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REVIEW ARTICLE

On the natural cell size of European honey bees: a "fatal error" or distortion of historical data?

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Summary

As a possible way to help control varroa mites, some beekeepers advocate the use of cells smaller than the regular size commonly used by beekeepers. This paper addresses two of their principal arguments, namely that honey bees built smaller cells under natural conditions in the past, and that a "fatal" error occurred at the turn of the 20th century when a new and allegedly misleading method of estimating cell density was introduced. Historical data show not only that cell sizes were not smaller in the past, but also that estimating cell densities was not an issue before the introduction of wax foundation. Moreover, not realizing that the two methods of estimating cell densities are equivalent, the proponents of small cells have erroneously corrected the data reported by the authors of the 17th, 18th and 19th centuries. In conclusion, the claim that cells were smaller in the past is not only not supported by the historical records, but rests on a distortion of the historical records resulting from an incorrect transformation of the original data.

Acerca del tamaño natural de las celdas de abejas europeas: ¿un "error fatal" o distorsión de los datos históricos?

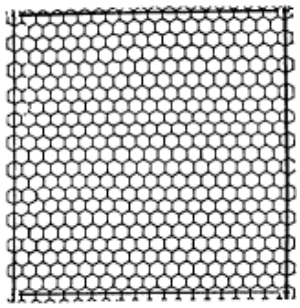
Resumen

Como una posible manera de ayudar a controlar a los ácaros varroa, algunos apicultores abogan por el uso de las celdas más pequeñas que el tamaño regular usado generalmente por los apicultores. Este trabajo aborda dos de sus principales argumentos, a saber: que la abeja de la miel construía celdas más pequeñas en condiciones naturales en el pasado, y que se produjo un error "fatal" al comienzo del siglo XX, cuando se introdujo un nuevo y supuestamente erróneo método de estimación de la densidad de celdas. Los datos históricos no sólo muestran que los tamaños de las celdas no eran más pequeños en el pasado, sino también que la estimación de las densidades de celdas no era un problema antes de la introducción de la fundación de cera. Por otra parte, sin darse cuenta de que los dos métodos de estimación de densidades de celdas son equivalentes, los proponentes de celdas pequeñas han corregido erróneamente los datos comunicados por los autores de los siglos XVII, XVIII y XIX. En conclusión, la afirmación de que las celdas fueron menores en el pasado no sólo no es apoyada por los registros históricos, sino que se basa en una distorsión de los registros históricos como resultado de una transformación incorrecta de los datos originales.

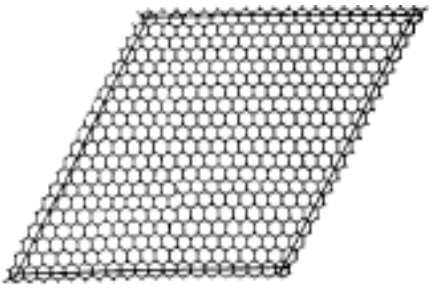
Keywords: honey bee, cell size, historical data

Introduction

Since the publication of two influential papers on the size of worker cells of the European honey bee, *Apis mellifera* (Erickson *et al.*, 1990a, 1990b), a community of "organic" beekeepers has been claiming that reducing the size of worker cells is one of the keys to controlling tracheal and varroa mites (Lusby, 1996a). In particular, the cell size is supposed to affect the reproduction of the varroa mites in several ways. Firstly, because varroa mites significantly prefer the large drone cells for their reproduction, it is suggested that large worker cells would also be more attractive to varroa than smaller cells. Alternatively, the mites' reproductive success might be negatively affected in smaller cells because of space reduction. It is also suggested that smaller cells positively affect the heat regulation in the brood nest, increases the rate of development of worker bees, as well as their number in the brood nest, which in turn favours their hygienic behaviour and increases the time spent on removing mites from infested cells (Lusby, 1996a, 1996b, 1997a).



A.



B.

Fig. 1. Diagrams presenting: ***A.*** Counting a square decimetre for number of cells using a square measurement; and ***B.*** Counting a square decimetre for number of cells using a rhombus measurement (reproduced from Lusby, 1997a).

As cornerstones of their approach, the proponents invoke two major arguments. Firstly they claim that the European honey bee used to build smaller cells before the introduction of wax foundation, and secondly, that a "fatal error" occurred around the turn of the 20th century when a new approach was introduced to estimate cell densities of honey combs (Lusby, 1997a). They therefore suggest that a cell width of 4.9 mm would be closer to the "natural" cell size than the width of 5.3 mm which is commonly used in marketed wax foundation.

On this basis, the proponents of small cells have proposed "retrogression" programmes to return to allegedly more "natural" cell sizes. Their claims also provoked scientists to conduct their own controlled studies in order to assess the effectiveness of cell size in mite control programmes, as well as the beekeeping equipment industry to produce and market wax foundation and artificial comb with smaller cell size.

Apart from the queen cells, which have their own distinct shape and protrude from the comb, three kinds of hexagonal cells appear in a hive: worker, drone and honey cells. Worker cells, in which worker brood is reared, are usually the commonest, the smallest and are located in the centre of the comb. Generally located in the periphery of worker brood cells, drone cells are about a third larger and much less numerous, while honey cells are the most variable in size. As far as cell size is concerned, authors usually refer separately to worker and drone cells, but rarely mention honey cells. The controversy about cell size only concerns worker cells reared on combs built using wax foundation.

The goal of this paper is not to enter into the controversy of the effectiveness of using smaller cells against the varroa mite (see Heaf**,** 2011**;** a review which shows that the majority of studies do not support this view), nor to address the erroneous claim of bees having built smaller cells in the past (see Vogt**,** 1911**;** Honegger**,** 1937**;** Stever**,** 2003**;** Zeissloff**,** 2007 and Heaf**,** 2012 for detailed reports of historical records), but to address the second argument, namely that there was a **"**fatal error**"** in estimating cell densities. To our knowledge, this specific point has not yet been discussed. Therefore, it is the goal of this paper to try to understand and explain this fatal error and its consequences.

