

Natural Cell Size

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This is the fourth edition of this paper. A researcher of T. W. Cowan's work has drawn my attention to the wide range of values reported in Cowan's writings. I have taken account of this. Also, my attention has been drawn to the data of François Huber, Abbé Collin, Jeffries Wyman and Pierre André Latreille which are now included.

This paper should be regarded as work in progress. More published data will be added if it comes to my attention. Readers' help with obtaining source material is much appreciated.

A school of beekeeping has arisen since 1990 which holds that the size of honey bees in USA and Europe has been artificially increased by rearing them on foundation whose cell size is larger than the natural cell size.¹ The 'small cell school' is not insignificant in size. Since the initial papers on the subject co-authored by Dee Lusby,^{2,3} an e-group has formed for discussing small cell, treatment free beekeeping,⁴ and it now has over 5,000 members. This paper is intended to examine some of the premises of the small cell school.

Erickson et al. (1990) examined early literature on cell size and concluded 'It is worth noting that the cell size range reported as natural for feral bees has varied little from the 1600's to the present time'.² This conclusion is first tested with reference to the early literature, quoting it where possible and making the appropriate conversions to metric measure according to the system of units applied by each author at the time. I take the literature before 1900 as most representative of pre-foundation beekeeping.

Data on natural cell size from the literature before 1900

*Swammerdam*⁵

'Wanneer dit werk regulier is, soo maaken vyf van deese Huyskens seer net een duym, ende uysen-vyftig een Hollantsche voet' and 'Quodsi aedificium hoc regulare est; tunc quinque harum cellularum quam exactissime pollicem aequant, & quinque supra quinquaginta Hollandicum pedem conficiunt.' (When this construction is regular, then five of these cells are exactly equal to one inch, and fifty-five make up one Dutch foot.) (p. 379)

As Swammerdam was working in Amsterdam we can take the Amsterdam version of the Dutch foot as his unit of measure. It is equal to 11 Amsterdam inches, thus explaining why 5 cells in an inch make 55 to a foot. The Amsterdam foot is equal to 283.133 mm. This makes Swammerdam's cell size 5.15 mm.

*Maraldi*⁶

'...nous avons vû faire en un jour un Rayon qui avoit un pied de long & six pouces de large, & qui suivant la grandeur ordinaire des Alvéoles, en pouvant tenir près de quatre mille.' ('we have seen a comb made in a day which was a foot long and six inches wide and which following the ordinary size of cells can hold about four thousand.') (Page 304)

The Parisian foot (Pied du Roi) is 324.83 mm. The area of the comb was therefore 52,752 mm², or 5.2752 dm². Maraldi's comb therefore had about 4000/5.2752 cells per dm², i.e. 758. This corresponds to an average cell size of 5.52 mm.

However, on page 306 we read:

'Nous avons trouvé dans divers Rayons qui avoient un pied de long depuis 60 jusqu'à 66 rangs d'Alvéoles...' ('We have found on various combs that are a foot long between 60 and 66 rows of cells.') Maraldi's cell size range, converting by the Paris foot (le pied du Roi), is 4.92-5.41.

Given the discrepancy between the average of 5.52 mm and the range of 4.92 to 5.41 mm the question arises which one to take as representative of Maraldi's investigations. The average has some uncertainty associated

with it as it is based on 'about four thousand [cells]'. It thus seems appropriate to take the range as the representative observation.

*Réaumur*⁷

"J'ai trouvé que 20 des petites cellules posées sur une meme ligne droite, remplissent ensemble une longueur de quatre pouces moins une demi ligne. Si on néglige la demi-ligne, le diametre de chacune de ces cellules sera de 2 lignes $\frac{2}{5}$. Et un gateau de 15 pouces de long, sur un peu plus de 10 pouces de large, sera composé d'environ 9000 alvéoles." (I found that 20 small cells on a single straight line comprised a length of four *pouces* minus half a *ligne*. And a comb 15 *pouces* long by a little more than 10 *pouces* wide will be made up of about 9,000 cells.) (page 397)

For the first measurement we need not neglect the half a *ligne*. The total length measured, based of course on the *Pied du Roi* was 108.28 minus 1.13 mm, i.e. 107.15 mm. This divided between 20 cells makes an average cell size of 5.36 mm.

For the area measure we have an approximation of an unknown magnitude. The area over which he counted cells was $2 \times 109,909$ mm, allowing for both sides of the comb. This is 10.99 dm². Therefore the number of cells per dm² is $9,000/10.99 = 819$. This corresponds to a cell size of 5.31.

Thus in the case of Réaumur, in contrast to that of Maraldi, there is good agreement between the linear and area estimates of cell size.

