

**CHARLES DARWIN ON THE ROUTES
OF MALE HUMBLE BEES**

R. B. FREEMAN

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R. B. FREEMAN

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I. INTRODUCTION

BETWEEN the years 1854 and 1861 Charles Darwin, with the help of five or six of his children, made a number of observations on the flight routes of male humble bees. These he recorded at the time in a series of field notes, but he never wrote them up for publication in England. In May 1872, however, he wrote a précis of them. It is these notes and a version of the précis which are printed below.

A German translation of this précis was published in 1886 by Ernst Krause in the second volume of his edition of some of Darwin's shorter works entitled *Gesammelte kleinere Schriften*, 1884-86. Krause describes, in a footnote, here translated from the German, how he came by the manuscript: "The present essay by Darwin was amongst the papers of Professor Hermann Müller of Lippstadt, the authority on the relationships between flowers and insects, who died on 25 August, 1883. It was sent to him in May, 1872. I have mentioned this in my biography of Müller where further details may be found. So far as I know it has never been published, but the observations that it contains are far too valuable to be forgotten. I owe this information to the son of my late friend, Dr. Hermann Müller, who is a secondary school master in Liegnitz".

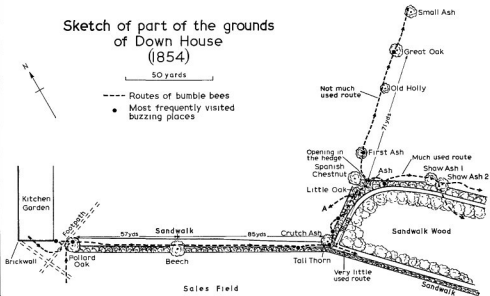
Darwin's original must have been written in English, because he had little German, and it must have been accompanied by a sketch of the relevant parts of his grounds at Down House, because a plan with German captions accompanies the translation. I have not been able to trace the whereabouts of the original manuscripts, either in English or in German. This précis was translated from the German into English and published, with the German plan, in my *Works of Charles Darwin*, 1965. The version published here is somewhat modified in the light of the words actually used by Darwin in his notes, and it also contains a few corrections.

The existence of Darwin's original field notes was brought to my attention by Mr. P. J. Gautrey of the Department of Western Manuscripts, University Library, Cambridge. They are written in ink on nineteen leaves of blue-tinted paper and on one, dated August 13th, 1861, of a much darker blue. The outside wrapper is of the same blue-tinted paper and bears on the front "Humble Bees / Cupboard IX / C3, 10 [10 is deleted] / For Letters", and on the back "(Humble Bees)". There is a rough pencil sketch of the grounds on the inside of this wrapper. They

Sketch of part of the grounds of Down House (1854)

50 yards

- Routes of bumble bees
- Most frequently visited buzzing places



are amongst a collection of Darwin manuscripts which were deposited in the Library by Sir Robin Darwin in 1963.

It is clear that they were set down shortly after the times of each original set of observations. There are no indications that they were altered or added to later, except for the addition of the general title on the outside cover, and possibly the addition of years, in pencil, at the top of some leaves. The notes are written in a condensed manner with many contractions and inconsistencies of usage. In the transcript given below I have expanded the contractions and straightened the inconsistencies. For example, Darwin wrote buz or buzz, sand-walk, sandwalk or swalk; I have used buzz and sand-walk throughout. I have not attempted to expand the condensations. In most places the sense is clear, and where it is not, a hypothetical expansion would be no aid to comprehension. In general, the notes are legible, but I am doubtful of the readings of a few words; these I have placed in brackets [] which Darwin uses only once. A line by line transcript without expansions has been deposited with the manuscript at Cambridge.

Neither of the two British books devoted to the humble bees, those of Sladen (1912) and of Free & Butler (1959), mentions Darwin's work, although the latter devotes several pages to the flight paths, as they are now called, of the males. A considerable amount of research on this subject has been undertaken in recent years which has confirmed and extended Darwin's observations, but his own work is not usually referred to, nor is his name mentioned. The best paper is that of Arthur Frank (1941) in which he describes closely similar flight paths for males of *Bombus hypnorum* and *Bombus terrestris*, but he is apparently unaware that accurate observations on the subject had been made nearly ninety years earlier. Haas (1952) has explained one of Darwin's difficulties by showing that the males mark their buzzing places with secretions from the mandibular glands, which attract others to the spot. Darwin's comment, in the field notes, about the dog and the corner stones shows that he had considered such an idea, but he does not mention it in the précis. The only paper that I have seen which refers to Darwin's work is one by Krüger (1951) which gives an excellent summary of his findings as they are given in the précis.