Problem statement

According to Lusby (1997a), worker cell density had been estimated in the past (allegedly back to antiquity) according to the "rhombus method", whereas since the beginning of the 20th century, this approach has been replaced by the "square method" (Fig. 1). The "square approach" became widely used following the work of Ursmar Baudoux (1867-1934), a Belgian professor in beekeeping science, whose goal was to produce larger bees harvesting more honey than bees of the usual size. The square and the rhombus are plane geometrical figures having four equal sides. Whereas a square has four right angles, a rhombus, or lozenge, is an oblique-angled parallelogram. Because of the architecture of the comb, there can be only one type of rhombus to measure cell density, namely a rhombus having pairs of opposite angles of 60° and 120°. The surface areas of the square and the rhombus differ in accordance with the ratio of their heights (cf. online supplementary material Fig. S3).

According to Lusby (1997a), the square and rhombus methods are not equivalent, and result in large differences in cell densities. As a consequence, an unnoticed leap in estimating cell density is alleged to have occurred around the turn of the 20th century, with modern cell densities corresponding to larger cell sizes as compared to those recorded in the past. For example, nowadays, a cell density of 830 cells/dm^2 corresponds to a cell width of 5.3 mm, while in the past the same cell density is alleged to have resulted from a cell size of 4.9 mm.

This alleged leap is summarized in Table 1, a table named "Square Decimetre Measurement Conversion Chart" (Lusby, 1997b). For a series of cell widths, this table compares cell density estimated according to the rhombus method (second column) and the square approach (columns 3-5). For example, a cell width of 5.3 mm would correspond

Table 1. The "Square Decimetre Measurement Conversion Chart" (Lusby, 1997b). The table named "Square Decimetre Measurement Conversion Chart" is central to understand the logic of the present paper. Since it has been published on the website "www.beesource.com" and might disappear from a future version of the website, it is reproduced in Table 1 as it appeared on the website in October 2012 (reproduced with Dee Lusby's permission, who asked to add the following comment "just reference it was put together by me from information in old beekeeping archives and posted on beesource.com under pov lusby for knowing what was in use in past and written about").

Square Decimeter Measurement Conversion Chart

Cell Width (cm for 10 Worker Cells)	Rhombic (Old World) Square Decimeter Measurement	USDA Square Square Decimeter Measurement with Cell Width Deviation where known	Baudoux Square Square Decimeter Measurement	Rietsche Square Square Decimeter Measurement
5.96	562	650 - 6.0	650	
5.9	574/575			
5,8	594			
5.75	604		700	
5.7	615	700 - 5.7		
5.6	637	725 - 5.6		750
5.55	649		750	
5.5	655	750 - 5.5		
5.44	675			
5.4	684	800 - 5.4		780 - 800
5.37	692		800	
5.35				
5.3	711	830 - 5.3		
5.21	737		850	
5.2	740	850 - 5.2		830 - 850
5.17				
5.15	751 (Vogt) 753			
5.1	763 (Castillon) 770			
5.06	780/781		900	
5.0	789 (Maraldi) 800	920 - 5.0		
4.92	821 (Georgandas) 827		950	
4.9	828 (Castillon) 832 (Reaumur/Klugel)	950 - 4.9		
4.83	838 (Langs./Dadant) 856/857 (L'Abbe Collin/Grout)			
4.8	860 (Fratelli Piana) 867/868		1000	1050
4.7	870 (Swammerdam) 905	1050 - 4.7	1050	
4.66	920/921			
4.6	940 (Rambaldi) 945			
4.58	953 954 (Maraldi)			
4.5	987			
4.4	1032			
4.3	1081			

Lusby - July 1997

to a cell density of 830 cells/dm^2 according to three modern computations using the square approach (USDA, Baudoux and Rietsche) whereas the cell density would be only 711 cells/dm^2 according to the "rhombic (Old World) square decimetre measurement" approach. In support of the claim that cells were smaller in the past, the historical records of some authors from the Age of Enlightenment would seem particularly convincing: according to Table 1, Swammerdam, Maraldi, and Réaumur allegedly reported cell sizes ranging between 4.6 and 4.9 mm. But as will be shown later (Table 2), the data presented in Table 1 for these authors do not correspond to the cell sizes reported in their original writings.

In a further step to understand the difference between the two approaches, the four datasets (columns 2 to 4 of Table 1) were plotted against cell widths (Fig. 2). On the one hand, USDA, Baudoux and Rietsche's measurements are very closely aligned along the non-linear "theoretical" curve given by the direct density estimates resulting from elementary geometry (see online supplementary material for details), which suggests that the calculations according to the square approach are correct. On the other hand, density estimates computed by Lusby according to the "rhombic" approach (column 2 of Table 1), plotted on the same diagram, appear to be aligned along a curve of similar shape (dotted curve on Fig. 2), but the curve crosses the vertical axis at a significantly lower level. The difference between the two series of estimates (square versus rhombic) amounts to 13.4% on average, which corresponds to a difference of approximately 0.4 mm in cell width, i.e. of the order of magnitude of cell size reduction which is recommended by the proponents of small cells.

