure the entrance size of the nest (the direction perpendicular to the ground is the length, and the direction parallel to the ground is the width), length of the tunnel, distance between the entrance and the first cell, tunnel diameter, distance between the cell and the tunnel, diameter and length of the cell, thickness of the cell wall, thickness of the cell partition, and distance between adjacent cells.

Statistical Analysis

The data were analyzed by SPSS 16. The Pearson correlation coefficient method in SPSS 16.0 was used to analyze the following correlations between variables: the correlation between the diameter and length of the tunnel, the correlation between the number of cells in a nest and the number of cell branches, the correlation between the number of tunnels in each nest and the diameter at the widest point of the tunnel, and the correlation between the tunnel length and the number of cells in the tunnel. The Mann-Whitney *U*-test was performed on two independent samples for significant difference analysis of the cell numbers in different nest structures, the diameter of the tunnel, and the distance between the entrance and the first cell. One-way ANOVA was used for significant difference analysis of the distance between adjacent cells for different types of cell structures, the length and diameter of cells, the wall thickness of cell, and the thickness of cell partitions. SigmaPlot 10 was used to plot the figures.

Results

Morphology and Breeding of *X. xinjiangensis*

Females are generally 16–18 mm (17.22 ± 0.54 mm) in length and black in color, and the thorax is covered with reddish-brown hair. The length of the head exceeds its width. The mandibles contain two sharp teeth, and the outer tooth is clearly longer than the inner one. The legs are covered with black hair. However, the inner side of the tarsus of the fore leg, the middle leg, and the tarsus and tibia end of the hind leg are covered with yellowish-brown hair. The wing is a shiny purple-black (Fig. 1A). Males average 15–17 mm (16.32 ± 0.49 mm) in length and black in color, and the head, thorax, and abdomen are covered with yellowish-brown hair with some black hair. The width of the head slightly exceeds the length. The prelabrum, labrum, and frontoclypeal area are all lemon yellow, and the wings are yellow and transparent (Fig. 1B).

X. xinjiangensis multiplies at the rate of one generation a year in the Manas area in Xinjiang and leads a solitary life. It nests in the soil and winters as an adult. Females fly to feed in early May of the following year and build their breeding nests near their wintering

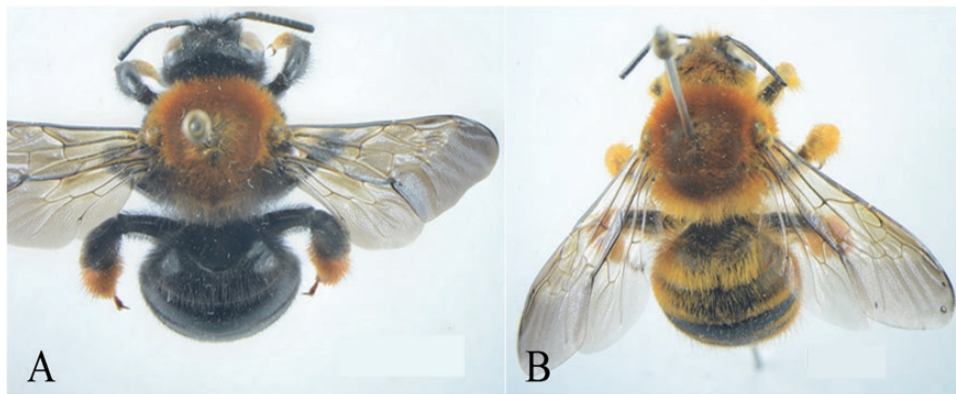


Fig. 1. Morphology of *X. xinjiangensis*. (A) Female. (B) Male.

nests. The cells constructed by a female in a lifetime average 5–14, with a mean of 8.65 ($n = 35$). The female-to-male ratio of the newly emerged offspring bees is approximately 0.86:1 ($n = 9$, ♀25, ♂29). During the development of the offspring bees, deaths occur in the egg stage and parasitism in the larva stage.

Nesting Sites and Choice of Nesting Substrate

The nests of *X. xinjiangensis* in the soil can be categorized into wintering nests and breeding nests. The nesting sites are mainly located on the sunny side of gullies, mounds, and cliffs. The nesting sites are mainly located in the gullies on the sunny side or in small mounds, dike cliffs, or high cliff walls where the soil layer is thick (Fig. 2). From early May to mid-July each year, *X. xinjiangensis* females build breeding nests in the middle and upper parts of gullies, small mounds, dike cliffs, or high cliffs. They build wintering nests near the bases of gullies, mounds, dike cliffs, or high cliff walls (wintering nests are usually near breeding nests) (Fig. 2).

