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ARAŞTIRMA MAKALESİ / RESEARCH ARTICLE

MAY THE HONEYCOMB ARCHITECTURAL DEVIATIONS REFLECT THE BEES ENGINEERING PROWESS?

Petek Mimari Sapmaları Arıların Mühendislik Yeteneklerini Yansıtabilir mi?

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ABSTRACT

This study affords the experimental evidences elucidate the putative mechanism of the bee comb establishing. Furthermore, the first time discerned skewed triangular prism in the bottom of the cells ab initio built up by *Apis mellifera carpatica* indicates that the traditional rhombic dodecahedra is not mandatory element of the comb architecture. The revealed oddity is inherent to about one third of the whole number of the cells constitute the analyzed patterns. The building abnormality presumably developed from the primeval manner of cells construction and may be triggered with the volatile natural factors e.g. geographic location and climatic zone, variety of floral shapes, duration of active season as well as bee race. Disclosed constructional diversity mirror the reaction of the colonies on the highlighted disturbances and might be stipulated by the bees' ability to engineering prowess.

Key words: *Apis mellifera carpatica*, Cells construction, Design fluctuation, Bees' ingenuity

ÖZ

Bu çalışma, arı peteği kurmanın varsayımsal mekanizmasını aydınlatan deneysel kanıtlar sunmaktadır. Ayrıca, *Apis mellifera carpatica* tarafından ab initio olarak inşa edilen hücrelerin alt kısmında ilk kez fark edilen çarpık üçgen prizma, geleneksel eşkenar dörtgen dodecahedra'nın tarak mimarisinin zorunlu öğesi olmadığını gösterir. Ortaya çıkan tuhaflık, analiz edilen kalıpları oluşturan tüm hücre sayısının yaklaşık üçte birine özgüdür. Bina anormalliği muhtemelen ilkel hücre yapımı tarzından gelişmiştir ve uçucu doğal faktörlerle tetiklenebilir, örn. coğrafi konum ve iklim bölgesi, çiçek şekillerinin çeşitliliği, aktif mevsim süresi ve arı ırkı. Açıklanan yapısal çeşitlilik, kolonilerin vurgulanan rahatsızlıklar üzerindeki tepkisini yansıtır ve arıların mühendislik hünerleri tarafından şart koşulabilir.

Anahtar kelimeler: *Apis mellifera carpatica*, Hücre yapımı, Tasarım dalgalanması, Arıların hüneri

GENIŞLETILMIŞ ÖZET

Amaç: Araştırma, tamamen Apis mellifera carpatica tarafından inşa edilmiş (ab initio) petek yapısının özgünlüğünün araştırılmasına yöneliktir.

Gereç ve Yöntem: Tüm petek örnekleri arı tarafından ab initio yapılmış ve en az beş Apis mellifera carpatica kolonisinden toplanmıştır. Büyüyen erkek arıları veya arı hücrelerini içeren analiz edilen desenler, çerçevenin alt tahtasına yapıştırıldı ve bir aktif sezon boyunca oluşturuldu. Bir durumda incelenen tarak çerçevenin içine dikilmiştir. Tüm koloniler 10-12 çerçeveli (435×300 mm) Dadant Blatt tipi kovanlarda yaşamış ve her birinin gücü 30-40 bin birey olarak tahmin edilmiştir. Arı kovanının yeri 49°34´ K, 22°47´ Doğu (Doğu Beskids, Ukrayna) idi. Numunelerin (yetiştirme dronlarından veya arılardan) boyutları (12-13) × (7-8) cm ila (16-18) × (9-10) cm arasında değişmiştir.

