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Contributed Paper

The Comb Structure of *Apis dorsata* F. (Hymenoptera: Apidae): 3-dimensional Architecture and Resource Partitioning

Ninat Buawangpong [a], Prakaimuk Saraithong [a], Kitiphong Khongphinitbunjong [a], Panuwan Chantawannakul [a]* and Michael Burgett [b]

[a] Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, 50200 Thailand.
[b] Department of Horticulture, Oregon State University, Corvallis, OR 97331 USA.
*Author for correspondence; e-mail: Panuwan@gmail.com

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ABSTRACT

The architecture of the comb structure of the giant honeybee *Apis dorsata* was examined, including cell sizes, comb area, comb volume, and gravimetric capacity. Regardless of comb area, the partitioning of comb between brood rearing and food storage centered around 83% of the comb surface being used for brood production. The potential gravimetric capacity of the total comb was variable displaying a range of 1–2 g per cm^2 of comb surface. The largest comb examined would have had a hypothetical weight of *ca*. 17 kg, while the smallest comb *ca*. 2.0 kg. These calculations do not include the weight of adult bees. A large colony would possess as much as 8 kg of adult worker bees based on an average worker weight of 160 mg.

Key words: *Apis dorsata*, comb structure, hexagon architecture, gravimetric capacity, comb partitioning

1. INTRODUCTION

Apis dorsata F. is one of two species of Asian giant honeybees with a range throughout the Indian subcontinent, Southeast Asia and numerous southwestern Pacific archipelagos [1]. The nest is characterized by a single comb which can develop to a large size accommodating adult bee populations in excess of 70,000 individuals [2]. Giant honeybee colonies are known to exhibit a migratory life style with several colony movements during an annual cycle [3, 4, 5]. As individual combs can be very large, with reported dimensions of 1.5 m x 1 m [6], each colony relocation therefore requires the construction of a new nest comb which represents a major investment of energy and wax material. The wax comb is comprised of hexagonal cells with the overall comb structure generally assuming a semicircular shape under most circumstances. The nest combs are apically attached to the underside of larger diameter tree branches, but often colonies will establish on anthropogenic structures such as water towers and overhanging building eves.

Both giant honeybee species *A. dorsata* and *A. laboriosa* are unique in the genus *Apis* in that the hexagonal cells used for rearing drone and worker brood are the same size, albeit this is a debated point *i.e.*, Tan (2007) [7] reports a statistically significant size difference between drone and worker cells, however previous research reports no consistent difference [6]. The majority of the comb area is used for brood production and the brood cells are comparatively uniform in both diameter and cell depth. The comb area used for colony food storage (nectar, honey, and pollen) is found in the upper top most section of the nest. Both the diameter and depth of honey storage cells are significantly greater than the cells used to rear brood [7].

Our objective was to examine a series of *A. dorsata* combs in Thailand to derive several metrics that would allow for an accurate summarization of comb architecture as it relates to total comb volume, partitioning of comb between brood and food storage, gravimetric holding capacity, and potential honey storage.

2. MATERIALS AND METHODS

We obtained recently abandoned combs from six *A. dorsata* colonies during January and February 2011 from the Chiang Mai University campus, and a private residence dormitory in metropolitan Chiang Mai, Thailand (18° 58′ N, 98° 59′ E). The nests had been established in late 2010 and early 2011. All of the examined combs were from colonies which had absconded prior to producing queens and swarms, *i.e.,* pre-reproductive phase.

The following comb parameters were measured: cell diameter, cell depth, total comb area (sub-divided into honey comb area and brood comb area), total number of brood cells, total honey storage cells, brood comb volume, and honey comb volume. Cell diameters were determined by both measuring series of 10 linear cells as well as measuring individual cells with an ocular micrometer. For calculating the volume of cells the internal cell wall diameter must be used; when calculated the number of cells per cm^2, the diameter of the cell was measured diagonally from the interior to the exterior of the opposing cell wall (septum). Cell depth was determined by measuring the distance from cell top to bottom from linear cell series cut along a sagittal plane through the comb. As the depth of the honey storage cells varies dramatically within a comb and between combs, cell depth measurements for each comb's honey storage area were taken both latitudinal and longitudinally and an average honey cell depth was calculatedfor each individual comb's honey storage area.