2. PRÉCIS

On September 8th, 1854, one of my sons¹ saw some humble bees enter a hole at the base of a tall ash tree. I looked into this hole hoping to find the entrance to a nest, but was unable to see one. Whilst I was examining the hole, another humble bee entered it, and, after flying off, returned almost immediately and, flying upwards for about a yard, flew away through a crutch between two large branches of the ash.

I now removed all the grass and other plants which were growing around the hole, but still could not find any entrance. After a minute or two, another humble bee appeared. It buzzed over the area that I had cleared and then flew up and passed, like the previous one, through the same crutch. I watched many others behaving in the same way, all coming from the same direction and arriving at intervals of a few minutes. The only exception was that some flew round the stem of the large

ash instead of through the crutch. I was later able to confirm that all these bees were males of *Bombus hortorum*. I made similar observations on many other occasions, and was able to follow the bees from the ash to a bare spot at the side of a ditch where they buzzed again, and then for several yards further to an ivy leaf where the procedure was repeated. I am going to call these spots where they stopped for a few seconds "buzzing places". From the ivy leaf they went into a dry ditch which was covered over by a thick hedge and flew slowly along the ground between the dense branches of thorn. I could only follow them along this ditch by making several of my children¹ crawl in, and lie on their tummies, but in this way I was able to track the bees for about twenty-five yards. They always came out of the ditch by the same opening, but from here there were three routes leading in different directions which I have indicated on the plan by dotted lines. I have marked them as far as I was able to follow the bees. There were several buzzing places on each of these routes, always a few yards apart. One of these was very odd because the bees had to fly down several feet to a fallen leaf at the bottom of a very thick hedge, and then fly back again by the way that they had come.

I then followed their route for about a hundred and fifty yards until they came to a tall ash, and all along this line they buzzed at various fixed spots. At the far end, near a pollard oak, the track divided into two as shown in the plan. On some days all the bees flew in the direction I have described, but on others some arrived from the opposite direction. From observations made on favourable days, I think that the majority of individuals must fly in a wide circle. They stop every now and then to suck at flowers. I confirmed that whilst in flight they move at about ten miles an hour, but they lose a considerable amount of time at the buzzing places. The routes remain the same for a considerable time, and the buzzing places are fixed within an inch. I was able to prove this by stationing five or six of my children each close to a buzzing place, and telling the one farthest away to shout out "here is a bee" as soon as one was buzzing around. The others followed this up, so that the same cry of "here is a bee" was passed on from child to child without interruption until the bees reached the buzzing place where I myself was standing.

After a few days the routes were slightly changed. The bees first buzzed at the base of a tall slender thorn in a hedge opposite the tall ash; they then flew slowly upwards close to the trunk of the thorn, and, ascending to a considerable height, crossed over a big branch of the ash where they buzzed, and were lost to view as they flew high over it. I saw scores of bees flying upwards by this particular thorn, but never saw one come down again. I kept up these observations for several years from the middle of July until the end of September. The best time for observation is the middle of a warm day.

Now I must describe the strangest part of the whole business. For several successive years male bees followed almost the same routes, and several of the buzzing places were exactly the same, for instance in the hole at the foot of the tall ash; furthermore the bees always flew away through the same crutch. They also travelled along the same dry ditches and flew in or out through the same small opening at the end of the hedge, although there were many similar openings at this spot which could have served their purpose just as well.

