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ECTD_028

TITLE: Charles Darwin and Bees.

SOURCE: *Bee World* 40: (12) 297 - 303

DATE: 1957

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BEE WORLD

Vol. 40 No. 12 DECEMBER 1959

CHARLES DARWIN AND BEES

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This year we are celebrating the centenary of *The origin of species*, which was first published in London on 24th November 1859, under the title *On the origin of species by means of natural selection, or The preservation of favoured races in the struggle for life.* The index of this book contains the names of well over two hundred different plants and animals, and it would seem that in this great variety, bees could only occupy a very minor position in Darwin's interests. Nevertheless on reading the two of Darwin's books which contain most of his references to bees (*The origin of species*, and *The effects of cross and self fertilisation in the vegetable kingdom* published in 1876), one certainly gets the impression that he was particularly interested in them, and that he devoted long hours to their observation, probably in his garden at Down in Kent.

COMB BUILDING BY HONEYBEES

In *The life and letters of Charles Darwin* (1887), his son Francis mentions that his father took no personal share in the management of the garden; but though that may have applied to the general care of the bees, Darwin did undoubtedly look through the hives on occasion. He was particularly interested in the way the comb was built, and in a letter to A. R. Wallace in 1859 he says ' this is an especial hobby of mine, and I think I can throw a light on the subject '. He carried out a number of experiments, described in *The origin of species.*

' Following the example of Mr. Tegetmeier,* I separated two combs, and put between them a long, thick, rectangular strip of wax : the bees instantly began to excavate minute circular pits in it ; and as they deepened these little pits, they made them wider and wider until they were converted into shallow basins, appearing to the eye perfectly true or parts of a sphere, and of about the diameter of a cell. It was most interesting to observe that, wherever several bees had begun to excavate these basins near together, they had begun their work at such a distance from each other, that by the time the basins had acquired the above-stated width (*i.e.* about the width of an ordinary cell), and were in depth about one sixth of the diameter of the sphere of which they formed a part, the rims of the basins intersected or broke into each other. As soon as this occurred, the bees ceased to excavate, and began to build up flat walls of wax on the lines of intersection between the basins, so that each hexagonal prism was built upon

* W. B. Tegetmeier, at one time Secretary of the Muswell Hill Beekeepers' Association, and founder of the Library which is now known as the Miller Memorial Library.

the scalloped edge of a smooth basin, instead of on the straight edges of a three-sided pyramid as in the case of ordinary cells.

'I then put into the hive, instead of a thick, rectangular piece of wax, a thin and narrow, knife-edged ridge, coloured with vermilion. The bees instantly began on both sides to excavate little basins near to each other, in the same way as before; but the ridge of wax was so thin, that the bottoms of the basins, if they had been excavated to the same depth as in the former experiment, would have broken into each other from the opposite sides. The bees, however, did not suffer this to happen, and they stopped their excavations in due time ; so that the basins, as soon as they had been a little deepened, came to have flat bases; and these flat bases, formed by thin little plates of the vermilion wax left ungnawed, were situated, as far as the eye could judge, exactly along the planes of imaginary intersection between the basins on the opposite sides of the ridge of wax. In some parts, only small portions, in other parts, large portions of a rhombic plate were thus left between the opposed basins, but the work, from the unnatural state of things, had not been neatly performed. The bees must have worked at very nearly the same rate in circularly gnawing away and deepening the basins on both sides of the ridge of vermilion wax, in order to have thus succeeded in leaving flat plates between the basins, by stopping work at the planes of intersection.

* * *

'From the experiment of the ridge of vermilion wax we can see that, if the bees were to build for themselves a thin wall of wax, they could make their cells of the proper shape, by standing at the proper distance from each other, by excavating at the same rate, and by endeavouring to make equal spherical hollows, but never allowing the spheres to break into each other. Now bees, as may be clearly seen by examining the edge of a growing comb, do make a rough, circumferential wall or rim all round the comb; and they gnaw this away from the opposite sides, always working circularly as they deepen each cell. They do not make the whole three-sided pyramidal base of any one cell at the same time, but only that one rhombic plate which stands on the extreme growing margin, or the two plates, as the case may be ; and they never complete the upper edges of the rhombic plates, until the hexagonal walls are commenced.

* * *

'It seems at first to add to the difficulty of understanding how the cells are made, that a multitude of bees all work together ; one bee after working a short time at one cell going to another, so that, as Huber has stated, a score of individuals work even at the commencement of the first cell. I was able practically to show this fact, by covering the edges of the hexagonal walls of a single cell, or the extreme margin of the circumferential rim of a growing comb, with an extremely thin layer of melted vermilion wax ; and I invariably found that the colour was most delicately diffused by the bees—as delicately as a painter could have done it with his brush—by atoms of the coloured wax having been taken from the spot on which it had been placed, and worked into the growing edges of the cells all round. The work of construction seems to be a sort of balance struck between many bees, all instinctively standing at the same relative distance from each other, all trying to sweep equal spheres, and then building up, or leaving ungnawed, the planes of intersection between these spheres. It was really curious to note in cases of difficulty, as when two pieces of comb met at an angle, how often the bees would pull down and rebuild in different ways the same cell, sometimes recurring to a shape which they had at first rejected.'