Nest Architecture and Structure

Wintering Nest

Newly emerged *X. xinjiangensis* females construct wintering nests. The wintering nest consists of an entrance and a bored tunnel. The height of the nest from the ground is 12–50 cm ($n = 10$), with a mean of 32.35 ± 14.15 cm. Wintering bees dig the linear tunnel from outside to inside, perpendicularly from the cliff. The depth of the tunnel is 27–40 cm ($n = 10$), with a mean of 35.19 ± 4.28 cm. The females collected in the samples all spent winter in solitary conditions (Fig. 3).

Breeding Nest

After females emerge from the wintering nest, they build a breeding nest to reproduce. Each female builds a nest independently.

In the Manas area, in early May of the next year, when the outdoor temperature reaches 19°C on sunny days, wintering bees begin to emerge from their nest in large numbers, first looking for nectar plants on which to feed, after which the females begin to build breeding nests. The breeding nest consists of an entrance, a tunnel, and several cells. Each cell consists of a cell wall and cell partition (Fig. 4). The nest building process is as follows: the wintering female selects a nesting place and bores an entrance, excavates part of a tunnel followed by the first cell, collects nectar to make bee bread, lays eggs on the bee bread, and makes the cell partition to close the cell. Then, she continues to excavate the tunnel inward to build different cells in sequence. A certain distance lies between the excavated tunnel and each cell, as well as between a cell and the adjacent cells.

The female first excavates a cylindrical cell and then secretes a glandular substance, which she applies to the inner wall of the excavated cell. The secretion forms a hard shell wall within the cell, and the inner wall of the cell is smooth. After the cell has been completed, the female collects nectar to make bee bread and lays an egg on the bee bread. After egg-laying, the female seals the cell entrance with a partition made from secretions and soil. The entrance of the cell is sealed sequentially from outside to inside. Rotiform lines can be clearly seen on the cell partition (Fig. 4C). Afterwards, the female continues to excavate the tunnel for the next cell, and the same procedures are repeated. In each cell, a single egg is laid.

X. xinjiangensis builds two types of breeding nest: the branching type and the straight-chain type. In the branching type, cells are tightly clustered along the tunnel, while in the straight-chain type, cells are sequentially constructed parallel to one another along the tunnel (Fig. 5). Among 35 dissected nests, the branching type accounted for 62.86%, while the straight-chain type accounted for 37.14%. The different types of cell architecture vary significantly in the number of cells built in the nest (Mann–Whitney $U2$ independent sample test, $Z = -2.695$, $n = 35$, $p = 0.007$): the average number of



Fig. 2. Nest locations of *X. xinjiangensis*. (A) Gully. (B) Small mound. (C) Dike cliff. (D) Cliff. Spots circled in red in the above figure indicate breeding nest locations, while spots circled in yellow indicate wintering nest locations.



Fig. 3. Wintering nest of *X. xinjiangensis*. (A) Female bee looking for a nesting location. (B) Female bee excavating wintering nest. (C) Entrance of wintering nest. (D) Depth of wintering nest.

cells in the branching type was 7.53 ± 2.06 ($n = 22$), and the average number of cells in the straight-chain type was 9.77 ± 2.01 ($n = 13$) (Table 1).

The length of the tunnel excavated by the female is approximately 9.79–31 cm, with a mean of 17.24 ± 5.51 cm; the distance from the entrance to the first cell is approximately 3.44–27 cm, with a mean of 8.46 ± 5.86 cm; and the diameter of the tunnel is 0.96–1.27 cm, with a mean of 1.10 ± 0.08 cm. The different types of nest structure excavated by *X. xinjiangensis* show no significant difference in the total length of the nest (Mann–Whitney *U*2 independent sample test, $Z = -1.492$, $P = 0.136$), the total distance from the entrance to the first cell (Mann–Whitney *U*2 independent sample test, $Z = -0.246$, $P = 0.805$), or the tunnel diameter (Mann–Whitney *U*2 independent sample test, $Z = -0.049$, $P = 0.961$). The results of Pearson correlation analysis show that the length of the tunnel constructed by *X. xinjiangensis* and the distance of the first cell from the entrance are significantly correlated ($r = -0.834$, $P = 0.02$), whereas the length of the tunnel and its diameter are not significantly correlated ($r = -0.118$, $P = 0.802$) (Table 1).

