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Original article

The cell bases of honeybee combs*

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Abstract – Pirk et al. [Naturwissenschaften 91, 350–353 (2004)] posited that beeswax is a thermoplastic medium that softens with increasing temperature and literally flows among an array of close-packed cylinders, which are actually the self-heated building bees and so hexagonal cells arise quite passively. But, it was further argued that the three apparent rhomboids of the cell base arise as optical artefacts. A re-examination of the cell bases of freshly drawn comb, old comb, and the silk residues of wax-extracted old combs prepared from a silicone-based moulding rubber preparation showed that three perfect rhomboids are seen to form the trihedral pyramid in the cell base (Fig. 1), those of old combs show hemispheres inside the cell bases (Fig. 2). Longitudinal sections of old combs clearly show the parabolic curvature of the inside of the cell base; but the edges of rhomboids are clearly visible on the outside of the cell base (Fig. 3). The silken cell "ghosts" exhibit rhomboids on the outside of the cells (Fig. 4) but a hemispherical base on the inside of the "ghost cell" (Fig. 3). Three rhomboids would be expected as a product of thermodynamic equilibrium in precisely the same way that soap bubbles form angular, not hemispherical, contact faces because the wax moves to a more probable state resulting in rhomboids, or a trihedral pyramid, which forms the cell base. Thus, the underlying geometry of the cell walls and bases are in keeping with mathematical laws on surface minima.

comb development / cells / silk / surface minima

1. INTRODUCTION

That the geometry of the cells in the combs of honeybees is parsimoniously explained by wax flowing in liquid equilibrium to occupy a minimal surface area was recently proposed (Pirk et al., 2004). These authors formulated a final hypothesis that because beeswax is a thermoplastic medium, it softens with increasing temperature and flows among an array of close-packed cylinders, which are actually the self-heated building bees (Bujok et al., 2002) and so hexagonal cells arise quite passively (Pirk et al., 2004). It was further argued that the three apparent rhomboids forming the base of each cell do not exist but arise as optical raster artefacts from looking through semi-transparent combs (Pirk et al., 2004).

The self-organization model posited by Pirk et al. (2004) for the hexagonal walls follows from mathematical and physical considerations (Kepler, 1611; Bartholin, 1660; Tóth, 1964; Hales, 2000). However, Pirk et al. (2004) incorrectly described the cell bases as hemispheres. This is prima facie paradoxical as their proposed self-organizing mechanism would predict rhomboid cell-bases for the same reason that it predicts hexagonal walls (Thompson, 1917; Taylor, 1976; Hales, 2000). On initial comb construction, all of the cells exhibit the laws of surface minima (Taylor, 1976) and the cell bases should consist of three real rhomboids in a trihedral pyramid and only become rounded on the inside after many generations of brood have been reared in them resulting in continued silk deposition. Here

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Figure 1. Mould of newly constructed drone comb showing trihedral pyramid structure of cell base.

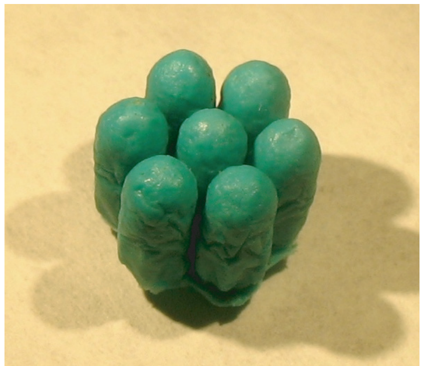

Figure 2. Mould of very old comb showing that the trihedral base of Figure 1 has become completely hemispherical.

we report new observations on the cell bases that prove that they begin indeed as rhomboids and only become hemispherical with continued use for brood-rearing.

2. MATERIALS AND MEHODS

To obtain precise impressions of the structure of the cells, worker and drone comb cells of *Apis mellifera capensis* Escholtz, and brood cells of *A. florea* Fabricius were filled with an exact replica, silicone-based moulding rubber preparation (Provil novo Light C.D. 2, Heraeus Kulzer GmbH & Co. KG, Hanau, Germany), which is non-exothermic and hardens at room temperature. Freshly drawn combs built without foundation, well-used blackened combs also built without foundation and the silken residual "ghosts" of cells obtained from combs after melting away the wax were examined. Ten separate samples of each kind of comb were tested. All cells were essentially the same for its kind. The male mouldings were then carefully removed from the female moulds (the cells) and the shape of the male cell impressions photographed and those from *A. m. capensis* are shown in the figures. The apical angles were measured by drawing the lines of the cells on sheets of transparent plastic and measuring them with a protractor.