The total comb area was determined by transferring the comb outline onto paper. This outline was then scanned to produce a digital .jpg image. This format was used as the input for the public domain software program "ImageJ" (U.S. National Institutes of Health) which calculated the area into cm^2. A separate scan was made for the honey comb area and the brood comb area for each of the six combs.

For determining a potential colony biomass, an average weight was determined for honey (1liter), and the combined capped brood, wax comb substrate (g/cm^2 of comb surface area). Honey and brood samples for weight determination were taken from three active *A. dorsata* colonies in January 2012. To compare the difference between the mean cell diameters of brood and honey cells, a one-tail ANOVA was used.

3. RESULTS

All six combs possessed the stereotypic semicircular form. The widths, as measured across the tops of the combs, ranged from 33.5 cm to 91 cm; the depths, measured from the top to the comb down to the bottom, ranged from 30.5 cm to 73 cm.The largest comb (C4) had an area (both comb sides) of 8,314 cm^2, while the smallest (C5) an area of 1,744 cm^2. The average cell sizes (diameter and depth) for both brood cells and honey cells are shown in Table 1 and Figure 1. They are in close agreement with previous studies [1, 6, 7]. The average diameter and depth of honey cells were larger than that of brood cells. Our range of brood cell diameters (5.1 – 6.1 mm) closely matches those reported by Tan (2007) [7] (5.2 – 6.1 mm). We were not able to discriminate any cell size difference between worker brood cells and drone cells as reported by Tan (2007) [7], albeit the combs in our study possessed no brood, therefore we were unable to determine if a brood cell had been used to produce a drone or worker. The difference between the mean cell diameters of brood and honey cells was statistically significant ($P < 0.001$, ANOVA test).

Table 1. Mean cell dimensions as determined from six *Apis dorsata* combs. A caveat is that honey cell depth will display large variations within a single comb and between multiple combs.

Cell Type	Dia. ± SD (mm)	Area ± SD (mm^2)[1]	Cells/cm^2 ± SD	Depth ± SD (mm)	Volume ± SD (mm^3)[2]
Brood	5.54 ± 0.16	26.58 ± 0.60	3.76 ± 0.09	16.79 ± 0.65	406.89 ± 14.98
Honey	6.25 ± 0.39	33.83 ± 1.15	2.96 ± 0.10	variable	variable

[1] The area of a hexagon = the diameter^2 x "3/2

[2] For cell volume determination, the cell interior diameter was used (*i.e.*, 5.29 mm for brood cells, 6.00 mm for honey cells)

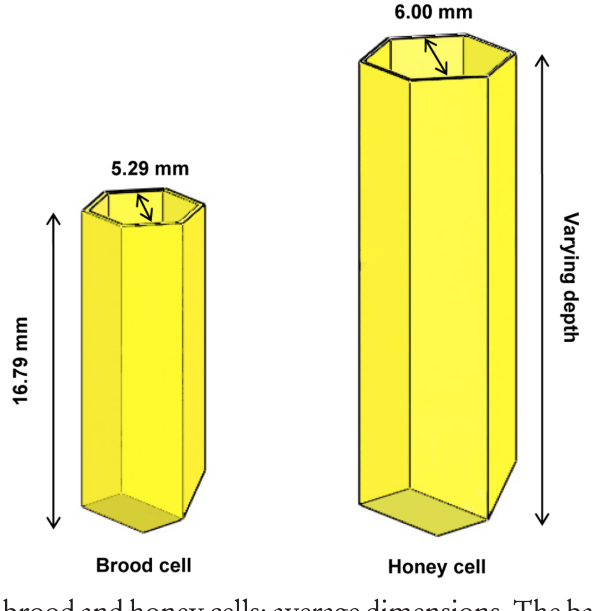

Figure 1. *A. dorsata* brood and honey cells; average dimensions. The bases of the hexagonal cells are trihedral, with only one of the three planes as shown. *Schematic by Mr. Prapat Thongjun, Post-Harvest Technology Research Institute, Chiang Mai University.