In the first year I saw dozens of bees coming through this particular opening and flying along the bottom of the ditch to the tall ash. But in the second year the bees visited the thorn mentioned above and flew upwards from there, and in the third they visited a different thorn nearby. At first I was astonished by these facts, and could not understand how bees born in different years could apparently learn exactly the same habits. But they seem to prefer to fly along hedges and paths, and they love to buzz around the feet of trees, so that I assume that the same routes and the same buzzing places have some kind of attraction for this species; but I am unable to understand in what this attraction consists. At many of their buzzing places there is nothing particular of note. When one of them has been frequently visited, it is possible to change its appearance completely without interrupting the visits. For instance I pulled up all the grass and plants from the one at the foot of the ash and sprinkled white flour on the spot, without this making any change in the visits. It is just as difficult to understand how individual males from the same nests in the same area follow the same routes and buzz in the same places in one particular year as it is to understand how the bees follow the same routes and choose the same buzzing places year after year; for I believe that they emerge one after another, and I have never seen two travelling together. I have also been unable to understand the purpose of this habit of always flying along the same routes and buzzing at the same places, thereby losing a great deal of time. I have kept a look out for queens on these flight paths, but have never seen one.

The males of *Bombus pratorum* also have buzzing places and behave in many respects like those of *Bombus hortorum*, but their habits and routes are somewhat different. On a visit to Devonshire I was able to confirm that males of *Bombus lucorum* visit buzzing places in the same way.

Mr. F. Smith⁸ of the British Museum knew nothing of this habit, but he referred me to a short note by Colonel Newman in the *Transactions of the Entomological Society of London* (New Series, Volume 1, part 6, 1851, p. 67). I have always regretted that I did not mark the bees by attaching bits of cotton wool or eiderdown to them with rubber, because this would have made it much easier to follow their paths.

3. FIELD NOTES

Sept. 8th—13th 1854. George¹ observed numerous humble-bees (I think all same species) go and buzz at spot at foot of ash. I cleared away all leaves and rubbish, feeling sure there was a nest—but none—this clearing made no difference. Then observed that bees mostly went through great fork of ash, or round bole, and buzzed at a spot on bole; then flew along side hedge and ditch and buzzed at (3/ bare ground, then along ditch to ivy leaves 4/, then along deepish dry ditch, lined by ivy and full of thorns (so go by only slowly) and out by round hole in hedge at end by (5/spanish chesnut². I think sometimes though rarely went straight along outside ditch.—One day all travelled in this course, other days a good many came travelling in back direction, but I think never so many.—Hoop-net which placed on (3/ buzz place, did not prevent bees coming and so caught. So not guided by vision.—Prudent bee flew away but afterwards returned.—

At buzz 5, there seems branching off. Some go obliquely across field towards flower garden: others to great ash, 5(a) but very many of these first went up hedge to south (probably to buzz 6.) and then returned in a Δ . From ash 5a I *think* they go to great oak—but most from hole in hedge by spanish chesnut (5/ do not buzz there but go [?about] south along hedge, to dead leaf in hedge (6/), this buzzing place singular as it lies rather in rubbish of hedge and bees have to fly in and out a good way out of course. From 6. they go a little along hedge and then over it to 6(a) or still further to between two ash branches (7 into the shaw. Here those that have gone over by 6a join same route. I have seen several fly from 6 to 5.—Here the bees come [?into] generally fly to near ground. Some buzz about and then go back out of shaw and apparently on southward, but others (I saw 3) go through thickest part of shaw obliquely into the sand-walk by seat on old fir.—These buzzing places must cause *extreme* delay. Do not come in afternoon 4-5. I have observed only 12-13. Come at about 1 per minute to buzz 1.

Sept. 14 Stormy. 12½ o'clock. Think bees flying about, but not one watched for ¼ hour on to track. At last they came quite quick in reverse course from buzz 2 to a new buzz (-1 Frank¹), deep in ditch, (just as if going into a hole) then down almost straight for 20 yards sand-walk; but Etty¹ says that some went towards kitchen garden. Others came from -1 to 2 and thence *towards* 2, 3, etc.

Sept. 15th 1854. Have quite deserted buzz 1. Now go back and forward from -1 Franky¹ buzz—to 2, and thence direct without calling at spanish chesnut, (5) thence some to ash and some round corner to 6 etc. — From -1 a few went to sand-walk, but most along hedge, calling at buzzing places every few yards to big beech, thence with many calls to pollard oak, thence over kitchen garden wall into Sales³ field.—Buzz 2. being quite white with flower⁴ made no difference in the calls when dusted at 2 always went direct to 5 then back to all calling places to the kitchen garden.—at 3½ none.