*Latreille*⁸

'J'ai mesuré une longueur de quatorze alvéoles ordinaires de notre abeille domestique, prise en ligne droite, et dans un rayon, allant du bord extérieur à l'alvéole destiné pour la femelle et placé vers le milieu du gâteau: j'ai trouvé 76 millimètres, chaque cellule donc un diametre de cinq millimètre et un peu plus de $\frac{3}{7}$.' (p.6) (I measured a length of fourteen ordinary cells of our domestic bee, taking a straight line, and on one comb, going from the outer edge of the cell destined for the female and situated towards the middle of the comb: I found 76 millimetres, each cell therefore a diameter of five millimetres and a little more than $\frac{3}{7}$ ths.) This means each cell is 5.43 mm wide on average. Further down the same page he writes '...la longueur d'une série de dix-huit alvéoles et de $\frac{4}{10}$ d'alvéole d'un gâteau de nos ruches égale un décimètre,...' (The length of a series of eighteen and $\frac{4}{10}$ ths cells of a comb of our hives equals a decimetre.) This also corresponds to an average cell size of 5.43 mm.

On the following page he writes: 'J'ai dit que j'avois mesuré les alvéoles du gâteau de nos ruches, en partant du bord et gagnant le milieu du plan. L'indication de cette manière de mesurer étoit nécessaire, m'étant aperçu que la même longueur, prise dans un sens à peu près parallèle au bord, ou transversalement, ne répondit pas exactement à la même quantité de cellules; ainsi les 76 millimètres qui ont servi d'éléments à mon premier calcul, au lieu de ne comprendre que quatorze alvéoles, en referment ici la moitié d'un de plus'. (I have said that I had measured the cells of the comb of our hives, starting at the edge and reaching the middle of the surface. The indication of this method of measuring was necessary because I had noticed that the same length, taken in a direction almost parallel to the edge, or transversally, did not fit exactly to the same number of cells; thus the 76 millimetres that served as part of my first calculation, instead of including only fourteen cells, here enclosed half of one extra.) Fourteen and a half cells in 76 millimetres corresponds to a cell size of 5.24 mm. The average of Latreille's two measurements is 5.34 mm.

*Huber*⁹

Le diamètre des cellules d'ouvrières est de 2 lignes $\frac{2}{5}$..." (The diameter of the cells of the workers is $2 \frac{2}{5}$ *lignes*) (p. 221-222). $2 \frac{2}{5}$ *lignes* corresponds to 5.4144 mm.

*Wyman*¹⁰

'The average *diameter* of a worker cell, measured on a line perpendicular to its sides, as deduced from the following table, is 0.201, or one fifth of an inch, but it may be increased or diminished in different parts of the same comb.' (p.5)

Wyman tabulated 36 values comprising measurements from three different parts of each of four combs by measuring in the three directions of the hexagons in each case.

'The greatest aggregate diameter of any one series of ten cells was 2.10 inches, and the least 1.85 inches, making a difference of 0.25 inch, or the diameter of a cell and a quarter.'

Wyman would have used imperial measure, so his mean was 5.11 mm and range 4.70 to 5.33 mm.

Compared with Root, who was also working in the USA, Wyman's mean and minimum are distinctly lower.

*Berlepsch*¹¹

"a. Kleine sechseckige Zellen, so groß, daß gerade eine Arbeitsbiene darin ausgebildet werden kann, also so lang wie eine Arbeitsbiene. 8 Linien tief und 2 2/5 Linien weit." ('a. Small six sided cells, large enough for a worker bee to be raised in, i.e. as long as a worker bee. 8 *linien* deep and 2 2/5 *linien* wide.) (p. 149)

2 2/5 *linien* corresponds to 5.4144 mm.

*Root*¹²

'Mr. Root then began measuring up many pieces of natural comb when he discovered that the initial cells, five to the inch, from his first machine were slightly too small. The result of his measurements of natural comb showed slightly over 19 worker cells to four inches linear measure, or 4.83 cells to one inch.

In later years, H. H. Root, about to begin work on a new foundation mill, confirmed the measurements of his father, namely, 19½ cells to four inches linear measure (4.83 cells to one inch), taken across the vertical cell walls. Measurements taken in the two diagonal directions downward between parallel walls were slightly more, if anything. This would make from 825 to 850 cells to the square decimeter, including both sides of the comb.'

4.83 cells to the inch corresponds to a cell size of 5.26 mm. 825 to 850 cells per dm² corresponds to a range of 5.21-5.29 mm.