COMB BUILDING BY OTHER BEES

Darwin was also interested in comb building by other species of bees, and in the letter to Wallace mentioned above, he says : 'If you can collect duplicates [of bees' combs] at no very great expense, I should be glad of some specimens for myself with some bees of each kind.' In *The origin of species* he writes :

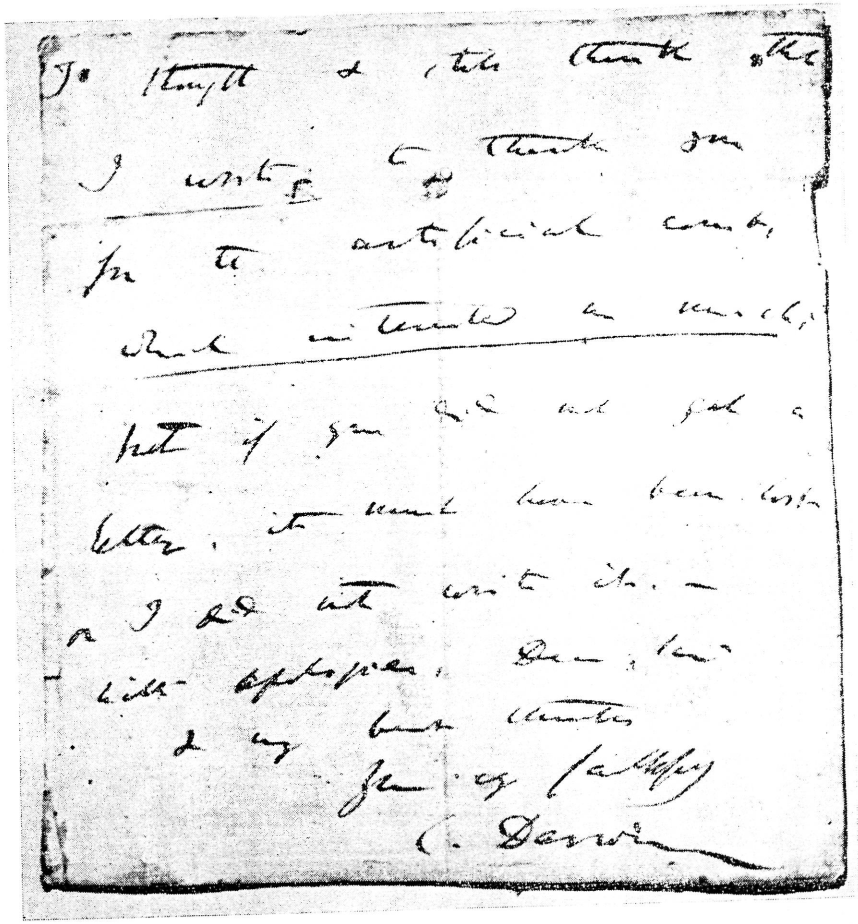
'In the series between the extreme perfection of the cells of the hive-bee and the simplicity of those of the humble-bee we have the cells of the Mexican Melipona domestica, carefully described and figured by Pierre Huber. The Melipona itself is intermediate in structure between the hive and humble bee, but more nearly related to the latter; it forms a nearly regular waxen comb of cylindrical cells, in which the young are hatched, and, in addition, some large cells of wax for holding honey. These latter cells are nearly spherical and of nearly equal sizes, and are aggregated into an irregular mass. But the important point to notice is, that these cells are always made at that degree of nearness to each other that they would have intersected or broken into each other if the spheres had been completed ; but this is never permitted, the bees building perfectly flat walls of wax between the spheres which thus tend to intersect. Hence, each cell consists of an outer spherical portion, and of two, three, or more flat surfaces, according as the cell adjoins two, three, or more other cells. When one cell rests on three other cells, which, from the spheres being nearly of the same size, is very frequently and necessarily the case, the three flat surfaces are united into a pyramid ; and this pyramid, as Huber has remarked, is manifestly a gross imitation of the three-sided pyramidal base of the cell of the hive-bee. As in the cells of the hive-bee, so here, the three plane surfaces in any one cell necessarily enter into the construction of three adjoining cells. It is obvious that the Melipona saves wax, and what is more important, labour, by this manner of building ; for the flat walls between the adjoining cells are not double, but are of the same thickness as the outer spherical portions, and yet each flat portion forms a part of two cells.'