Bulgular ve Tartışma: Farklı kolonilerden alınan çok sayıda geri çekilmiş petek deseninin görsel şeklinin incelenmesi, elementlerin yapısındaki sapmanın ortaya çıkmasına neden olmuştur. Mesele şu ki, tam hücre sayısının yaklaşık %30-40'ının taban profili, ya yetiştirici erkek arılardan oluşuyor ya da arılar, geleneksel üç eşkenar dörtgenden farklıydı ve eğik üçgen prizma olarak tasvir edildi. Geometrik simülasyon nedeniyle, tarağın yapımı, seminal hücrenin yalnızca gelecekteki tarağın bir tarafında temel alınmasından başlayabilir. Bu hücrenin yuvarlak şekilli tabanı tamamlandıktan hemen sonra, ikinci ve üçüncü (sağ veya sol kenarı) petek çekirdeğin her iki yanında aynı anda oluşmaya başlar. Önemli olarak, tarak plakasının bir karşı tarafında bulunan hücrelerin merkezleri, karşı parçaya kıyasla çapının yarısına eşit mesafelerle kaydırılır. Yani hücre tabanının kenarı en yakın komşularla birer nokta temas eder. Başlangıçta, çevreleyen komşuların sayısı iki (hücrelerin bir sırası), sonra dört (hücrenin iki sırası) ve son olarak altıdır (hücrelerin üç ve daha yüksek sırası). Bu mimari sayesinde ve çalışan arıların yükselttiği sıcaklıkla, karşıt yarım küre şeklindeki hücrelerin ortak tabanları neredeyse anında ve kendiliğinden, prizmatik tabanlarla birleştirilmiş iki katmanlı altıgen hücre dizisini oluşturur hale gelir. Böyle bir temas esastır çünkü yokluğunda (örneğin ahşap kovan çerçevelerinin tahtaları bu tür bir bindirmeyi engelliyorsa/ayırıyorsa) hücre tabanının profili yarım küre şeklinde kalır. Önerilen geometriye göre, her hücrenin alt kısmında çarpık üçgen prizmaya sahip olması gerekir. Oysa hücrelerin sadece üçte biri bu kuralla eşleşir. Açıklanan uyumsuzluk, fiziksel (hava durumu, coğrafi konum, besin temeli, Dünya manyetik alanının gücü) ve biyolojik (arı ırkı) dahil olmak üzere çeşitli faktörlerden kaynaklanabilir. Öte yandan, bu tür bir etki üzerindeki tepki oranı, eninde sonunda örneğin, hücre elemanlarını düzeltmek için arıların içgüdüsel ustalıklarından gelebilir.

Sonuç: Son olarak, bu sonuçlar, petek oluşumundan sorumlu olabilecek temel faktörler (arıların fiziksel güçleri veya becerisi) hakkında yüzyıllardır devam eden anlaşmazlığın çözülmesine yardımcı olacaktır.

INTRODUCTION

The visible (even not global) changes of dead Nature in most cases modify the living specimens both the shape and behavior. This postulate become the cornerstone of evolutional theories either classical natural selection (Darwin 1859) or modern genetic (synthetic) (Koonin 2009) ones. Although the replies of living Nature at such impact are postponed and at the first glance not so noticeable as the formers, it has great impact on evolution of the individual species and higher taxonomic ranks. Considering the social insects (e.g. bees) the spotlighted effect may be also reflected with alteration of their engineering capability in the way that “Slight changes in the rules followed by cell builders can cause radical shifts in the final nest architecture” (Oldroyd et al. 2015). As authors claimed, such changes may be triggered by several factors, including bees race, climatic zone (i.e. geographic region), variety of floral shapes, duration of active season, etc. Actually, these elements influence the building process of others kinds of collective insects too. For example, “…termites can be induced to build structures that radically depart from normal nests through targeted interference at critical stages of construction.” (Turner 2010). On the other hand, the building action frequently demands connecting the larger drone cells with the smaller ones of workers or encounters the obstacles. In these cases, the bees incorporate the transition zones where the shapes of the comb are often distorted (Sparavigna 2016). Admittedly, such behavior might evolve from the engineering capability of colony.