Table 2 summarizes the metrics of the six combs. Determining the total number of cells per comb was done by multiplying the known comb area (cm^2) by the number of cells per cm^2 (3.76 and 2.96 cells per cm^2 for brood and honey cells respectively). Our largest comb (C4) possessed nearly 5 times as many cells as the smallest comb examined (C5). As the combs used in this study were from colonies that had absconded prior to reproductive maturity and therefore represent colonies of varying ages, it was not unexpected to see a broad range of variation in comb area and the total number of cells between the six combs. One measure that possessed only a small difference between colonies was that of the proportion of comb area devoted to brood production *vs*. food storage. On average, 82.7% of the total comb area was used for brood production with a range of 80.2% to 88.0%, with the remainder of the comb used for food storage, primarily nectar and honey. The average volume of abrood cell was 406.9 mm^3. A universal average volume for a honey storage cell could not be computed due to the great variability in honey cell depth. However, by calculating an average honey cell depth for each individual comb's honey storage area we were able to derive a mean honey cell volume on a per comb basis. Following the determination of average brood and honey cell volumes, it is astraight-forward matter to calculate the total volumes for both the brood comb and the honey storage comb for each examined colony.

Table 2. Summarized metrics for *Apis dorsata* combs 1-6.

	C1	C2	C3	C4	C5	C6
Σ comb area (cm^2)	2,790	6,366	6,956	8,314	1,744	3,120
Honey combarea (cm^2)	552	764	1,252	1,568	322	526
Brood comb area (cm^2)	2,238	5,602	5,704	6,746	1,422	2,594
% brood comb	80.2	88.0	82.0	81.1	81.5	83.1
Σ cells	10,043	23,317	25,140	29,991	6,296	11,310
Honey cells	1,628	2,254	3,693	4,626	950	1,557
Brood cells	8,415	21,063	21,447	25,365	5,346	9,753
Σ comb vol. (l)	4.97	11.07	13.57	20.29	3.08	6.73
Honey comb vol. (l)	1.21	1.67	3.99	8.96	0.69	2.76
Brood comb vol. (l)	3.76	9.40	9.58	11.33	2.39	3.97

A hypothetical gravimetric capacity for a comb can be obtained by summing the weights of the honey and brood. *A. dorsata* honey weight varies slightly according to the moisture content, but from a series of honey samples taken from separatelyharvested honey combs, we obtained a weight of 1.35 kg/l. Brood weight estimates are based on capped broodsamples which averaged 0.9 g/cm^2 of comb surface area. Table 3 provides estimates of the gravimetric holding capacity for the six combs examined. An additional weight, which we have not taken into consideration, is that of the adult bees. From samples of curtain bees taken from living *A. dorsata* colonies, we derived an average worker bee weight of 160.5 ± 21.8 mg which is *ca*. 6,230 worker bees/kg. Because the combs used in this study had been abandoned, we have no way of knowing the populations of adult bees prior to absconding.Worker bee density per unit area of comb has only been determined for the European honeybee *A.*

mellifera[8]and as no published data exist regarding *A. dorsata*worker bee density per cm^2 of comb, we were unable to estimate adult bee populations from the comb area for the combs used in this study.

4. DISCUSSION AND CONCLUSION

Our observations for brood and honey cell width are in agreement with previously reports. Tan (2007) [7] reported a statistically significant cell width difference between brood cells used for rearing drones *vs*. cells used to rear workers. While we do not dispute his finding *per se*, we note that his range of widths for 'worker' brood cells is 5.2-6.1 mm, and the range for 'drone' brood cells is 5.5-6.1mm. Our brood cell range was 5.1-6.1 mm. Our interpretation is that within the combined ranges Tan reported (5.2-6.1 mm), drones are produced in the mid- to upper rangecell widths, while worker brood are successfully reared in any cell size within the entire range of brood cell diameters.