In agreement with Lusby's claim, there seems to be only one explanation for these puzzling results: an error must have occurred at some time. From a theoretical point of view, cell density estimates should not depend on the sampling method: a linear or a surface area measurement, (whatever the shape, e.g. square, rectangle, rhombus, triangle or even circle), should yield the same results. On the one hand, the modern density estimates using the square approach of Baudoux, USDA and Rietsche are in agreement with elementary geometry (solid line on Fig. 2). They can therefore reasonably be considered as accurate estimates. On the other hand, it seems unlikely that the illustrious minds of the Age of Enlightenment mentioned above repeated the same mistake over decades in the 17th, 18th and 19th centuries. In order to try to solve this puzzle, two lines of reasoning were followed. The first was to go back to elements of geometry in order to understand from a theoretical point of view the differences between the rhombic and the square approaches. The second was to go back to the original writings of the authors of the 17th, 18th and 19th centuries in order to understand how they did their measurements and their computations using the "rhombic" approach.

Evidence from the geometry of comb

The geometry of comb has long fascinated mathematicians. In antiquity, Pappus (4th century AD), probably inspired by the work of Zenodorus (2nd century BC), raised the question of finding the most parsimonious way to tile a plane. He suggested, that among the three possible figures (square, triangle or hexagon) which divide a surface into regions of equal area without leaving empty spaces, the hexagon had the least total perimeter with respect to the enclosed area, and hence the highest honey capacity with respect to wax use. This problem, known as the honey comb conjecture, has only been recently solved by Hales (2001) who confirmed Pappus' intuition. In the middle of the 18th

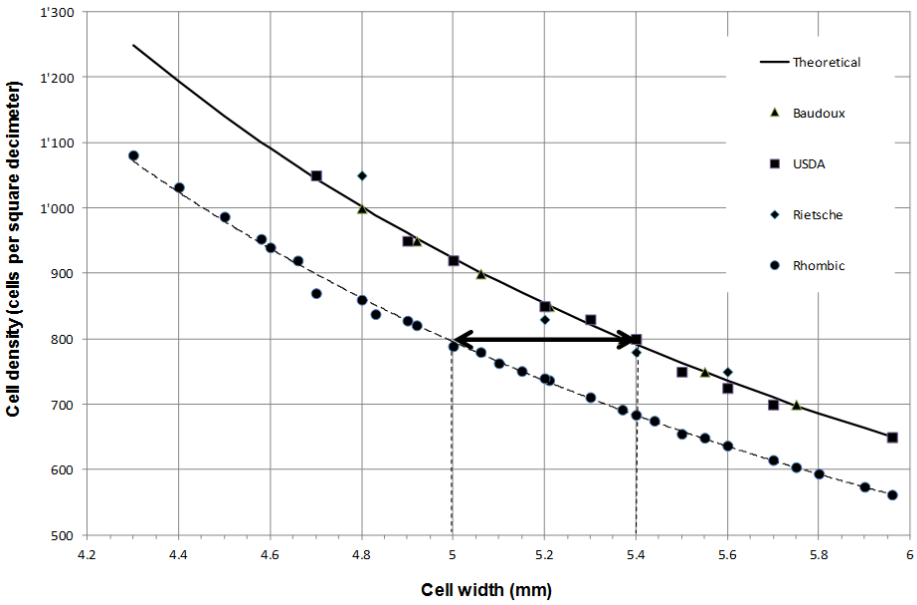


Fig. 2. Data plot of the four datasets of cell densities of Table1 (Lusby's "Square Decimetre Measurement Conversion Chart" (1997b) against cell widths. The arrow (between the dotted vertical lines) depicts the approximately 0.4 mm difference in cell size resulting from converting densities using the square approach to density estimates using the rhombic method.

century, Réaumur challenged the best mathematicians of his time, asking them to determine whether the three-dimensional geometry of the bottom of the cells, with the special configuration of their basal wax plates, was also optimal in terms of wax use. Solutions to this also very difficult problem were proposed by König and L'Huillier who confirmed some of the findings published earlier by Maraldi in 1712 (see Thompson, 1945, pp 525-544, for a review). Fortunately, estimating cell density is a much simpler task involving only very elementary concepts of mathematics and geometry (see online supplementary material). In short, estimating cell density can be viewed as estimating the number of hexagonal cells that are contained in a given area (square, rhombus or whatever planar geometrical figure), the first step being to estimate the area of an average cell. An hexagonal cell can be encompassed in a circumscribed circle and can itself encompass an inscribed circle (Fig. S1, online supplementary material). The diameter of this inscribed circle, or small diameter, d_i, corresponds to the cell width as measured by beekeepers when a series of contiguous cells are measured from wall centre to wall centre. The area of an average hexagonal cell can then be estimated as the sum of six equilateral triangles whose dimensions can be deduced using the Pythagorean theorem.

It should be stressed that this is a model-based approach, since cell density is estimated on the basis of a single measurement: the average cell width. Most important is to realize that this model has two implicit assumptions, namely that cells are regular hexagons and that they are all the same size. This approach works particularly well when estimating cell densities from wax foundation where these two assumptions are likely to apply.

Using this approach, estimating cell density as the number of cells encompassed by a given surface area (e.g. the square decimetre) is an extrapolation of an average cell area from a reference area. But at no stage is a square actually measured on the comb, nor a rhombus or whatever figure is chosen. Therefore, a cell density estimation based on a cell width measurement does not depend on a geometrical surface area measured on the comb: the square decimetre is a unit of area, whereas the decimetre is a unit of length. In addition, it is shown in the online supplementary material that Equation 1 reported by Erickson *et al.* (1990a) for estimating cell densities using cell widths measurements is drawn from the same model with the same assumptions.

Finally, the approach of actually measuring a square or a rhombic area on the comb is also examined. This approach is model-free: the base and the height of the square or the rhombus are measured and the number of cells per row and the number of rows are individually counted. The total number of cells for the square or the rhombus is obtained from a multiplication of the number of rows by the number of cells per row. While the total number of cells directly yields the cell density per dm^2 when the measurement is conducted on a square with a 1 dm base, the total number of cells still has to be transformed to get the density in cells per dm^2 with the rhombus approach. Since the ratio height/base of a rhombus with 60° angles is approximately 0.866 ($h = \frac{\sqrt{3}}{2} b$; cf online supplementary material), a rhombus of base, b = 1 dm, has a height of approximately 0.866 dm and an area of approximately 0.866 dm^2. Therefore, the total number of cells counted on a rhombus of base 1 dm has to be divided by the same ratio, or alternatively to be multiplied by its inverse, (approximately 1.155) in order to express the cell density in square decimetres.