Then the origin of honey bee awesome architecture intrigued the generations of many brilliant scientists. Up today the true manner of the bees construct their nests remains ambiguous that is reflected with two opposite hypotheses. One of it admits participation solely the physical laws in shaping of the comb cells. The adherents of this postulate, e.g. Middle Age Danish mathematician Bartholin (Bartholin 1660), Thompson (Thompson 1917) Pirk and Karihaloo (Pirk et al. 2004, Karihaloo et al. 2013) suggested that honeybees neither have to measure nor construct the highly regular structures of a honeycomb, and the observed shape of combs can be explained by wax flowing in liquid equilibrium. They theorized that the perfect regular structure results from wax as a thermoplastic building medium, which softens and hardens as result of increasing and decreasing temperatures. Whereas their opponents (Pappus of Alexandria 5th century AD), (Darwin 1859), (Nazzi 2016), (Gallo et al. 2018) advocate the essential role of the individuals and their participation in the whole stages of comb construction all through it foundation to the full size erection. The adepts of the second theory arguing that hexagons on the honeycomb, "…besides perfectly economize labor and wax, also symbolize communication, balance, precision, union, equality and integration thus reflect the bees' masterpiece of art in engineering" (Darwin 1859). Continuing of such approach, Bauer (Bauer et al. 2013) has shown that many of the bees are engaged in direct construction in a way encompasses a regular sequence to manipulate the wax. In this case, some bees have to support their colleagues work by actively warming the wax. The authors reasoned that the wax temperature during the construction of the hexagonal cells was between 33.6 and 37.6 °C whereas existing the wax in the liquid equilibrium (essential for self-organized building) demands 40 °C. Both of these postulates (although utilize the different approaches) devoted to the elucidation a putative mechanism of cells erection. Regardless the long-lasting story of this dispute and apart from a couple theoretical works (Narumi et al. 2018, Narumi et al. 2022), the highlighted hypotheses still lack the consistent experimental data concerns the interim (particularly the ones proceeding right after the cell foundation) stages of honeycomb construction. Then the final decision yet encountered with the key assertion combines the bees architectural creativeness and physical laws.

Cited oddities and claim inspired us to undertake thorough analyze the elements of honeycomb setting up. We reckoned that the cells bottom as the construction fundament may afford the valuable clue concerning the comb architecture. On the other hand, mentioned moiety deviation might also encode the information relates the evolution of comb design. For this aim the patterns of honeycomb both the rearing drones and bees made up fully (ab initio) by the bees were selected. We intentionally did not explore the cells built up on the artificial wax plate as the later already possess the triple-rhomboids printed at it base. The results of such approach are presented therein.

MATERIALS AND METHODS

Honeycomb patterns analysis

All samples of honeycombs were *ab initio*-made by the bee and collected from at least five colonies *Apis mellifera carpatica.* The analyzed patterns, comprised either rearing drones or bee cells, were attached to the bottom plank of the frame and built up during one active season. In one case the examined comb was erected inside the frame. All colonies lived in *Dadant Blatt type beehives with 10-12 frames (*435×300 mm*) and the strength of each was estimated as 30-40 thousands of individuals. The* location *of apiary was 49°34´ N, 22°47´ E (Eastern Beskids, Ukraine).* The samples (either from rearing drones or bees) sizes varied within (12-13) × (7-8) cm to (16-18) × (9-10) cm. Magnifying glass was used for inspection the withdrawn comb patterns. Such methodology belonged to the most cheap, handy, non-invasive and non-destructive one thus used broadly for studying the stagnant objects both living and dead Nature (Headstrom 1968). The surface areas of the analyzed samples were calculated by Area Calculator program Scetchandcalc (free trial version is accessible in the net). The percentage (*n*) of comb surface occupied by the cells possess the bases differed (S_{STP}) from the triple-rhomboid ones was estimated as:

$n = S_{STP}/S_{tot}$, where: S_{tot} - the total area of the comb pattern.

Few examples of such modellings are presented at Fig. S3.

Instruments

The photos of the specimens were taken by Cannon CX 620 HS and HP Photosmart R 707 cameras. Hand lens 5× (occasionally 10×) was used for visual inspection the honeycomb samples.