Sept. 17th Things go as usual at -1 Frank¹ buzz going in 3 ways thence, but some went through hedge. Observed there a different species buzzed all along straight hedge of sand-walk, at shorter intervals and never on ground, and very uncertainly at each buzzing place. But certainly they have numerous buzzing stages.—

Sept. 25th Much cold weather but saw some bees go to buzzing places at pollard oak by kitchen garden.—The other humbles by straight sand-walk quite active.—

Sept. 29th Very fine day. Several bees out, all visited Backy's¹ buzzing place, then went up either side of the thorn bush, then crossed over head to great limb of ash, and so up the limb, half up tree to where lost to view.

Oct. 2nd. Saw bees going up thorn and crossing over with greatest precision to one spot of great limb.—never have seen one come in reversed direction, but all from kitchen garden along walk.

Footnote: v. Trans. Entomolog. Soc. (New S.) Vol. 1 Part 6th. p. 87 1851.⁵

July 23rd, 1855. George¹ and Franky¹ observed yesterday and 2 or 3 days ago several humble bees at buzzing places.—This day I saw them going to identical spot under crutch, where they were first seen last year.—Some now go round and towards spanish chesnut tree. Others go along walk, buzzing every now and then:

they buzz in hole on south side of great beech, instead of on north side, and at almost identical spot, if not very identical spot, on old oak pollard.—Bees went both ways. Willy¹ is almost sure that one bee stopped at flower and then went on course.—Several of the bees seemed only slightly to pause over the beech buzzing places; and some seemed to have difficulty in finding their buzzing places.

July 24th. After rainy morning watching at oak pollard 3 first bees came from west.—Ascertained some stop to visit flowers on road.—3 bees at intervals came from ash pollard to oak pollard, and buzzed in rather different way from others, which go on visiting some leaves and flying about and then turned and went back, visiting the buzzing places on walk-side and going back to big beech. Surely it is too early and too many for all these bees to be mere promenaders.—4' 50" Bees yet visiting pollard oak. They do *suck* flowers on road.—

July 25th at 10.30 am. Bees at oak pollard. Often suck flowers on road. Seems almost general rule. At oak pollard at least 2 roads diverge.—I saw 2 bees enter hole by spanish chesnut (where hurdle was put), and fly along ditch; I think do not come out on other side of hedge.—It is impossible the bees could have hit accidentally 2 years successively on so obscure a hole: describe how long we were before we could find out this hole.

July 28th. Saw 5 bees enter hole by spanish chesnut; one or two entered 18 [?] inches, word omitted] above hole. Also saw them at crutch.—

July 29th 11½ am. Watched hole by spanish chesnut and saw during 1½ hours from 40–50 bees enter, and not one come out of hole. The greater number went (as by plan) from field ash to foot of *little ash* and then through hole to *base* up little oak, then up oak and then *east* of little ash (making circle and then by a very long flight to shaw ash 1 & 2.—I saw some crawl through hedge by little ash, so as to cut off circle and yet come back and go through proper route. Some few of them instead of going as described turned to west and flew apparently towards crutch ash.—

Again some thought by Willy¹ to be larger and more buzzing bees, came along ditch from south to foot of ditch oak and then turned to west and apparently flew back towards crutch ash. At crutch ash (having no effect) some go along well west to great beech etc.—often into sand-walk, and others round tree up towards spanish chesnut, apparently turning into ditch.—

Note at left of page: Bees flew in longest range from spanish chesnut hole and shaw ash 1 in 6½ seconds, a little over 10 miles an hour.

Aug. 17th Splendid day 12½ to 1 o'clock. Watched for 20' and saw not one bee enter hole by spanish chesnut.—but saw 3 enter hedge about 3 yards south of spanish chesnut turn by A, in reverse course to that formerly marked by Willy¹.—Ash. Watched crutch and cob-web shows quite given up that place. In fact very few bees about. ?Has one set died and another not yet born.—

Aug. 22nd. Saw 3 bees at crutch B. 2 flew towards spanish chesnut and one along walk.—From spider's web I do not believe any have buzzed before here.—I looked large and bright yellow.—Saw queen visiting tealze flower.