3. RESULTS

There were no differences except for size between worker and drone cells. The moulds

Figure 3. Longitudinal section of very old comb showing the hemispherical structure inside of the base and the edges of two rhomboids below the cell base.

of the cell bases and walls of freshly constructed drone combs of *A. m. capensis* are shown in Figure 1 in which three perfect rhomboids are seen to form the trihedral pyramid of the cell base. Moderately old comb contains transitional cells in which there is an intermediate phase of rhomboid deterioration (not shown) while those obtained from very old and blackened combs show perfect hemispheres instead of the rhomboids inside the cell bases (Fig. 2). Exactly the same results were obtained from *A. florea.*

When fresh combs are cut in the longitudinal axis, the rhomboid nature of the base is quite apparent. Likewise, old combs cut longitudinally clearly show the parabolic curvature of the inside of the cell base; but the edges of two rhomboids are clearly visible on the outside of the cell base (Fig. 3). In the trihedral

Figure 4. The silken cell "ghosts" exhibit clear-cut rhomboids on the bottom outside of the cells.

pyramid, as in soap bubbles, the three apical angles were measured at close to co-equal angles of approximately 109°. The silken cell "ghosts" exhibit clear-cut rhomboids on the bottom outside of the cells (Fig. 4) but a hemispherical base on the inside of the "ghost cell" (Fig. 3). The same results were obtained from *A. florea.*

4. DISCUSSION

The images of the old blackened combs in which many generations of brood have been reared derive from the gradual accretion of silk and larval faeces, which slowly changes the "apparent" shape of the cell bottom from the real underlying rhomboid to a superimposed hemisphere. The explanation for the results of Pirk et al. (2004) as to a hemispherical base of the cell is simply that they made resin moulds of cells in old brood comb but photographed freshly constructed comb in which the rhomboids are obvious. So the rhomboids of freshly constructed combs are very much a reality that becomes obscured in time.

Just as importantly, our results from *A. m. capensis* and *A. florea* bear directly on the self-organization, thermodynamic equilibrium hypothesis (Pirk et al., 2004): regular and precise patterns are frequently observed in systems with self-organising properties (Thomson, 1882; Bénard, 1900; Leduc, 1911; Weaire and Phelan, 1994). And, indeed, three rhomboids would be expected as a product of equilibrium in precisely the same way that soap bubbles form angular, not hemispherical, contact faces. During the working process the thermoplastic wax moves to a more probable state (Boltzmann, 1905) and as a result rhomboids, or a trihedral pyramid, form the cell base. This is readily observed in such contexts as soap bubbles (Taylor, 1976) or in the steam developing at the lid of a glass-topped rice pot. Thus the underlying geometry of the cell walls and bases are in keeping with mathematical laws on surface minima.

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Les bases des cellules des rayons d'abeilles domestiques.

***Apis mellifera* / cellule / rayon / cire animale / construction animale / cocon de soie / surface minima**

Zusammenfassung – Der Zellboden von Honigbienenwaben. Pirk et al. (2004) postulierten, dass Bienenwachs als ein thermoplastisches Medium, das mit steigender Temperatur weicher wird, in dem Bereich der von den sich aufheizenden Bienen gebildeten Zylindern sozusagen flüssig ist und hierdurch die hexagonalen Zellen völlig passiv entstehen. Außerdem wurde argumentiert, dass die drei sichtbaren Rhomboide an der Zellbasis durch ein optisches Artefakt entstehen. Eine erneute Untersuchung der Form von frisch ausgebauten Waben, alten Waben und einer Modellierung von Waben aus den nach Auflösung des Wachses zurückbleibenden Seidenresten der Puppen mit einer Silikonmodellmasse ergab, dass die dreibeinige Pyramide am Zellboden von frisch gebauten Waben durch drei perfekte Rhomboide ausgebildet wird (Abb. 1). Alte Waben zeigen am Zellboden eine halbkugelige Form (Abb. 2). Längsschnitte der alten Waben zeigen ebenfalls eine parabelförmige Krümmung in der Innenseite des Zellbodens, aber die Ecken der Rhomboide sind auf der Außenseite deutlich sichtbar (Abb. 3). Der Abguss von den seidenen Zellresten weist Rhomboide auf der Außenseite der Zelle auf (Abb. 4), innen dagegen aber eine halbkugelige Form (Abb. 3). Diese Ergebnisse stützen direkt die Hypothese des sich selbst organisierenden, thermodynamischen Fließgleichgewichts, weil als Produkt eines Gleichgewichts drei Rhomboide erwartet würden, genau wie Seifenblasen winklige und nicht gebogene Formen an ihren Kontaktstellen formen. Während des Bauprozesses bewegt sich das thermoplastische Wachs zur Form der höheren

Wahrscheinlichkeit und als Ergebnis zu Rhomboiden bzw. zu einer dreiseitigen Pyramide, die den Zellboden bildet. Demnach stimmt die grundlegende Geometrie der Zellwände und ihrer Basis mit den mathematischen Gesetzen über ein Minimum der Oberfläche überein.

***Apis mellifera* / Wabenbau / Zellen / Seidenkokon / Oberflächenminima**

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