The distance of each cell constructed by the female from the tunnel is 1.42–14.98 mm, with a mean of 6.62 ± 3.05 mm. The different types of nest structure show a significant difference in the distance of the cells from the tunnel (according to one-way ANOVA, $df_{(1,53)} = 14.571$, $P < 0.01$). The distance between adjacent cells is 1.57–22.31 mm, with a mean of 7.06 ± 4.25 mm. The different types of nest structure show no significant difference in the distance between adjacent cells (according to one-way ANOVA, $df_{(1,52)} = 0.115$, $P = 0.735$).

The cell constructed by *X. xinjiangensis* is shaped like a long oval cylinder. The length of a cell (the distance from the cell partition to the far end of the cell) is 11.57–24.55 mm, with a mean of 14.95 ± 1.45 mm; lengths of 14–16 mm account for 80.18% of the total sample (Fig. 6A).

No significant difference was found in the cell length between the different types of nest structure (according to one-way ANOVA, $F_{(1,109)} = 0.039$, $P = 0.844$). The diameter of the cell is 8.14–12.90 mm, with a mean of 10.37 ± 0.91 mm; diameters of 10–11 mm account for 48.6% of the total number of samples (Fig. 6B). No significant difference was found in the cell diameter between different types of nest structure (according to one-way ANOVA, $F_{(1,105)} = 0.035$, $P = 0.852$). The wall of the cell is rather thin. Its thickness is 0.62–2.41 mm, with a mean of 1.27 ± 0.34 mm, and cell wall thicknesses of 1–1.5 mm account for 59.43% of the total number of samples (Fig. 6C). No significant difference was found in the cell wall thickness between the different types of nest structure (according to one-way ANOVA, $F_{(1,103)} = 0.580$, $P = 0.448$). The cell partition (located at the cell entrance, used to separate the cell from the tunnel) is also rather thin. The partition thickness is approximately 1.03–2.90 mm, with a mean of 1.84 ± 0.46 mm, and partition thicknesses of 2–2.5 mm account for 40.66% of the total number of samples (Fig. 6D). No significant difference was found in the cell partition thickness between the different types of nest structure (according to one-way ANOVA, $F_{(1,89)} = 0.924$, $P = 0.339$; Table 1).

Interestingly, after wintering, some females use the nest built by the mother for reproduction rather than building a new nest. Of the 10 nests dissected on May 23–25, 2015, two females made use of the old nest. Using the old nest appears to take less time than building a new one, as the reproductive schedule for these females is quicker than that of females constructing a new nest. Females excavating new nests build five cells at most. By contrast, females using the old nest build at least five cells and at most eight.

Discussion

Among the 31 subgenera of *Xylocopa*, only *Proxycopa* nests in soil. Little literature exists on the nesting biology of *Proxycopa*. This



Fig. 4. The structure and composition of nests of *X. xinjiangensis*. (A) Nest entrance. (B) Female going home. (C) Cell. (D) Male at entrance. (E) Bee bread with egg laid on it. (F) Bee bread with larva feeding on it.

study investigated the nesting biology of *X. xinjiangensis*, a species of *Proxycopa*. The results of this study reveal that females average 16–18 cm in body length, and males average 15–17 cm in body length, which is basically consistent with the measurement reported by Wu (2000). Species in the subgenus *Proxycopa* are generally smaller than species in the other subgenera (13–30 mm; Michener 2007) in the *Xylocopa* genus. *X. xinjiangensis* selects nest locations in gullies, mounds, dike cliffs, or high cliff walls where the soil layer is rather thick. The number of cells per nest constructed by *X. xinjiangensis* ranges from 5 to 14, with a mean of 8.65. *X. xinjiangensis* bears certain similarities to *X. olivieri*, another species of *Proxycopa* described by Gottlieb et al. (2005), in nesting location, nest architecture, and cell structure. However, the number of cells per nest constructed by *X. olivieri* ranges from 3 to 6 (Gottlieb et al. 2005).