Aug. 23rd. Saw bees at crutch, and they went *through* crutch, and towards spanish chesnut tree, entering by last year's ivy leaf buzz, but did not come out by

hole by spanish chesnut tree. One or two went up young thorn south of thorn of last year.—

Aug. 29th Saw bees *several* go to exact spot at bottom of thorn (last years Franky¹ buzzing place); but not up the tree. Thence most went round ash to near or about old ivy. Buzzed and then turned through hedge at bottom to some sand, and then apparently along hedge bottom—Some, however, went to crutch buzz. All then came from kitchen garden way. Two bees after going to Franky¹ went about 4 feet back towards kitchen garden, buzzed and again came to Franky buzz. Now there are scores of trees like Franky¹ buzz. It certainly appears they keep to same buzzing places though course altered.

Sept. 7th. Saw bee at crutch buzz.

Sept. 26. Fine day: saw several bees at crutch: some went through: none called at thorn.—also saw 2 or 3 go into hole within one foot of old hole by spanish chesnut: some also buzzed at foot of spanish chesnut at old place.

Sept. 27th. Many at crutch. Called at marked place on *south* side of great beech, and at old buzzing place on old oak pollard.—

1856. July 10th. I several times watched before this date and saw none. Observed bees coming out of 2 or 3 [This is male of *Bombus pratorum*]⁴ near holes at end of hedge in sand-walk by ash and crossing walk buzzing a little about hedge to left of a hole in hedge, then fly into hole and then flying along bottom of hedge westward. Today (11th) saw one coming opposite course. 12th saw another coming opposite course. Also today 11th saw *Bombus hortorum* at bottom of Franky's¹ thorn: came in there and then flew *towards* big beech.—one other crossed towards old ivy-leaf buzzing place.—12th Saw both species, as before.—

July 25th. Saw *B. hortorum* go to tree-foot, next to Franky's¹ thorn, then fly along walk to south side of big beech tree.—one from this place went to surface of old ash, 18 inches from old buzzing place, then round towards old ivy leaf and then I believe to bottom of hedge near hole by spanish chesnut tree. I saw two go into the very old hole (and one by hole within foot's distance) by the spanish chesnut tree: I suspect come out near crutch buzzing place. One buzzed at oak by garden and then came to Franky¹ buzzing place and then towards spanish chesnut. Some went into sand-walk from new crutch place.—

July 26th. Saw bee go ivy-ash and then to Franky¹ buzz and then along sand-walk to beech. Saw many go from Franky¹ buzz towards spanish chesnut tree, and some called at ground buzzing place about yard from hole. One turned back at this buzzing place and went into the hole.

Note at left of page: How on earth do bees coming separately out of nest discover same place, is it like dogs at corner-stones?

Several called at buzz within yard of hole, coming from along the hedge running eastward, and went in to holes and then buzzed at foot of same young *ash* as last year and then went along bottom of hedge.—Lenny¹ thinks two kinds call at Franky¹ buzz, coming from big beech, and all go up, *towards* spanish chesnut, but only a few, *the larger* ones, come to the ground buzzing place within yard of hole: I am inclined to believe true.—I have as yet seen bees only go *into* hole.

July 30th. Saw several go to Backy's¹ thorn, then buzz about 18 inches to east,

then go to west side of old ash, then to the east side where covered by ivy and then round corner into sand-walk.

Aug. 2nd. Saw bee go to seek old crutch buzzing place.—

1857. Aug. 28th. After having several times casually watched, saw bees at old used crutch buzzing place, after going into hollow, they flew a little up to right hand to some ivy leaves, and then straight down walk towards summer house.

Sept. 16th. Saw 2 bees go to thorn by the old ash: they went not to root, but low down, and then went high up where I lost sight of them.

Sept. 17th saw several on same thorn—one flew up towards branch of big ash tree, as [?anciently]—the rest just flew round big ash, towards corner with spanish chesnut.—I saw what I *fancied* was female come and find with difficulty the tree: and it rested on twigs and seemed to sting them.

Note at left of page: Do not females find males by their buzzing places? Several females and not nearly so many males as with hive bee.

1858. I watched many days and saw none until Leny¹ saw one on Sept. 14. To-day (15th) I also saw them at old identical crutch spot; several then flew first round gate to another little hollow at foot of tree: and some flew through the crutch and then went up towards spanish chesnut; but it did not come out of hole by spanish chesnut tree.