The "fatal error" explained

Referring to Fig. 1 and comparing the square and the rhombic approach, Lusby (1997a) correctly observes that *"in counting the number of cells by the square measurement method (...) you gain three extra rows of cells to count"*. This results in 20 rows of 20 cells = 400 cells/comb side using the rhombic approach (Fig. 1B) as compared to 23 rows of 20 cells = 460 cells using the square method (Fig. 1A). The difference of course occurs from the fact that the ratio height/base is larger in a square than in a rhombus, respectively 1.00 and 0.866 (cf. Fig. S3, online supplementary material). Referring again to the diagrams reproduced in Fig. 1, Lusby (1997b) wrote: *"Counting the number of cells by each method, you would find that with the rhombus count you would have 800 cells total. (...). In counting the number of cells by the square measurement method (...), you would find that you would have 920 cells total"* (for the two sides of the comb).

Apparently considering that a rhombus with a base of 1 dm has an area of 1 square decimetre (instead of 0.866 dm^2) Lusby incorrectly estimates that the cell/density measured using a rhombus is equal to 800 cells/dm^2, which indeed is significantly smaller than the 920 cells/dm^2 resulting from the square method. However, the cell density using the rhombic approach should be (correctly) expressed as 800 cells/0.866dm^2 which corresponds to 923.8 cells/dm^2. Lusby's example, with rows of 20 cells for a square or a rhombus with a 1dm basis refers to an average cell width of 5.0 mm. As Table S1 (online supplementary material) shows, this corresponds to a cell density of 923.8 cells/dm^2, independently of the approach used (either direct, Equation 1 of Erickson *et al.*, 1990a, square or rhombus).

Lusby's error is explicit in the wording of the title of Table 1, i.e. "Rhombic (old world) square decimetre", as well as in the following quotation: "*Combs are measured in what is called a "square decimetre", but a square decimetre can be measured one of two ways. It can be measured either with a perfect square or by a rhombus method. By changing to a perfect square measurement, we have gotten into deep trouble because the numbers arrived at in the totals are vastly different (...). By trying to approximate the old US Standard of 856 and the Old World Standard of 800 cell sizes to the square decimetre many beekeepers have used foundation bases geared to a square decimetre using square measurements rather than a square decimetre using rhombus measurements. The error is proving fatal to say the least.*" (Lusby, 1996b).

In another paper Lusby (1997b) writes the following paradoxical statement: "*the cell count from using the square measurement method for a square decimetre is only good in the laboratory, not in the field. The cell count from using the rhombus measurement method for a square decimetre has direct correlation to the field*". Obviously, the reader is expected to believe that both kinds of measurements are both correct and can coexist in parallel worlds... depending on whether she/he is a beekeeper or a scientist...

In a next step, Lusby transferred her calculation error to the historical data of the 18th and 19th century by estimating cell widths from densities allegedly computed according to the rhombus approach, into cell widths as they would be calculated from modern cell density estimates resulting from the square approach. For instance, a cell width of 5.0 mm, which corresponds to a modern cell density of 923.8 cells dm^2, is assumed to have been reported as a density of 800 cells/dm^2 in the past, which means that a density of 923.8 cells dm^2 as reported by early authors would actually correspond to a modern cell density of 1091.4 cells dm^2, i.e. to a cell width of 4.6 mm. This erroneous and confusing conversion, as reported in the "Square Decimetre Measurement Conversion Chart" (Lusby 1997b; Table 1), results in a difference of 13.4% in cell densities and in an average difference of cell widths of approximately 0.4mm (Fig. 2). As will be shown below, this last step was totally unjustified. If any "fatal" error occurred, it is to be found in transferring Lusby's calculation error to the historical data.

Back to the historical records: the rhombus approach has never been used in the past

As explained above, the second line of reasoning for the present paper was to go back to the original writings of the authors whose data have been converted in the "Square Decimetre Measurement Conversion Chart" from Lusby (1997b). There are three major difficulties to be overcome in this quest. The first is to get access to the original texts. Apart from reading texts in public libraries, this step was facilitated by reports already published by Honegger (1937), Stever (2003), Zeissloff (2007) and Heaf (2011), as well as by the fact that many original texts are nowadays available in electronic form on the web. The second difficulty lies in dealing with the original languages, among which are Dutch and Latin (Swammerdam), French (e.g. Réaumur and Huber), German (e.g. Klügel and Vogt) and English (e.g. Cowan and Wyman), as well as old typographic characters. The last difficulty, by far the most sensitive, is to deal with old measurements systems, i.e. identify in which system data have been reported and properly translate them into the metric system (Parisian foot for the French authors, Hannoverian foot for Klügel; Imperial Prussian foot for most German authors, etc.). Much of this conversion work had already been achieved by the quoted authors, but all records have been seen and checked for exactitude. The results of this detailed reading are reported in Table 2.

The following conclusions can be drawn from this quest. Firstly, it confirms the reports of Honegger (1937), Stever (2003), Zeissloff (2007) and Heaf (2011) which show beyond any doubt that the honey bee cell sizes reported from natural combs by Swammerdam in the 17th century and most authors during the 18th and 19th centuries were not smaller than those of wax foundation marketed during most of the 20th

Table 2. Comparison of table "Cell Tell" of Erickson *et. al.* (1990a), transformations by Lusby (1997b) and historical records after Vogt (1911), Honegger (1937), Stever (2003), Zeissloff (2007), Heaf (2011, 2012) and author's inputs.