The literature on the nesting biology of carpenter bees (*Xylocopa*) in wood structures is extensive (Hurd 1978; Gerling et al. 1983; Bernardino and Gaglianone 2008; Ali et al. 2017; Lucia et al. 2015, 2017). However, no literature addresses the difference between the breeding nest and the wintering nest. Most carpenter bees nesting in wooden structures winter in the breeding nest built by the mother, and females emerge from the nest after wintering to build breeding nests for reproduction. For example, *Xylocopa tranquebarorum* females winter together in the breeding nest built by the mother. After wintering, these sisters emerge from the nest, looking for sites to build their own nests. Some of the wintering bees use the old nest, while males do not construct nests (He et al. 2009). *X. xinjiangensis*

constructs nests in the soil. The newly enclosed females construct wintering nests solely for the purpose of wintering. The wintering nest is positioned deep below the ground surface, possibly due to the low winter temperatures in the Xinjiang area (the average daily temperature of the coldest month (January) in Manas is -18.4°C , and the lowest daily temperature in -37.4°C). After the wintering bees emerge from their nests to feed, they build breeding nests near the wintering nest for reproduction. *X. xinjiangensis* winters solitarily. Therefore, the nesting characteristics of *X. xinjiangensis* and carpenter bees that nest in wood structures are significant for further study on the evolution of *Xylocopa* from solitary to social wintering.

To date, numerous studies on the nesting biology of *Xylocopa* in wood structures have been published, and the materials reported to be used for nesting include hollow plant stalks and soft wood (Gerling et al. 1989, Ali et al. 2017). A *Xylocopa* female nesting in a hollow stalk first bores an entrance and then sequentially builds cells from the interior of the stalk toward the outside (entrance), taking advantage of the hollow structure (Maeta et al. 1996, He et al. 2009), while a *Xylocopa* female nesting in a soft wood structure bores the entrance and tunnel first and then builds cells sequentially from the inside toward the outside (i.e., toward the entrance) (Hongjamrassilp and Warritt 2014, He et al. 2017). In this study, we investigated the nesting behaviors of *X. xinjiangensis*, which nests in soil. The results showed that when *X. xinjiangensis* females were constructing a breeding nest in the soil, they first excavated a section of tunnel, then began to build the first cell. Afterward,



Fig. 5. Nest architecture of *X. xinjiangensis*. (A) The branching type. (B) The straight-chain type.

Table 1. Parameters of the nest structure and composition of *X. xinjiangensis* in Xinjiang, determined for all the nests examined ($n = 18$, 2013; $n = 8$, 2015; and $n = 9$, 2016)

Nest characteristics	Branching tunnel			Straight-chain tunnel		
	<i>n</i>	min–max	Mean \pm SD	<i>n</i>	min–max	Mean \pm SD
Nest entrance length (mm)	14	8.99–11.19	10.19 \pm 0.81	12	8.89–11.49	9.97 \pm 0.76
Nest entrance width (mm)	14	9.22–11.94	10.51 \pm 0.94	12	9.12–11.96	10.41 \pm 0.83
Tunnel length (cm)	13	9.89–31	16.40 \pm 6.20	6	16.67–22.2	19.40 \pm 2.42
The distance between the nest entrance and the first cell (cm)	13	3.45–27	9.04 \pm 6.80	6	5.35–8.91	6.96 \pm 1.74
Tunnel diameter (cm)	13	1.03–1.27	1.10 \pm 0.08	6	1.05–1.21	1.11 \pm 0.06
Cell length (mm)	59	11.73–24.55	14.93 \pm 1.72	52	11.57–16.68	14.98 \pm 1.09
Cell diameter (mm)	59	8.14–12.9	10.38 \pm 0.97	48	8.18–12.06	10.35 \pm 0.84
Cell wall thickness (mm)	54	0.62–2.41	1.24 \pm 0.38	51	0.78–1.98	1.29 \pm 0.30
The distance between the cells and the tunnel (mm)	34	1.42–11.92	5.48 \pm 2.27	22	4.42–14.98	7.93 \pm 2.70
The distance between adjacent cells (mm)	36	1.57–18.39	6.80 \pm 3.81	18	3.22–22.31	7.21 \pm 4.62
Number of cells per nest	19	5–12	7.53 \pm 2.06	13	6–14	9.77 \pm 2.01
Cell partition thickness (mm)	51	1.03–2.89	1.80 \pm 0.47	40	1.05–2.90	1.89 \pm 0.45

n = number of observations.