1859.—Aug. 12th. *Very* few humble bees—saw few buzzing at tall thorn, (not former one) but close within iron-hurdle within sand-walk—they apparently flew up the ash tree. They began buzzing high up the thorn.—

Aug. 18th & 19th The bees now buzz in old thorn trees, as during former years; but they do not begin at base, but 3 or 4 foot up and then go up to top and so up to big ash.—N.B. I never saw bees go *down* thorn trees or come back through crutch, so must be to certain extent a *circuit*:

Aug. 24th. Today bees visiting old place in numbers under ash-crutch; but they buzz a few inches higher above weedy ground.—they go and come after buzzing by 3 routes (1) from sand-walk. (2) after buzzing they just go round tree, as formerly, and rebuzz and go along walk to kitchen garden. (3) they come from latter course, buzz, and then instead of flying through crutch, they take new line and go into hedge close on N.E. side of ash, and apparently go along hedge, but I could not see any coming out at hole by spanish chesnut.—A few got buzzing up thorn tree—I now think same liking of same place causes similarity on successive years.—

Aug. 13th. 1861. Torquay. *B. lucorum*. Saw *humble bees* different from Down species many buzzing repeatedly [deleted] at same spot a foot or two up stem of Pinaster on edge of walk—went round tree and buzzed longer than old species. Three times I saw bees alight on several leaves and stem of tree and apparently examine them closely—from this tree, they fly in 2 courses along the walk, and high up to another Pinaster above. I *fancy* I saw large female buzzing in this tree.—They always come from one way—I have now seen them for a full week, many buzzing—After about a fortnight they changed and gave up this tree.

Humble bees. Sept. 9th 1861. I have watched occasionally during last fortnight. The original spot at foot of crutch almost deserted—I have watched whilst

many bees have gone to neighbouring places many times and have seen only one go to base of crutch and through the crutch—some come out of hole of hedge on sand-walk side of old ash and many buzz at the thorn tree which they used to go up and on both trees near. There are many buzzes.

At hole in hedge by spanish chesnut on west side there is ivy covered thorn at which very many buzz this is new.—several came along bottom of hedge, but instead of coming out by hole by hurdle, they turn within the shaw and buzz at foot of little ash close by and then at another ivy ash close by.—I am convinced the bees instinct may lead them to same sort of places.—Journal of Horticulture or Cottage Gardener 1861 Oct. 22 p. 767 on humble bees fertilized on ground or on flowers or coming out of nest—does not favour idea of buzzing connected with marriage.—

F. Smith* has seen them in union on flowers.

4. NOTES

1. The five children that Darwin refers to were: 1. Willy (William Erasmus b. 27th December, 1839), 2. Etty (Henrietta b. 25th September, 1843), 3. Georgy (George Howard b. 9th July, 1845), 4. Frank, Franky, Backy (Francis b. 16th August, 1848), and 5. Lenny, Leny (Leonard b. 13th May, 1850). Elizabeth, known as Bessy, (b. 8th July, 1847) may also have taken part but is not mentioned by name. The field notes show that the son mentioned in the first line of the précis was George.

2. Chesnut is spelt consistently without a middle t.

3. Sydney Sales owned land adjoining Darwin's. He is mentioned in correspondence between Leonard Darwin and solicitors in 1881, preserved in the University Library, Cambridge.

4. Spelt "flower" in the manuscript, but flour is clearly intended.

5. Newman, H. W. Habits of the Bombinatrices. *Proc. ent. Soc. Lond.* Meeting of 2nd June, 1851, pp. 86-94. On page 91, in a general comment on the males of all species Newman states "and each of the males of all the species making a round of visits in fine weather, in the early part of the day, to particular spots, and each species varies its flight in this respect, on the ground, in a manner that a little resembles the workers"; and on page 92 of *B. muscorum* "The male of this species . . . may be distinguished by his low flight along hedge-rows, and his stopping frequently as if intending to go into the ground; this he will continue for a mile together, and if watched, he will be seen to return to the same place more than ten times in an hour."

6. The brackets are Darwin's.

7. Newman, H. W. Is the female *Bombus* fertilized in the air? *J. Hort. & Cottage Gardener*, 1861, October 22, pp. 76-77. A query by Darwin and reply by Col. Newman that copulation occurs on the ground, on flowers, and in the nest; and that pairs may fly *in cop.* but do not start copulation there.

8. Frederick Smith, the hymenopterist on the staff of the British Museum. The original German of the Précis refers to him as J. Smith, in error.

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6. ACKNOWLEDGMENTS

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