Data from Erickson et al. 1990a					Data from Lusby, July 1997 *		Data after Vogt[1] (1911), Honegger[2] (1937), Stever[3] (2003), Zeissloff[4] (2007), Heaf[5] (2011) with author's inputs[6]				
Source	Year	Original unit of measure	Cell width (average) (mm)	Cell width (range) (mm)	Cell width (cm for 10 cell workers)	Cell density Rhombus (Old World)	Date	Cell width (average) (mm)	Cell width (range) (mm)	Density cells /dm² both sides	Method of measurement as reported in the original publications
Swammerdam	1600's	cells/dm²	5.1	-	4.7	870	written: 1669-1673 Published: 1737-1738	5.15		870.7	p.379: Horizontal linear measurements of 5 and 55 cells (foot of Amsterdam = 283.133 mm)[1,2,3]
Maraldi	-	cells/dm²	-	5.0-5.4	4.58 / 5.0*	789/954	1712	5.17	4.92-5.41	789-954	p. 306: linear measurements of several combs (60-66 cells /foot (Parisian foot=324.839 mm))[1,2,3,4,5]
								5.52		757.9	p. 304: Surface estimation: almost 4000 cells on a comb one foot long and 6 inches wide (=5.276 dm²)[1,2,3,4,5]
Réaumur	1700's	cells/dm²	5.3		4.9	832	1741	5.36 (5.41)		803.8	p. 397: Horizontal linear measurements of 20 cells (Parisian foot)[1,2,3,4,5] (Réaumur rounded his measurement resulting in an average width of 5.41 instead of 5.36 without rounding)
								5.31		819	Surface estimation: 9000 cells on a piece of comb of 10.1 dm²[1,2,3,4,5]
Klügel	-	cells/dm²	5.3		4.9	832	1772	5.27		831.5	Cell side = 1½ Duodecimallinien, i.e. r_c=3,04mm--> d_i=5,27mm (foot of Hannover=292,100)[1,2,3,6]
de Castillon (= Lhuillier)	-	cells/dm²	-	5.3-5.5	4.9 / 5.1*	763/828	1781**	5.40 ±0.074	5.28-5.50	763-828	pp. 299-300: Horizontal linear measurements;average of 10 measurements; series of 15 to 46 cells (Parisian foot; measurements are given in units of the inscribed radius r_i)[1,2,3,4,5,6]
Latreille	1800's	cells/dm²	5.4				1804	5.24-5.43		783-841	pp.387-388; Horizontal measurement; 14 cells =76 mm horizontally; 14,5 cells =76 mm in diagonal[1,2,6]
Vogt	-	cells/dm²	-	5.3-5.5	5.15	751	1911	5.37±0.09 a 5.34 b 5.25±0.08 c 5.14 d		800.8 809.9 837.9 874.1	pp 19-23 & Table 1: Average of 72 measurements (mm) in 3 directions on the two sides of 4 combs of unused (a ,b) and used cells (c, d) (b , d = horizontal measurements)[2,3,5,6]
Collin	1865	cells/dm²	5.2		4.83	856	1878 (5th ed.)	5.20		854	Average measurements (mm) of the radius of the inscribed circle for worker and drone cells; radius of the circumsribed circle and cell area calculated according to concepts of elementary geometry (see appendix); measurement method not explained[6]
Langstroth/Dadant	-	cells/dm²	5.3		4.83	838	1889	5.25	5.07-5.46	852.5 838	pp. 97-98: "It is generally admitted that five worker-cells measure about 5 cells to the inch, or twenty-five to the square inch, but this is incorrect. If five worker-cells measured exactly an inch, the number contained in a square inch would be about twenty-nine. As they are usually somewhat larger, the average number in a square inch is a trifle over twenty-seven". p. 152: "As every square inch of comb contains 55 cells, 27 to 28 on each side" (modern inch)[5,6]
							1927	5.25		838	Grout (1931) reports that "Langstroth (...) calculated that there were 838 cells per square decimeter and Charles Dadant confirmed his results"[6]
Root	1876	cells/inch	5.2				1877	5.26	5.21-5.29	825-850	Horizontal measurements of rows of cells (modern inch)[5]
Cheshire	1886	cells/inch	5.1	5.06-5.45			1888	5.26	5.08-5.64	726-895	Horizontal measurements of rows of cells of several hundreds of combs (imperial inch)[5]
Cowan	1889	cells/in²	5.1	4.72-5.36			1889, 1890, 1896	5.10	4.72-5.36	804-1037	p. 12. Horizontal inear measurements Series of 10 to 60 cells (modern inch)[5]
Cook	1904	cells/in²	5.1	5.06-5.45			1904	5.27	5.07-5.46	775-898	p. 183: "I find the worker-cells per square inch vary from 25 to 29"[6]
Miller	1910	cells/in²	5.1	5.11-5.29			1910	5.11	5.04-5.17	864-	Average: horizontal measurement; range: diagonal measurements (modern inch)[6]
Grout	1937	cells/dm²	-	4.95-5.49			1	5.23	4.96-5.50	764-940	p. 263-264 "Various measurements (...) by Collin, Langstroth and Charles Dadant(...) recording a variation of from 764 to 940 cells per square decimeter for various races of bees".[6]
Taber & Owens	1970	mm/cell	5.2	4.99-5.45							reference not found
Dadant	1946	cells/dm²	5.2	5.06-5.20			1946	5.48	5.24-5.72		p.162: "vary from five cells measuring 1 1/32 inches to 1 1/8 inches"[6]
Dadant	1975	cells/dm²	5.2								reference not found
Message & Gonçalves	1985	mm/cell	5.1	5.07-5.11							experimental study with bees of different origins, including africanized bees[6]

*: Maraldi and de Castillon are quoted twice in Lusby July 1997

century. Secondly, the major and most surprising finding of this study of the original literature is that none of the authors whose data could be checked, and whom were cited by Lusby, used the rhombic method! As Table 2 shows, all the earlier authors estimated cell size on the basis of linear measurements of rows of contiguous cells (as is still done nowadays). Thirdly, early authors only seldom reported estimates of cell densities, and in such cases, they calculated estimates of total numbers of cells on rectangular surface areas (e.g. Swammerdam, Maraldi, Réaumur): no mention of surface estimates using the rhombus approach could be found.