they continued to excavate the tunnel to build the second cell. The cells were constructed sequentially from the outside (i.e., from the entrance). This cell-constructing sequence differs completely from that of *Xylocopa* nesting in wood structures. *Xylocopa* nesting in

wood structures construct cells sequentially from the inside; that is, the first offspring bee is located deepest inside the nest. The breeding time span of female bees is normally long (more than 40 d). In *X. xinjiangensis*, if the outermost offspring was not eclosed, the

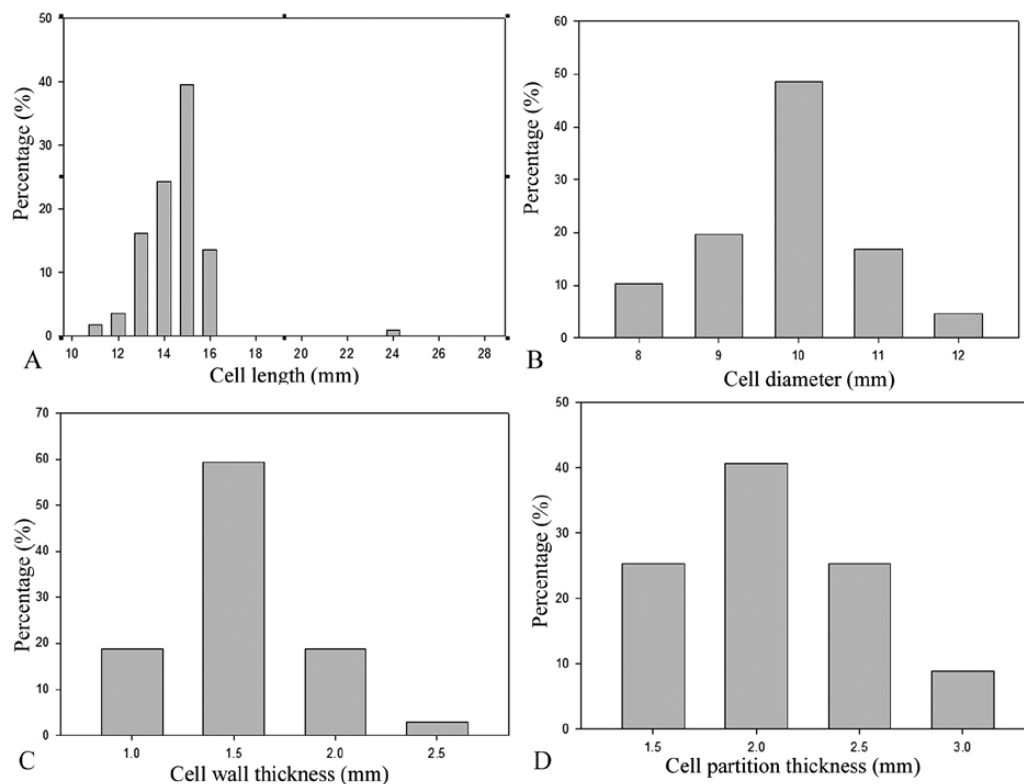


Fig. 6. Nest characteristics of *X. xinjiangensis*. (A) Cell length ($n = 111$). (B) Cell diameter ($n = 107$). (C) Cell wall thickness ($n = 106$). (D) Cell partition thickness ($n = 91$).

innermost offspring would not go out to feed and to guard the nest (He et al. 2009, Hannan et al. 2012, He et al. 2017). Therefore, presumably, this difference in nesting order is related to the brood development and guarding behavior.

The large carpenter bees are an important group for research on the early stages of the social evolution of insects. For the first time, we observed and described the nest building and nesting behavior of *X. xinjiangensis*, which are clearly different from those of the large carpenter bees that nest in wood structures. These differences are of great significance for further study of the evolution of *Xylocopa* from solitary to social habits as well as for species resource protection.

Acknowledgments

Thanks go to Dongshuo Yang from Luoyang Normal University and Yichang Yang from Henan Experimental High School for their kind help in the field collection. We are grateful for the financial support given by the National Natural Science Foundation of China (U1304308) and the Henan Provincial Department of Science and Technology (162102110101).

Conflict of interest

The authors declare no conflict of interests.

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