RESULTS

The manner of the bees may start to erect the honeycomb is imprinted at Fig. 1. Meticulous examination of this fully bee-made pattern unraveled some interesting features. First of all, regardless the edges of the bottoms of starting cells (rows *1* and 2) have a circular full-faces, it profiles, even in a very beginning period of construction, were not plane and encompass the junction structures (Fig. 1a, inset drown in grey). Starting already from the initial rows this "pre-comb" was constructed from the cells shared it circular-shaped closed bases. Importantly, the manner of the rows are built up implies the horizontal shifting of the cells centers both at the back and front sides of the comb plate on the distance equal the half of cell diameter *d* (Fig. 1, *a* and *b*). Due to such technique, each cell base contacts by it edge with six surrounding neighbors. Locations of contacts are pointed out by the green double-sided arrows (Fig. 1*a* and inset). Such mode, on the other hand, affords a triple junction among neighboring circular cells on the both moieties of the same comb plate. It led to formation the curved triangle-looks gaps (pointed by the red arrows, Fig. 1*a* and inset).

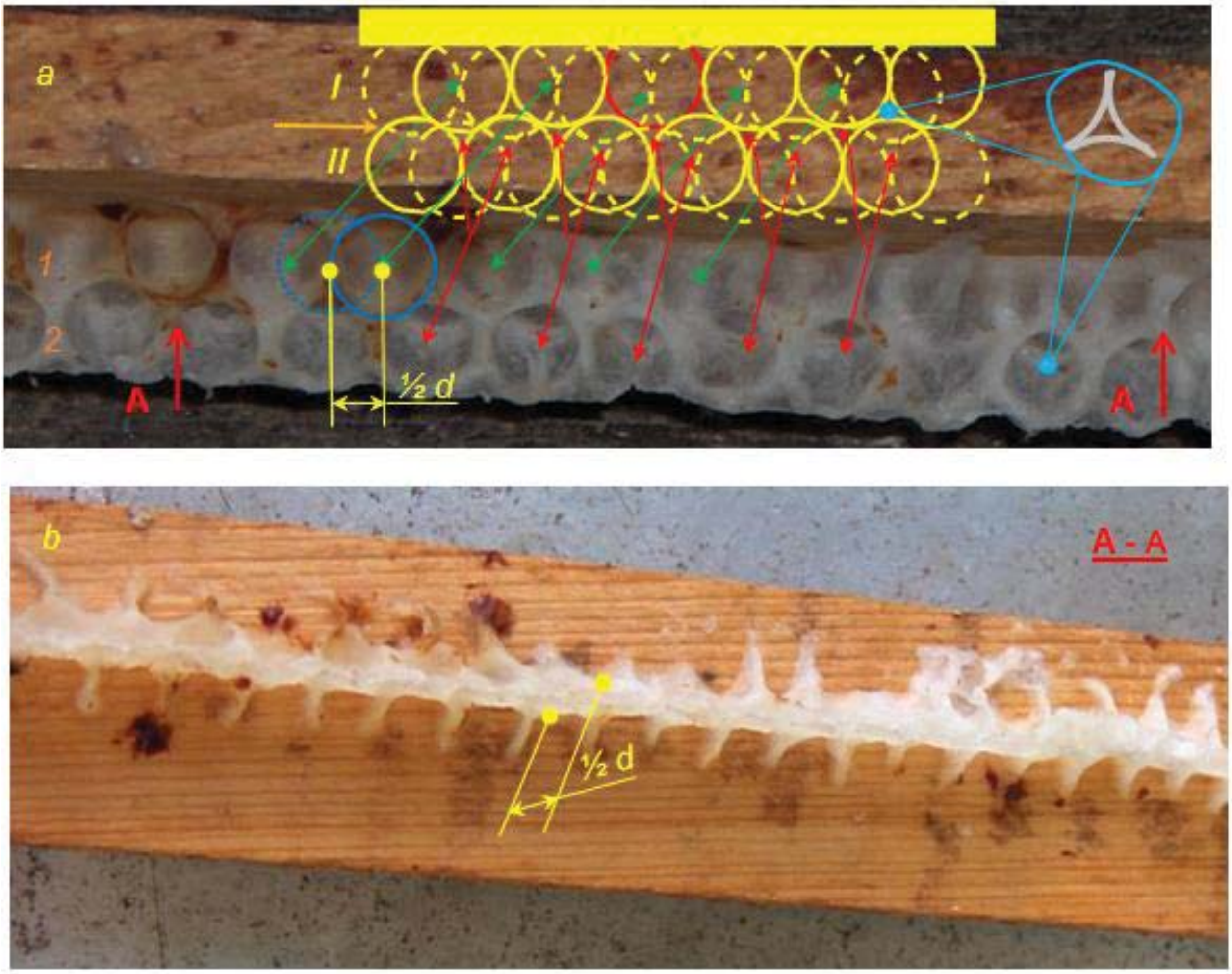

Fig. 1. Two photos on the same section of pattern withdrawn in the very beginning period of it growing. Images represent the front (*a*) and interior (*b*) (A-A) side of the same top plank of the wooden hive frame. The edges of the cells bottoms create the rows *1* and *2* are circular (cylinder). The inset at (*a*) simulates the full face of the cells bottoms where the back and the front moieties are outlined with the dash and solid lines, respectively. The top edge of the putative seminal cell is marked by the red circle. The centers of the back (blue dotted circle) and front (blue solid circle) cells at (*a*) are pointed with the yellow spots (*a*, *b*).