Last, but not least, while all the cell widths were correctly reported in the first publication of Erickson *et al.* (1990a) in a table named "Cell Tell" and correspond closely to the data found in the literature, the spuriously converted cell widths reported later by Lusby (1997b) in the "Square Decimetre Measurement Conversion Chart" gives a series of distorted cell widths, reduced by approximately 0.4 mm as compared to the figures published as cell widths in the original reports of the early authors. For instance, while Swammerdam and Reaumur published average cell widths (and not cell densities) of approximately 5.15 and 5.31-5.36 mm respectively, their figures have been improperly converted as explained above to 4.7 and 4.9 mm in Lusby's (1997b) "Square Decimetre Measurement Conversion Chart". Since Swammerdam and Reaumur only published cell widths, this suggests that the original data have probably not been consulted, and that the original cell widths reported in Erickson *et al.* (1990a) were assumed to have been derived from cell densities calculated according to the rhombus. They were then transformed into modern densities according to the square approach, from which incorrect reduced cell widths were inferred. This confusing approach results in the "Square Decimetre Measurement Conversion Chart" which provides in the column named "Rhombic (Old World) Square Decimetre Measurement" cell densities corresponding to incorrectly inferred cell widths. In conjunction with the fact that the cell widths reported by the early authors have been incorrectly reduced by approximately 0.4 mm, and that these authors did not use the alleged "rhombic" approach, it means that the figures given as cell widths in this table is a strong distortion of the facts.

It can be stressed that estimating cell density probably only became an issue after the introduction of wax foundation, when beekeepers could experimentally manipulate this parameter. Indeed, there is no evidence that early scientists developed methods for estimating cell densities. In addition, no reference to the "rhombic" approach could be found in any of the historical records that have been reviewed in this paper. Not only was I unable to find a published document explicitly referring to the "rhombic" approach, nor could Lusby quote a single reference when asked by e-mail.

The relationship between the height and the base of the rhombus also suggests that the rhombus approach, which needs relatively complicated calculations, is not easy to use in practice as a field method. For instance, the dimensions of a rhombus encompassing a surface area of 1 dm^2 can be estimated to 1.075 dm for the base and 0.931 dm for the height using the relationship $h = \frac{\sqrt{3}}{2} b$.

It is finally worth noting that Equation 1 of Erickson *et al.* (1990a), namely *"Equation 1: cells/dm^2 = 2.31*N^2 (where N is the number of cells per linear dm)",* can also be interpreted as an application of the rhombus approach. If the number of cells on a 1 dm row is known, the total number of cells, N^2, of a rhombus of base 1 dm is also known and the cell density is obtained by multiplying N^2 by 1.155*2 = 2.31 (the ratio basis/height multiplied by 2 to account for the two sides of the comb; see online supplementary material for details). This also suggests that the rhombic approach is of little significance in practice and can be replaced by linear measurements, while its mere interest could rest in a pedagogical explanation of Erickson's *et al.* (1990a) Equation 1.

Additional data on natural cell sizes and shapes

In addition to the data examined in Table 2 on the basis of the list of authors quoted in Erickson *et al.* (1990a), data on cell sizes have been reported by many other authors (see Vogt, 1911; Honegger, 1937; Stever, 2003; Zeissloff, 2007 and Heaf, 2011 for reviews). For instance, François Huber, the famous naturalist who became blind when he was about 20 years old and wrote the most detailed description ever published on the construction of the honey comb (Huber, 1814, vol. II, pp. 112-230), reports a natural cell size of 5.4 mm for the region of Geneva, Switzerland, at the end of the 18th century (p. 222). Similarly, in an interesting and detailed study, Wyman (1866) reports an average cell width of 5.11 mm (range 4.70-5.33) for three rows of 10 cells measured in three directions on natural combs of European honey bees in North America. In addition, Wyman provides much information on the range of variation in cell size and shape. Also worth mentioning are the cell sizes given by von Berlepsch, Christ, Lombard, Féburier, Dzierzon, Ludwig and de Meyer (Zeissloff, 2007). All these data fall in the range of cell sizes given in Table 2 and, therefore, also support the claim that cell sizes were not smaller in the past.

The data reported by Abbé Collin (1878 p. 31) are also worth comment. The French priest reports cell size as follows: "*The cells of workers and drones are all hexagonal. The apothem, or small radius, of a worker cell has a length of 2 mm and 6 tenths, i.e. 2.6000 mm. Every side of the same cell has therefore a length of 3.0020 mm. The area in square millimetres is therefore of 23.4156. Therefore a comb of one square decimetre encompasses 427 cells on each side or 854 for the two sides*" (author's translation from the French). The wording used by Abbé Collin clearly indicates that, like de Castillon (1781), he refers to the geometrical properties of the hexagon, as described in the online supplementary material. He gives measurements of the two radiuses (r_i and r_c, cf. online supplementary material). It is noteworthy

that he does not introduce at all the geometrical properties of the hexagon, taking for granted that his readers have mastered them. It is also worth noting that his figures correspond exactly to figures of Table S1, online supplementary material, for a worker cell width of 5.2 mm, as do his figures for drone cells (small radius: 3.3000 mm; large radius: 3.8110 mm; density: 530 cells/dm^2). Interestingly enough, he gives density estimates relative to the square decimetre and not to the rhombus approach.