Table 4 summarizes previous reports of comb cell metrics between five *Apis* species. For both dwarf honeybee species (*A. andreniformis* and *A. florea*), and the cavity nesting *A. cerana* and *A. mellifera*, there are two distinct cell types involved in brood rearing; the larger brood cells for rearing drones and the smaller cells for rearing worker bees. Additionally for the two dwarf honeybee species, the honey storage cells are much deeper (elongated) that cells used for rearing brood (Burgett pers. obs.) and therefore an average depth is not attainable except on a per colony basis.

Our study of giant honeybees comb architecture reiterates that cells for rearing both drone and worker brood are of a uniform size, albeit with *ca*. an 18% variability. Honey storage cells are greater in both width and depth than brood cells which are more uniform, suggesting that there is natural adaptation to have larger honey cells that while economizing surface area, also possess greater volume, resulting in an efficient use of wax.

Concerning honey storage Tan (2007) [7] reported that colonies can possess *ca*. 4 kg of honey 3-4 weeks following nest initiation. From a large sample size of 152 colonies he reported a maximum of 15.7 kg of honey. The six combs we examined varied in potential honey storage (based on the volumes of the honey storage areas), but our largest colony could have theoretically held *ca*. 12 kg of honey.

Table 3 summarizes hypothetical colony weights for the six combs we examined, which ranged from a low of 1.97 kg (C5) to a high of 16.96 kg (C6). This does not include the weight of the adult bees. Relying on the limited data of Morse and Laigo (1969) [2], who reported colonies with as many as 70,000 workers, a colony large enough to have such a population would possess *ca*. 11 kilograms of adult bees in addition to the weight of the comb, brood and food stores. In a study examining the mechanical properties of wax from four honeybee species, Buchwald etal. (2006) [9] reported that the wax from *A. dorsata* was the strongest and stiffest wax of the four species examined. Due to the weight of the single comb nest, attached to the underside of a substrate, the findings of Buchwald et al. are not unanticipated, and, as they point out, conform to the nesting ecology of this giant honeybee species.

Table 3. Potential gravimetric capacity; combs 1-6.The potential is based on the assumption that the honey storage area is completely utilized and the brood comb is at 80% capacity.

Comb	Brood (kg)[1]	Honey (kg)[2]	Σ brood & honey (kg)
1	1.61	1.63	3.24
2	4.03	2.25	6.28
3	4.10	5.39	9.49
4	4.86	12.10	16.96
5	1.04	0.93	1.97
6	1.86	3.73	5.59

[1]brood wt.=0.9 g/cm^2 capped brood

[2]honey = 1.35 kg/l

Table 4. Comparisons of cell width and cell depth between five honeybees species.

Cell Type	*A. andreniformis*	*A. florea*	*A. cerana*	*A. mellifera*	*A. dorsata*
Worker					
Width (mm)	2.78±0.23[1]	2.98±0.15[1]	3.6-4.9[2,3,4,5]	5.2[6]	4.5-5.9[7,8,9]
Depth (mm)	7.60±0.20[1]	9.30±0.70[1]	10.1[2]	11.0[6]	16.0-19.0[7,8,9]
Drone					
Width (mm)	4.18±0.24[1]	4.88±0.21[1]	4.7-5.3[3]	6.2[6]	5.81±0.14[9]
Depth (mm)	14.50±7.10[1]	13.30±0.70[1]	ND	12.5[6]	19.0±0.4[9]
Honey					
Width (mm)	ND	ND	ND	ND	6.39±0.3[9]
Depth (mm)	ND	ND	ND	ND	variable[9]

[1]Rinderer et al. (1996)
[2]Inoue et al. (1990)
[3]Crane (1993)
[4]Tingek et al. (1996)
[5]Ruttner (1988)
[6]Seeley and Morse (1976)
[7]Doedikar et al. (1977)
[8]Thakar and Tonapi (1961)
[9]Tan (2007)
*ND: No data available

We would suggest that based on size (comb area), the number of adult bees and weight, colonies of the giant honeybee *A. dorsata* should be considered as a species of the mega-faunal community in the tropical ecosystems where they exist; playing a vital role as pollinators contributing to the botanical biodiversity wherever they occur. We are in agreement with Oldroyd and Wongsiri (2006) [6] who comment that a colony of *A. dorsata* "...is a thing of wonder..."

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