The last ones are created by the arcs of each series of three contacted cells (Fig. 1*a*, inset drown in grey) along the imaginary border separates the bottom of the row ***I*** and top of the row ***II*** (indicated with the gold arrow, Fig. 1*a* inset). Secondly, the circular-shaped bottoms of the newly-founded cells instantly transformed into the ones formed with trihedral sections of rhombic dodecahedra (Fig. S1; Fig. 2*a*, the cells spotted by red). Interesting, but when the cells were erected on the solid support it orientation was vertically up or down and hemispherical bottoms remained intact all the way through foundation till full size erection (the red-dotted cells, Fig. 2*b, c*). Thirdly, scrutinizing the several patterns of honeycombs fully (without using the artificial wax plate) made by the bees revealed the intriguingly feature of it construction (Fig. 3 and S2). The matter is that the bottom structure of the *ca.* 30-40 % of the comb cells differs from the traditional tetrahedral one (Fig. S1, S3). Instead, the shape of figure in the base of many cells was associated with the one we called "skewed triangular prism" (Fig. 3 inset). Again, the exhibited oddity was intrinsic exclusively to the honeycomb made fully *ab initio* by the bees (i.e. the cells erected on the artificial wax plates did not display such abnormality which, in fact, was comprehensible due to the triangular prisms originally stamped at it surface). Fourthly, such kind of cells were located compactly i.e. not scattered over the whole area of the comb (Fig. 3, Fig. S2, S3).