*Collin*¹³

"L'apothème ou petit rayon d'un alvéole d'ouvrière a une longueur de 2 millimètre 6 dixièmes." (The apothem or small radius of a cell of a worker is 2 millimetres and 6 tenths long.) (page 31). He is referring to the radius of the inscribed circle of the hexagon. Thus the diameter between two parallel sides is 5.2 mm.

*Cheshire*¹⁴

"Very careful measurements of some hundreds of combs, built by numerous colonies of black bees, showed only inconsiderable variations and an average of 14 ½ cells, measured across their parallel sides, to each 3in." (p. 210)

'Natural worker-comb seems to vary between the extremes of 30 and 27 cells to the 6in., ...' (p. 212)

Cheshire's average, based on the Imperial inch, corresponds to cells of 5.26 mm diameter. His range corresponds to 5.08 to 5.64 mm cells.

Langstroth (Dadant edition)¹⁵

Page 98: '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.'

Page 152: 'As every square inch of comb contains 55 cells, 27 to 28 on each side,...'

55 cells to the square inch is 852.5 cells to the square decimeter. This corresponds to a cell size of 5.2 mm.

*Cowan*¹⁶

'Worker cells are smaller than those of drones, five of the former measuring 1 inch in width.' (p. 11)

'There are 28.86 and 18.47 drone cells to a square inch on each side.'

Although these figures were taken from the 14th edition of *British beekeepers guide book to the management of bees in movable comb hives* dated 1896 they were already present in the French edition of 1887, and are very likely in the first edition of 1881.

Cowan would have been using the imperial inch of 25.4 mm. This makes his cell size 5.08 mm.

It has been suggested by Hawker (2011) that data from Cowan are unreliable, as different editions of his book give different values.¹⁷ Also, some of his books simply cite data from Abbé Collin.

But in his *The honey bee: its natural history, anatomy and physiology* (1890) Cowan writes:¹⁸

'The average size of a worker cell between the parallel sides is 1/5th of an inch, or 0.02 (A, Fig. 65, which is taken from a natural comb). We say 'average,' because considerable variation exists in different parts of the same comb, as Réaumur and Huber found. In carrying out our experiments, we took our measurements on three parts of each comb, and in each case in the three directions of the parallel sides. Thus, each comb furnished us with nine measurements. In order to reduce the possibility of errors occurring from measuring only one cell, we selected ten cells, which, allowing 1/5th of an inch to each cell, should occupy the space of 2 inches. In all, thirty-six measurements were taken, and we found the greatest aggregate diameters of any one series of ten cells to amount to 2.11 inches, and the least to 1.86, a difference of the diameters of a little more than a cell and a quarter. We next measured a large piece of comb, and took sixty cells, which theoretically ought to occupy the space of 12 inches. The measurements were made on three different combs, but they showed much variation. For instance, one row of cells taken 2 inches from the top measured 12.10 inches, and 4 inches from the top 12.00, and 2 inches lower down 12.01 inches. Taking ten cells in either of the above rows also showed considerable variation. In the first row the aggregate diameter of ten cells taken at one end was 2.07, in the middle 1.98. and at the other end 2.08. In the second row the diameters were 2.10, 1.95 and 1.98. In the third row 2.00, 1.95 and 2.05. From this it will be seen that the variation is not regular, but generally speaking the cells increase in size towards the ends, although this is not invariably the case. All these combs were worked by black bees in the natural way; but we would mention that measurements taken on combs worked by Carniolan bees showed the same variations, but the average size of their cells was larger.'

Cowan's range of 1.86 to 2.11, corresponding to 4.72–5.36 mm, is large, but fits well with his average, reported elsewhere in his writings, of 5.08 mm. Even so, this is somewhat below the average worker cell size observed by other researchers.

Conclusions regarding natural cell size from the literature before 1900

Other pre-1900 texts that report comb cell size are not available to me. Zeissloff examined the early literature and identified reports of authors who measured cell size themselves and did not simply copy earlier reports. To the above list we can add only his data from L'hullier¹⁹ who found the average cell size to be 5.40 mm.²⁰

From the above data, the widest cell size range reported is 4.70 mm (Wyman) to 5.64 mm (Cheshire). With the higher values there is a risk that the investigator concerned has included some honey storage comb in the measurements. Furthermore, it is possible that patches of smaller cells were present in combs investigated but the low values were lost in the averaging process. The average of the averages from all the above investigators is 5.25 mm.

Data on natural cell size from the literature since 1900, including recent measurements

Data on the cell size of natural comb since the introduction of foundation are liable to the criticism that they may be influenced by bees that were previously habituated to foundation of an unnaturally large cell size. However, this criticism would be ruled out if the values found accord with the early data, say from 1712 (Maraldi) to 1881 (Cowan).