COMB FOUNDATION

It is not surprising that Darwin should have taken an interest in comb foundation, which had been invented in 1857. T. W. Woodbury, who introduced movable-frame beekeeping into Britain in 1862, evidently sent some of the new 'artificial comb' to Darwin, for the Beekeeping Museum of the Bee Research Association has the original letter which Darwin wrote to Woodbury (p. 300) : 'I thought and still think that I wrote to thank you for the artificial comb, *which interested me much* ; but if you did not get a letter, it must have been lost or I did not write it.—With apologies, Dear Sir, and my best thanks, Yours very faithfully, C. Darwin '. One gathers that letter writing was rather a burden ; since so many letters were received, some rather foolish, it is not surprising that Darwin should sometimes have wondered whether he had or had not replied ; he used to say 'that if he did not answer them he had it on his conscience afterwards '.

BEES AS POLLINATORS

Darwin's main interest in bees arose from their function as pollinating agents. He writes that he 'was led to attend to the cross fertilisation of flowers by the aid of insects from having come to the conclusion, in my speculation on the origin of species, that crossing played an important part in keeping specific forms constant'. Subsequently he studied the adaptation of flowers for cross-fertilisation for many years, concentrating on the orchids; he came to the conclusion that for some reason, then unknown, it was usually necessary for pollen to be transported from one flower to



I write to thank you for the artificial comb, which interested me much;

but if you did not get a letter, it must have been lost

yours very faithfully

C. Darwin

Letter from Charles Darwin to T. W. Woodbury

another. These results were published in the book *On the various contrivances by which orchids are fertilised by insects* (1862). Darwin then went further and, as a result of a chance observation which was followed up by a long series of detailed experiments, he discovered that seed from a plant that has been cross-fertilised gave rise to offspring superior in growth and vigour to those from a self-fertilised plant. This very important result explained the necessity for the complicated floral mechanisms which

ensure cross-fertilisation, and made it possible to understand how 'natural selection can act on, and mould floral structures'. The proof of all this is given in his book *The effects of cross and self fertilisation*. Francis Darwin calls this 'the most unreadable of all his books to any but a professed naturalist', but beekeepers should be included in this term, for the book is full of interesting observations on the behaviour of honeybees and bumble bees. Darwin's experiments were carried out on 57 plant species belonging to 30 families, and he handled 2177 plants in all, from germination to maturity; in nearly every one the crossed plants had the advantage. Although these experiments were so important, they were carried out under extremely domestic conditions at Down, his home; the seeds were all germinated on 'the chimney piece in a warm room'.

A chapter of this book is devoted to 'The habits of insects in relation to the fertilisation of flowers', in which observations on the constancy of honeybees and bumble bees are mentioned. 'All kinds of bees and certain other insects usually visit the flowers of the same species as long as they can, before going to another species. This fact was observed by Aristotle with respect to the hive-bee more than 2000 years ago, and was noticed by Dobbs in a paper published in 1736 in the Philosophical Transactions. It may be observed by any one, both with hive and humble-bees, in every flower-garden; not that the habit is invariably followed. Mr. Bennett watched for several hours many plants of *Lamium album*, *L. purpureum*, and another Labiate plant, *Nepeta glechoma*, all growing mingled together on a bank near some hives; and he found that each bee confined its visits to the same species. The pollen of these three plants differs in colour, so that he was able to test his observations by examining that which adhered to the bodies of the captured bees, and he found one kind on each bee.

'Humble and hive-bees are good botanists, for they know that varieties may differ widely in the colour of their flowers and yet belong to the same species. I have repeatedly seen humble-bees flying straight from a plant of the ordinary red *Dictamnus fraxinella* to a white variety; from one to another very differently coloured variety of *Delphinium consolida* and of *Primula veris*; from a dark purple to a bright yellow variety of *Viola tricolor*; and with two species of Papaver, from one variety to another which differed much in colour; but in this latter case some of the bees flew indifferently to either species, although passing by other genera, and thus acted as if the two species were merely varieties.

* * *

'That insects should visit the flowers of the same species as long as they can, is of great importance to the plant, as it favours the cross-fertilisation of distinct individuals of the same species; but no one will suppose that insects act in this manner for the good of the plant. The cause probably lies in insects being thus enabled to work quicker; they have just learnt how to stand in the best position on the flower, and how far and in what direction to insert their proboscides'.