Ironically, an opposite controversy on cell size arose around 1935, with the claim that bees reared on wax foundation became smaller following the introduction of wax foundation (Honegger, 1937)! According to Honegger (1937), Johannes Mehring, who invented wax foundation around 1857, designed the first foundation on the basis of his own cell size measurements of natural honey combs, namely 18 cells/dm, corresponding to a cell size of 5.55 mm and a density of 750 cells/dm^2. Later on, some producers of wax foundation turned to smaller cells and much higher cell densities (e.g. 920 cells/dm^2 in Belgium before Baudoux's work (1933), 905 cells/dm^2 in Zürich; Honegger 1937). Honegger (1937), quoting the data of Swammerdam, Maraldi, Reaumur, Klügel, Castillon and Latreille, concluded that differences in wax foundation reflected the diversity of cell sizes of natural honey combs and that there were no reasons to believe that the size of honey bees had been affected by the introduction of wax foundation.

Illustrating the pitfalls of properly identifying copies from original reports as well as of using the correct conversion units, Kober (2003), a German advocating use of small cells, quoted a book published as early as 1770 by Thomas Wildman in England. Wildman apparently reported the lowest cell sizes ever found in the historical literature. Quoting Kober: "*Thomas Wildman described in England honeycombs with 60 to 66 cells per foot (305 mm); this corresponds to a cell width of 4.62 to 5.08 mm*". A careful reading of Wildman's book (1768) shows that he also reported that a comb one foot long and half a foot wide encompasses almost 4,000 cells. Table 2 shows that these figures and the wordings are identical to those of Maraldi (1712), which suggests that Wildman copied from Maraldi's writings. Indeed, Wildman's treatise, begins with a chapter entitled "An account of bees, extracted from the memoirs of the Royal Academy of Sciences at Paris" (Book 1 pp. 1-41) which is a translation of Maraldi's 1712 publication, augmented from Wildman's own remarks and from quotations drawn from Reaumur's treatise (1742). Wildman translated Maraldi's data without converting them to the British foot. Calculating cell width using a British foot of 304 mm, as Kober did for Wildman's data, therefore yields an incorrect range of 4.62 to 5.08 mm for cell size instead of 4.92-5.41 mm using the Parisian foot of 324.839 mm usually applied to Maraldi's data (Table 2). Therefore, Wildman's data should be discarded from the list of original historical records, because Wildman did not conduct any personal measurements.

Little is known about the shape of combs and cells under natural conditions in historical times. Nevertheless, drawings of traditional skeps show that combs, although usually aligned in a linear way, may also be curved. Such curves, which are usually absent from hives fitted with frames, call for an adaptive response from the bees in order for them to build usable combs. Wyman (1868) and Cowan (1890) give detailed reports of the variety of cell shapes and sizes found in combs built under natural conditions. Wyman even concludes from his extensive work and observations of natural cells that "in nature, the type-form", i.e. the hexagonal cell, "*is an ideal one, and, with this, real forms seldom or never coincide*".

The recent interest of organic beekeepers who let their bees build combs under conditions closer to nature (e.g. in skeps or by using top bars, or frames without wax foundation) reveals much variability in cell sizes and shapes. This offers new opportunities to observe the amazing adaptive building capacities of the bees under diverse and adverse conditions, but also complicates the estimation of cell densities.

In such cases, the assumptions of the model-based methods for estimating cell densities are clearly no longer valid, since cell sizes and forms may vary to a large extent. Analyses of combs (e.g. in Wyman, 1868 or Cowan, 1890) show that it is often difficult to follow and identify continuous rows of contiguous cells. The number of cells per row may vary from row to row, and the number of rows of cells may vary from the left to the right of the comb, or from one side of the comb to the other. In such cases, careful measurements should take account of these irregularities in order to obtain accurate cell density estimates.

Conclusions and final remarks

The present paper demonstrates that two premises of the proponents of the small cell approach, namely that a new method (the square approach) replaced the "Old World rhombic" approach to estimate cell density at the turn of the 20th century and that a hidden error occurred at this time, do not hold. As previously shown by all the reviews conducted during the last hundred years (Vogt, 1911; Honegger, 1937; Stever, 2003; Zeissloff, 2007; Heaf, 2012), the claim that the cell size of the European honey bee was smaller before the introduction of wax foundation is not supported by the facts. This paper also explains by which mechanism the original data of the 17th, 18th and 19th century have been distorted in order to support this wrong claim. As a consequence, the use of the expression "retrogression to natural cell size" is clearly inappropriate, as are the programmes conducted on the basis of this argument. Moreover, it should be stressed that Baudoux (1993), on whose shoulders much of the responsibility for the allegedly "fatal error" was set, not only did not introduce a new method for estimating cell densities (and therefore did not hide any discrepancy with the rhombic method which had never been a standard), but published correct cell density estimates in full accordance with the theory and the measurements of his illustrious predecessors of the Age of the Enlightenment.

As already mentioned, the aim of this paper is not to enter into the controversy about the effectiveness of small cells for controlling varroa mites. Nevertheless, its significance within the framework of the small cell approach is worth highlighting. The present study addresses the premise of this theory. It reveals a major misunderstanding which in part led scientists to undertake costly field and experimental studies, as well as encouraging the beekeeping industry to produce and market artificial comb and wax foundation of unusually and in fact "unnatural" small sizes. Added to the fact that most field and experimental studies bring little support to the small cell theory, that cell sizes were not smaller in the past, and that varroa tolerant bees also appeared on several instances on regular cell size combs, the findings of the present study leaves the small cell approach with little supportive evidence.

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References

BAUDOUX, U (1933) The influence of cell size. *Bee World*, 14(4): 37-41.