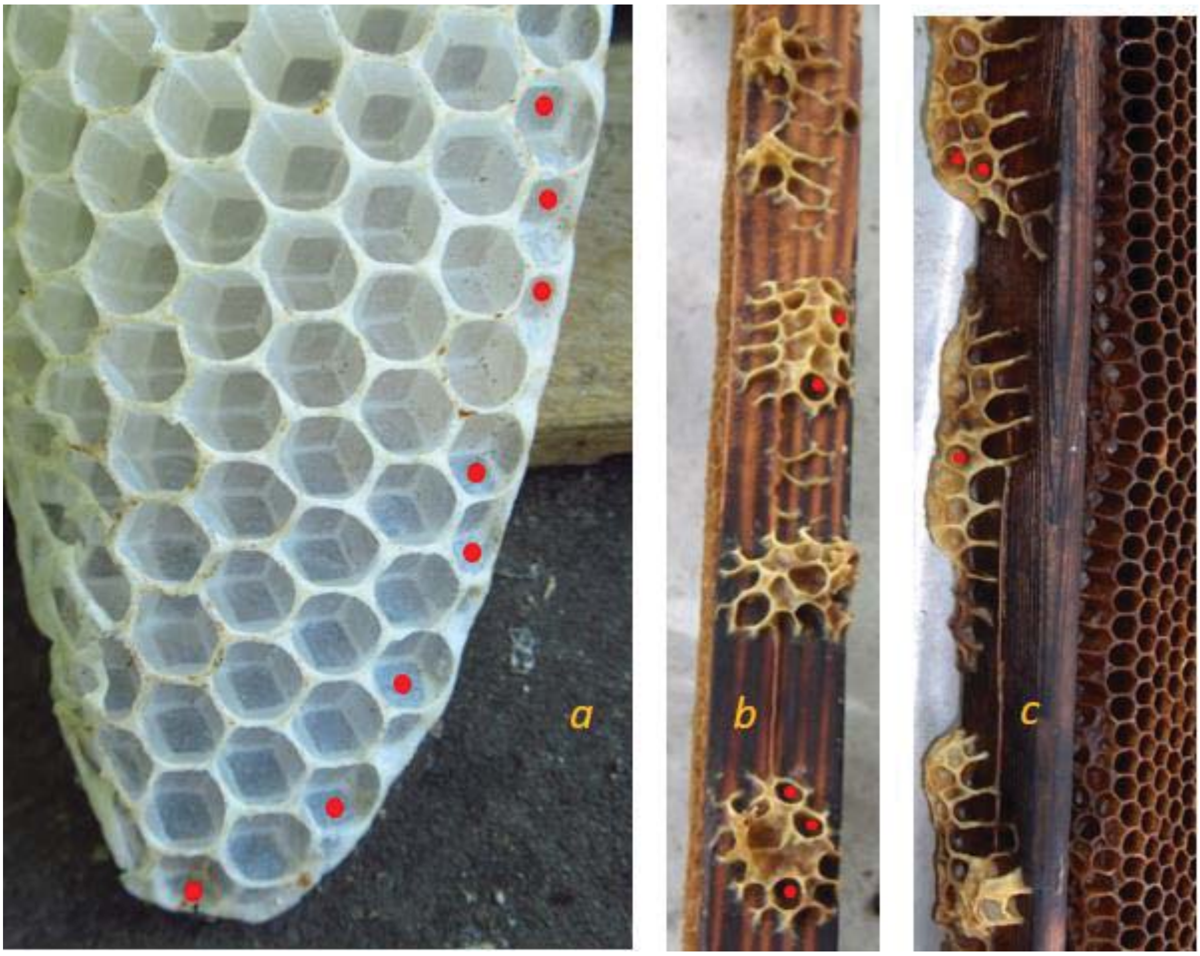

Fig. 2. The totally bee-made segment of the honeycomb (*a*) and the bee wax structures glued to the exterior part of the top (*b*) and floor (*c*) planks of the wooden hive frames. The red spots mark the new-founded cells.