BEES' RECOGNITION OF FLOWERS

Darwin then goes on to describe his observations on the bees' recognition of colours and shapes. 'That the coloured corolla is the chief guide cannot be doubted. On a fine day, when hive-bees were incessantly visiting the little blue flowers of *Lobelia erinus*, I cut off all the petals of some, and only the lower striped petals of others, and these flowers were not once again sucked by the bees, although some actually crawled over them. . . . The colour alone of the corolla serves as an approximate guide: thus I watched for some time humble-bees which were visiting exclusively plants of the white-flowered *Spiranthes autumnalis*, growing on short turf at a considerable distance apart; and these bees often flew within a few inches of several other plants with white flowers, and then without further examination passed onwards in search of the Spiranthes. Again, many hive-bees which confined their visits to the common ling (*Calluna vulgaris*), repeatedly flew towards *Erica tetralix*, evidently attracted by the nearly similar tint of their flowers, and then instantly passed on in search of the Calluna.

'That the colour of the flower is not the sole guide, is clearly shown by the six cases above given of bees which repeatedly passed in a direct line from one variety to another of the same species, although they bore very differently coloured flowers. I observed also bees flying in a straight line from one clump of a yellow-flowered Œnothera to every other clump of the same plant in the garden, without turning an inch from their course to plants of Eschscholtzia and others with yellow flowers which lay only a foot or two on either side. In these cases the bees knew the position of each plant in the garden perfectly well, as we may infer by the directness of their flight; so that they were guided by experience and memory. But how did they discover at first that the above varieties with differently coloured flowers belonged to the same species? Improbable as it may appear, they seem, at least sometimes, to recognise plants even from a distance by their general aspect, in the same manner as we should do. On three occasions I observed humble-bees flying in a perfectly straight line from a tall larkspur (Delphinium) which was in full flower to another plant of the same species at the distance of fifteen yards which had not as yet a single flower open, and on which the buds showed only a faint tinge of blue. Here neither odour nor the memory of former visits could have come into play, and the tinge of blue was so faint that it could hardly have served as a guide.

'The conspicuousness of the corolla does not suffice to induce repeated visits from insects, unless nectar is at the same time secreted, together perhaps with some odour emitted. I watched for a fortnight many times daily a wall covered with *Linaria cymbalaria* in full flower, and never saw a bee even looking at one. There was then a very hot day, and suddenly many bees were industriously at work on the flowers. It appears that a certain degree of heat is necessary for the secretion of nectar; for I observed with *Lobelia erinus* that if the sun ceased to shine for only half an hour, the visits of the bees slackened and soon ceased.'

These examples are enough to show what long periods Darwin must have spent watching bees at work. He also records his observations on the speed of flight of bees, and on the number of flowers they visit. He observed that bees from different hives may visit different kinds of flowers, and he comments that in one garden they visit a plant whereas in another a few miles off they do not.

COROLLA BITING

One aspect of bee behaviour that interested Darwin especially was corolla biting, because if the flower is bitten it is not cross-fertilised. 'The plants, the fertilisation of which actually depends on insects entering the flowers, will fail to produce seed when their nectar is stolen from the outside; and even with those species which are capable of fertilising themselves without any aid, there can be no cross-fertilisation, and this, as we know, is a serious evil in most cases. The extent to which humble-bees carry on the practice of biting holes is surprising: a remarkable case was observed by me near Bournemouth, where there were formerly extensive heaths. I took a long walk, and every now and then gathered a twig of *Erica tetralix*, and when I had got a handful all the flowers were examined through a lens. This process was repeated many times; but though many hundreds were examined, I did not succeed in finding a single flower which had not been perforated. Humble-bees were at the time sucking the flowers through these perforations. On the following day a large number of flowers were examined on another heath with the same result, but here hive-bees were sucking through the holes. This case is all the more remarkable, as the innumerable holes had been made within a fortnight, for before that time I saw the bees everywhere sucking in the proper manner at the mouths of the corolla.'

He found however that if a plant was growing alone, instead of in a group, it was rarely bitten, a feature which perhaps saved the species from extermination. 'If a plant suffers from being perforated, fewer individuals will be reared, and if its nectar is highly important to the bees, these in their turn will suffer and decrease in number; but, what is much more effective, as soon as the plant becomes somewhat rare so as not to grow in crowded masses, the bees will no longer be stimulated to gnaw holes in the flowers, but will enter them in a legitimate manner. More seed will then be produced, and the seedlings being the product of cross-fertilisation will be vigorous, so that the species will tend to increase in number, to be again checked, as soon as the plant again grows in crowded masses.'

But Darwin's best known observation on bees comes in *The origin of species*, where he describes how he has proved that bees are necessary for the fertilisation of clover, and stresses the vital importance of bumble bees to the production of red clover seed, a matter not appreciated before. He then goes on in a more light-hearted vein to suggest that since mice destroy bumble bees' nests and cats destroy mice, the frequency of certain flowers in a district may depend, unlikely as it may seem, on a high cat population. This train of reasoning has since been carried even further to equate a high cat population with an abundance of old maids, but this addition should not be attributed to Darwin.