Author	Date	Cell size (mm)
Vogt ²¹	1911	5.28-5.46 ²²
Armbruster ²³	1920	<i>awaiting data</i>
Seeley & Morse ²⁴	1976	5.2

Lee & Winston ²⁵	1985	5.15-5.25 ²⁶
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Dennis Murrell has measured cell size in natural feral comb and in near natural comb from top-bar hives.²⁷ He found a range from below 4.6 to 5.6 mm. In samples of top-bar hive come from other beekeepers he also found up to 25% was below a cell size of 4.9 mm.

Conclusions

Taking averages from the above table, we obtain a mean worker cell size of 5.27 mm which is almost identical to the pre-1900 average of 5.25 mm (see above). Even if Murrell's range of 4.6 to 5.6 mm is included, the mean for post-1900 comb cell size is 5.22 mm. My running average for ongoing measurements of cell size in feral comb from natural nests and foundationless comb from Warré hives is 5.3 mm.²⁸

We can therefore conclude that worker cell size in naturally constructed comb has not changed appreciably (<0.5%) throughout recorded beekeeping history, not even since the introduction of foundation in the late 19th century.

Acknowledgement

This paper was compiled with the help of data from early authors already identified by Erickson,^{2,3} Zeissloff,¹⁸ Stever,²⁰ Murrell^{25,29} and Hawker.¹⁵ The author thanks Michael Bush, Francis Saucy and Larry Garrett for drawing his attention to the data of François Huber, Abbé Collin and Pierre André Latreill respectively.

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¹ Stiglitz, D. & Herboldsheimer, L. (2008) *The complete idiot's guide to beekeeping* Alpha/Penguin.

² Erickson, E. H., Lusby, D. A., Hoffman G. D. & E. W. Lusby (1990) On the size of cells. Speculations on foundation as a colony management tool. Part I. *Gleanings in Bee Culture*, *Gleanings in Bee Culture* 118:98-101.

³ Erickson EH, Lusby DA, Hoffman GD, Lusby EW (1990) On the size of cells. Speculations on foundation as a colony management tool. Part II *Gleanings Bee Cult* 118:173-174.

⁴ <http://groups.yahoo.com/group/Organicbeekeepers/>

⁵ Swammerdam, Jan (1737/8) *Bybel der Natuure*. Pub: Herman Boerhaave. (written 1669-1673) Page. 379.

(http://www.dbnl.org/tekst/swam001bybe01_01/downloads.php)

⁶ Maraldi, Giacomo Filippo (1712) *Observations sur les abeilles* Pages 304, 306.

⁷ Réaumur, René Antoine Ferchault de (1742) *Mémoire pour servir à l'histoire des Insectes* Page 397.

⁸ Latreille, P. A. (1811) in *Recueil d'observations de zoologie et d'anatomie comparée: faites dans l'Océan Atlantique, dans l'intérieur du nouveau continent et dans la Mer du Sud, pendant les années 1799, 1800, 1801, 1802 et 1803*, Part 2, Volume 1. Authors: Alexander von Humboldt, Pierre André Latreille, A. Bonpland, Georges Cuvier (baron). *Voyage de Humboldt et Bonpland. Dèxieme Partie. Observations de Zoologie et d'Anatomie Comparée. Premier Volume*. F. Schoell, Paris. Pages 266 & 267. The same memoir appears in an earlier publication: *Annales du Museum d'histoire naturelle* Vol. 4, 1804 pp. 383-395, together with a figure on page 382. The relevant pages are 387 & 388.

⁹ Huber, F. (1814) *Nouvelles observations sur les abeilles* Page 222. Seconde édition, Tome Second, Paschoud, Paris & Genève.

¹⁰ Wyman, J. (1866) *The cells of the bee*. pp. 5-6. (From Proceedings of the American Academy of Arts and sciences, VII, 9 Jan. 1866) Cambridge: Welch Bigelow & Co.

¹¹ Berlepsch, August Freiherr von (1869) *Die Biene und ihre Zucht auf beweglichem Rahmen*. Page 149.

¹² Root, A. I. (1877, first edition) *The ABC and XYZ of Bee Culture*. A. I Root & E. R. Root, Taken from 36th Edition, 1975. This part does not appear in later editions.

¹³ Collin, Abbé (1878) *Le guide propriétaire d'abeilles* Cinquième édition. page 31. Berger-Levrault, Paris & Nancy.

¹⁴ Cheshire, F. R. (1888) *Bees and beekeeping; scientific and practical. Vol. II – Practical*. The Bazaar Exchange and Mart Office, London. Pages 210 & 212.