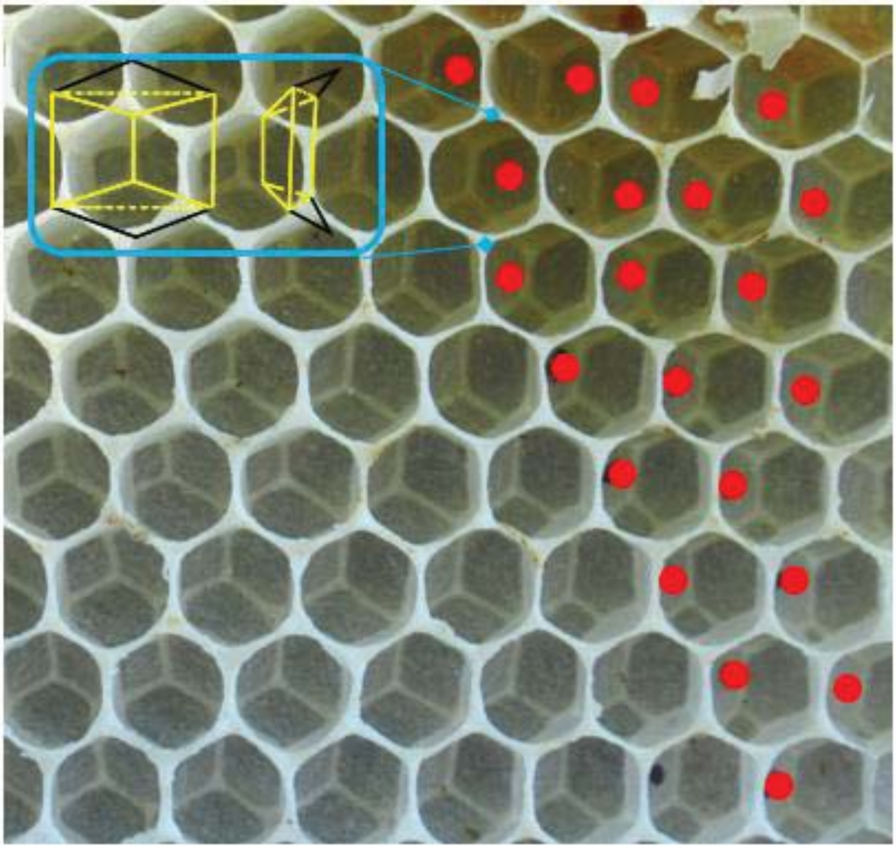

Fig. 3. Photo of the drones comb fragment fully made by the bees visualizes the new shape of cells base structure (yellow-lined figures inside the blue rectangle, left half-part of the view). The best visible “imperfections” (the cells possess the skewed triangular prism bottoms) are spotted by the red circles. The left moiety of the inserted figure (inside the blue-lined rectangle) was obtained by the revolving the right one on 90°.

DISCUSSION

Given the above data, one can assume that construction the initially hemispherical bottoms of the cell at the both sides of the same plate may start from it reciprocal horizontal shifting by the half-cell diameter (Fig. 1). Synchronized building/heating procedures causes the hemispherical bases instant transformation at proper (34-37 °C) temperature (Bauer et al. 2013, Narumi et al. 2018) into it pyramidal derivatives consisting of three rhomboid plates (Fig. 2*a*, the cells spotted by the red dots). In the absence of superimposed cells (i.e. the cells situated at the opposite sides of the same comb plate and share the same bottoms) the closed ends of the cells remain hemispherical. For example, the planks of wooden hive frames prevent such superimposition (Fig. 2*b, c*). In this case, the cells can be oriented vertically up and down only (there are no cells oriented horizontally). Last peculiarities hamper the transformation of hemispherical cells bottoms into three rhomboids (Fig. 2). The revealed instant conversion of circular cell base into rhomboids, in some aspect conflicts with Pirk (Pirk et al. 2004) postulate (“The three apparent rhomboids forming the base of each cell do not exist but arise as optical artefacts from looking through semi-transparent combs”). Nevertheless, on the other side, our results complement the cited work (as well as attachment-excavation model (Narumi T et al. 2022)) in the sense of the comb origination from the wax softening/hardening as result of increasing/decreasing temperature (Karihaloo et al. 2013). Again, the discovered peculiarities of construction relate to the comb fully (ab initio) made by the bees.

Finally, the graphical simulation of building process (Fig. 4 and 3, inset) indicates that geometrically the cells bottoms should be skewed triangular prisms. Whereas in fact the major part (rendering 60-70%) of naturally produced comb is built up from the cells have in it base the rhombic dodecahedra (Fig. 1, 3, S2). This paradox motivated us to undertake thorough inspection the numerous patterns of the combs withdrawn from the different families. Such scrutinizing succeeded in unravelling the already mentioned cells possess the predicted skewed triangular prism-shaped bottoms (Fig. 3 and S2). (Except the base, the other cell elements e.g. it depth, hexagonal shaped rim, the top (opened) area and the slope *upward* value were the same as in the ones possessed the rhombic dodecahedra bottoms). The discussed observations correspond with the ones distinguished by (Nazzi 2016). For example, similarly as postulated by the cited work, the addition of the new cell between two pre-existing ones (Fig. 4) generates two triple junctions that may exhibit the involvements both the liquid equilibrium process (Pirk et al. 2004) and alternative mechanism (Bauer et al. 2013, Narumi et al. 2022). The construction of the cell walls starts as soon as the cell base reaches a certain size. Consequently, the two sides of the honeycomb grow in synchrony in the manner that the beginning of the construction of the cell base coincides with the construction of the lateral walls of a cell on the opposite side. The described geometry rule consists with the one promoted by Nazzi and accompanies it with the revealed new kind of the cell base.