DE CASTILLON (1781) In M Lhuillier. Mémoire sur le minimum de cire des alvéoles des abeilles et en particulier sur un *minimum minimorum* relatif à cette matière. *Nouveaux Mémoires de l'Académie Royale des Sciences et belles-lettres*, Berlin, Germany. 277-300.

CHESHIRE, F R (1888) *Bees and beekeeping; scientific and practical. Vol. II – Practical.* The Bazaar Exchange and Mart Office; London, UK.

COOK, A J (1904) *The bee-keeper's guide; or manual of the apiary (18th Ed.).* 543 pp.

COWAN, T W (1890) *The honey bee: its natural history, anatomy, and physiology*. Houlston; London, UK, 220 pp.

DADANT, C P (1927) *The honey bee (23rd Ed.).* Dadant & Sons ; Hamilton IL, USA.

DADANT, H P (1946) The honey comb. In *R A Grout (Ed.). The hive and the honey bee (Revised edition of 1949).* Dadant & Sons; Hamilton, IL, USA. pp. 153-166.

ERICKSON, E H; LUSBY, D A; HOFFMANN, G D; LUSBY, E W (1990a). On the size of the cells. Speculations on foundation as a colony management tool. *Gleaning in Bee Culture*, 118(2): 98-101.

ERICKSON, E H; LUSBY, D A; HOFFMANN, G D; LUSBY, E W (1990b). On the size of cells. Speculations on foundation as a colony management tool. *Gleanings in Bee Culture*, 118(3): 173-174.

GROUT, A (1931) A biometrical study of the influence of size of brood cell upon the size and variability of the honey bee (*Apis mellifera* L.). MS thesis, Iowa State College, USA. 198 pp.

GROUT, A (1937) The influence of size brood cell upon the size and variability of the honey bee (*Apis mellifera* L.). *Iowa State College of Agriculture Experiment Station Research Bulletin,* 218: 260-279.

HALES, T C (2001) The honey comb conjecture. *Discrete and computational geometry*, 25(1): 1-22.

HEAF, D (2011) Do small cells help bees cope with varroa. A review. *The Beekeepers Quarterly*, 104, 39-45.

HEAF, D (2012) Natural cell size. Downloadable at: http:// www.dheaf.plus.com/warrebeekeeping/ natural_cell_size_heaf.pdf

HONEGGER, A (1937) Großzellen ja oder nein? *Schweizerische Bienenzeitung*, 60(3): 149-152.

HUBER, F (1814) *Nouvelles observations sur les abeilles. Seconde édtion, revue, corrigée et considérablement augmentée. Tome II.* Paris & Genève: J J Paschoud. 479 pp.

KLÜGEL, G S (1772) Mathematische Betrachtungen über den kunstreichen Bau der Bienenzellen. *Hannoversches Magazin*, 23: 353-368.

KOBER, T (2003) Zurück zur kleinen Biene? Teil 1: Die Geschichte der Zellgrössen. *Allgemeine Deutsche Imkerzeitschrift*, (4): 8-10.

LANGSTROTH, L L (1889) *On the hive and honey bee.* C DADANT and Son; Hamilton IL, USA. 521 pp.

LATREILLE, P A (1804) Sur un gâteau de ruche d'une Abeille des Grandes Indes, et sur les différences des Abeilles proprement dites, ou vivant en grande société, de l'ancien continent et du nouveau. *Annales du Museum National d'Histoire naturelle,* 4: 383-394.

LUSBY, D A (1996a) Small size foundation for mite control. *American Bee Journal*, 136(7): 468-470.

LUSBY, D A (1996b). Small size foundation for mite control. *American Bee Journal*, 136(11): 758-759.

LUSBY, D A (1997a) More on small cell foundation for mite control. *American Bee Journal*, 137(6): 411-412.

LUSBY, D A (1997b) Square decimetre conversion chart. Downloadable at: http://www.beesource.com/point-of-view/ed-dee-lusby/historical-data-on-the-influence-of-cell-size/square-decimeter-measurement-conversion-chart/

MARALDI, G P (1712). Observations sur les abeilles. *Histoire de l'académie royale des sciences Mémoires de l'Année 1712*, 1731, Paris, France. pp 297-331.

MESSAGE, D; GONCALVES, L S (1985) The effect of the size of the honey bee cells on the rate of infestation by Varroa jacobsoni. *Proceedings of XXXth International Apicultural Congress, Nagoya, Japan.* p. 250.

MILLER, C C (1910) A study of natural honey comb. *Gleanings in Bee Culture*, 38(1):23-24.

DE RÉAUMUR, R A F (1742) *Mémoires pour servir à l´histoire des Insectes* Tome 5. Paris, France. 728 pp.

ROOT, A I (1975) *The ABC and XYZ of Bee Culture (36th Ed.).* A I Root; Medina, OH, USA.

STEVER, T (2003). Verkleinerte Bienen - Irrweg der Züchtung oder Wunderwaffe gegen Varroamilben? *Bienenpflege*, (3): 93-95.

SWAMMERDAM, J (1737/8) *Biblia Naturae /Bybel der Natuure.* Pub: Herman Boerhaave; Amsterdam, Netherlands. Vol. 1. 550 pp.

THOMPSON, W D (1945) *On growth and form*. *A new edition.* Cambridge and New York: University Press, Macmillan Company. 1118 pp.

VOGT, H (1911) Geometrie und Ökonomie der Bienenzelle. *Festschrift der Universität Breslau.* 68 pp.

WILDMAN, T (1768) *A treatise on the management of bees*. Cadell; London, UK. 169 pp.

WYMAN, J (1866) Notes on the cells of the bee. *Proceedings of the American Academy of Arts and Sciences*, 7(1): 1-18.

ZEISSLOFF, E (2007) Natürliche Zellgröße. *Journal Apicole Luxembourgeois*, (3): 73-78.

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