¹⁵ Langstroth, L. L. (1889) *Langstroth on the hive and the honey bee*. Charles Dadant & Son. Page. 152.

¹⁶ Cowan, T. W. (1896) *British beekeepers guide book to the management of bees in movable comb hives*. Houlston & Sons. Page 12.

¹⁷ Hawker, B. (2011) Personal communication: "The above reference is to a later edition of Cowan's *Guide Book*. The early editions only mentioned 5 and 4 cells to the inch (5.08 worker cells per mm).

In the mid 1880s Cowan introduced the figures of Abbé Collin of 27.5 and 17.09 cells per sq. inch. He removed these after a few editions and inserted his own figures of 28.87 and 18.48.

The reference used by McMullan & Brown (2006, see below) is to the 2nd edition of Cowan's *The honey bee; its natural history, anatomy and physiology* (1904, Houlston & Sons, London, UK, 220pp.). Cowan made a slight change from the 1st to the 2nd editions. In the first, he quoted the Abbé Collin figures, but added 'not more than 25 (worker) and 16 (drone) cells per square inch will be found and these numbers have generally been adopted'. By the second edition Cowan had replaced the reference to Collin and inserted his own figures of 28.86 [worker, corresponds to a cell size of 5.08 mm including wall thickness] and 18.47 [drone] removing the quoted passage, adding 'taking the average of a large surface, 28 [worker, corresponds to a cell size of 5.15 mm including wall thickness] and 18 [drone] will be found sufficiently near the mark for general calculation'.

This was the bit that he confronted Root with when he was in America, regarding an article by Miller, forcing Root to publish an apology and do penance by criticising Cheshire. It is typical Cowan. He continued by stating that he had measured wild comb of the British black bee, Ligurians, Carniolans and American bees, but only gave details of his work on the British bee. He made measurements on four comb sides, measuring on three separate parts, three different ways (= 36 statistics). Each measurement was of 10 cells and resulted in a range 1.86 – 2.11 inches (4.72–5.36 mm)."

Reference: McMullan, J. B. & Brown, M. J. F. (2006). Brood-cell size does not influence the susceptibility of honey bees (*Apis mellifera*) to infestation by tracheal mites (*Acarapis woodi*). *Experimental and Applied Acarology* 39: 273-280.

¹⁸ Cowan, T. W. (1890) *The honey bee: its natural history, anatomy and physiology*. Houlston & Sons, London. pp. 180-181.

¹⁹ Lhuillier, M. (1781) *Mémoire sur le minimum de cire des alvéoles des abeilles*. Nouveaux Mémoires de l'Académie Royale des Sciences de Berlin.

²⁰ Zeissloff, E. (2008) *Natural cell size*. http://www.dheaf.plus.com/warreekeeping/zeissloff_cell_size_en.pdf

²¹ Vogt, H. (1911) Geometrie und Ökonomie der Bienenzelle. *Festschrift zur Jahrhundertfeier der Universität Breslau*. Breslau, Trewendt & Granier, 1911.

²² Quoted by Stever, T. (2003) Verkleinerte Bienen – Irrweg der Züchtung oder Wunderwaffe gegen Varroamilben? *Bienenpflege – Zeitschrift des Landesverbands Württembergischer Imker e.V.* 3, 93-95.

<http://www.franziproske.de/downloads/kleinebienengegenvarroa.pdf> or

http://www.bienenarchiv.de/veroeffentlichungen/2003_zellengroesse/zellengroesse.htm

²³ Armbruster, L. (1920): Zum Problem der Bienenzelle – Eine vergleichende Instinkt-Biologie des Nestbaues bei Bienen und Wespen; Leipzig, Berlin, Freiburg: *Bücherei für Bienenkunde IV*.

²⁴ Seeley, T. D. & Morse, R. A. (1976) The nest of the honey bee (*Apis mellifera* L.) *Insectes Sociaux* 23(4), 495-512.

²⁵ Lee, P. C. & Winston, M. L. (1985) The effect of swarm size and date of issue on comb construction in newly founded colonies of honey bees (*Apis mellifera* L.) *Can. J. Zool.* 63, 524-527.

²⁶ Quoted in: Winston, M. L. (1987) *The biology of the honey bee*. Harvard University Press. p. 81.

²⁷ Murrell, D. (2011) Natural comb. <http://beenaturalguy.com/observations/natural-comb/>

²⁸ Heaf, D. J. (2012) *Comb worker cell size measurements*

http://www.dheaf.plus.com/warreekeeping/cell_size_measurements.htm

²⁹ Murrell, D. (2011) <http://beenaturalguy.com/small-cell/a-i-root-and-cell-size/>