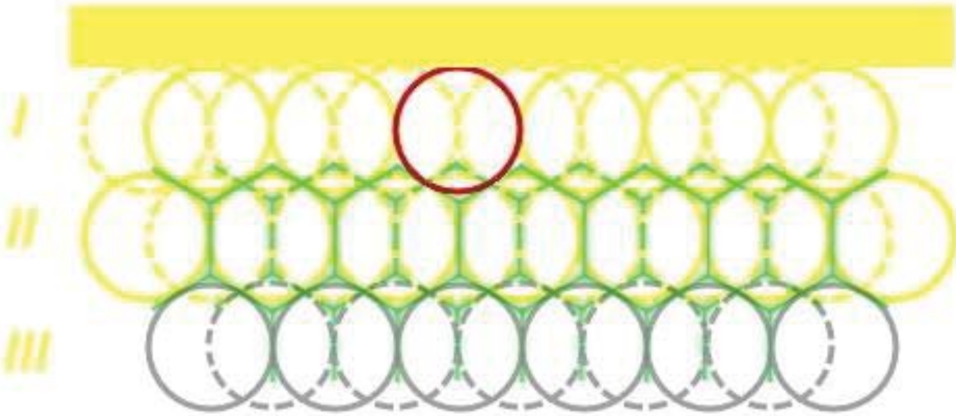

Fig. 4. The graphical simulation the initial three rows of the comb construction. The top of cells and embracing it hexagons are drown with solid (front) and dash (back) circles, respectively. Similarly, the cells of the imaginary rows *III* are represented by the solid (front) and dashed (back) grey rings. The purple circle depicts the putative seminal cell.

By now, it is hard to proffer the unequivocal explanation the simultaneous existence two kinds of structures (traditional tetrahedral and newly disclosed skewed triangular prism ones) of the cells bottoms. Supposedly, the discovered diversity of the cells bases may reflect: *(i)* the engineering prowess of the bees (imprinted with their ability to build up the same-purposed but differently-shaped structural elements); *(ii)* the traces of bees relict architecture; *(iii)* sort of "architectural mistake" (actually, the last rationale supports the item *(i)*). Nevertheless, the reasons of "correction" the forecasted by geometry skewed triangular prism-shaped bottoms to the well-known tetrahedral ones remained to be clarified. To narrow the discussion down the subject related with the deformation the initial circular cell walls to rounded hexagons was not reviewed within the undertaken research (Fig. 4). The detailed putative mechanism of that as well as further transformation the close packed cylinders into hexagonal prisms can be find in the literature (Talukdar et al. 2019, Nazzi 2016). Again, this study pursued the disclosing of evidences, rules and objectives owing to which the comb may start to originate and lead to the newly revealed kind of cells bottom.

Conclusion

The new kind of the cell bottom profile (skewed triangular prism) was disclosed. The putative mechanism of comb building leads to the revealed oddity presumably evolved from the bees' ingenuity and triggered by the volatile natural factors. The bee response on such impact eventually depends on the colony/species adaptation to the stress. The velocity of reaction presumably differs from the one to another bee race but still implies the creativeness of individuals imprinted by e.g. their mastering to correct the cell elements. Although such aptitude has been developed by the previous millions honeybees' generations one still might expect to find out the footprint of this ancient mastering. Last suggestion is grounded on the newly revealed shape of the cells base different to the traditional triple-rhomboid ones. This kind of deviation might be explicated by the primal manner of cells construction. Acquired data, on the other hand, may point out that either physics (self-organizing)- or cognitive (behavioral)-grounded approaches are likely involved in honeycomb construction. In truth, both of it are intentional i.e. origin from the coordinated efforts of many inhabitants the bee colony thus cannot be separated from each other. Finally, these results would assist in resolving the centuries-lasted dispute about the key factors (physical forces or skill of bees) may be responsible for the honeycomb formation.

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Author contributions: Conceptualization: APP, Methodology: APP, Investigation: APP, Visualization: APP, ABZ, Writing – original draft: APP, Writing – review & editing: APP, ABZ

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