A CONTRIBUTION TO THE KNOWLEDGE OF THE BIONOMICS OF BREMUS VAGANS (F. SM.) (HYMENOPTERA).

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A. Introduction.

The present paper is the fourth of a series of papers dealing with the biology of species of bumblebees found in Illinois. In the first paper (1928), the prominent facts in the life history of *Bremus bimaculatus* (Cress.) were recorded in detail. In a second paper (1929b) similar information was published relating to *B. impatiens* (Cress.), and a third paper concerning *B. americanorum* (Fabr.) is now in press. For details regarding how much of the data used in this paper were obtained, the reader should consult my previous papers, particularly that relating to *B. bimaculatus.*

B. Systematic Notes.

Bremus vagans (F. Sm.) belongs to the subgenus *Pratobombus* Vogt (1911); a subgenus of bumblebees ranging through the Palaearctic, Oriental, Nearctic and northern part of the Neotropical faunal realms. In addition to being the most widely distributed subgenus of bumblebees, this subgenus contains more species than any other subgenus and is readily divisible into several subordinate complexes. In North America, *B. vagans* is most closely related to such species as *flavifrons* (Cress.) and *centralis* (Cress.) which have the tips of the sagittae of the genitalia conspicuously dilated, the hypopygium somewhat carinate, and with a long malar space. *Pratobombus,* together with the subgenus *Terrestribombus* Vogt (1911), form a section of bumblebees designated by Krüger (1917) as *Anodontobombus.*

This study of the biology of *B. vagans* conclusively shows that the forms of *Pratobombus* occurring in Illinois, and recognized as species by the writer, are biologically distinct unities; thus, confirming their separation into species on the basis of certain structural characters.

In Illinois, *B. vagans* is abundant in the northern part of the state, less common in the central part, and virtually absent in southern Illinois. It ranges in North America through the lower limits of the boreal zone of Merriam from British Columbia to

Maine, throughout the transitional zone, and in the central and eastern portions of the upper austral zone.

C. Specific Life History Studies.

The writer has examined two nests of this species started by queens under natural conditions and studied in detail one colony which was founded by a queen in an artificial nest.

1. *Experiment 19, 1919.*

This experiment was started on June 8, 1919, with two queens of *B. vagans* which were collected at Antioch, Illinois, on June 4, 1919. Previous to placing the queens in an artificial nest, they were kept under conditions intended to cause them to become "broody." The next day after placing the queens in the nest I found one of them dead; presumably killed by the living queen. Another queen of the same species was introduced into the nest-box on June 10, and on the following day one of them showed a special interest in the pollen lump. Egg cells were constructed on June 11 and eggs laid during the next few days. On June 18, there was every indication that larvae were now in the cells, and on June 19, I actually saw them. The larvae grew very rapidly and by the twenty-first of June several of them had attained considerable size.

During this early period in the development of the comb, both of the queens took a great interest in the comb, but it was evident that one of them—the largest queen—"ruled" supreme. The colony had progressed so nicely by June 22 that a record of the developmental stages was begun. On this date several new egg cells were found on the tops of recently spun cocoons. An examination of these cells showed that there were not more than two eggs in each of them. On July 1, normal workers emerged and three more came out during the next few days. On July 5, the smaller queen was removed from the box and the nest left to the care of the larger queen.

The comb continued to grow and on July 20 two more workers emerged. Previous to this date, new egg cells were laid from time to time. Two of the cells examined on July 16 contained four eggs each. These cells were laid contiguous to one another in a horizontal position. The workers were allowed the privilege of foraging for nectar and pollen on July 21. As the nest grew in size additional honey-pots were constructed of wax and pollen on

the edge of the comb. Several of these cells averaged fifteen millimeters in height by eight millimeters in breadth.

By August 1 the number of workers in the nest had increased to twelve. At this date there was some surplus of pollen which was stored in empty cocoons. No surplus of honey, however, was found in the nest. It is interesting to note that the queen had now become so interested in the comb that she could not be induced to leave the comb while I examined the cells. Such was not the case, however, with the workers which were ready to use their stings at every opportunity. On August 9, another worker emerged and it was noted that nearly twenty-four hours were required for her pubescence to attain its normal color. On this same date many egg cells were in evidence on the tops of cocoons and in the depressions between them. The egg cells were made as usual from wax and pollen. On the side of the comb nearest the entrance to the nest-box, the bees had built up a protecting shield of wax-pollen composition. Another one of their performances during the early part of August was the dragging into the nest-box from the outside a large amount of oat-chaff.

During the remainder of August, the comb continued to grow unretarded and the colony attained considerable size. On August 17, there were fourteen cocoons in the nest, about sixty larvae in various stages of development, and many eggs. The number of eggs in a cell varied from three to six. For the first time, too, in the history of this colony, a surplus of honey was found in the nest on this latter date. This was stored in large wax-pollen honey-pots on the outer margin of the comb, whereas most of the pollen was stored in renovated cocoons from which workers had emerged. The old mother queen was still producing wax and I frequently saw her scraping it from the dorsum of her abdomen. Only ten workers were in the nest when it was examined on August 17, but many others were foraging in the field. The first males were found in the nest on September 4 and emerged from cocoons which contained pupae on August 22. Workers were also found in the nest on September 4, which had but recently emerged. When the nest was next examined on September 16, two young queens, fourteen workers and ten males were found. The old mother queen was still active and looked almost as sleek and trim as when her first eggs were laid. Two new egg cells were present on cocoons, one of which contained eight eggs and the other nine. These eggs were contiguous and horizontal as

before, but overlapped one another at one end. A queer find was an old sealed-over male cocoon, partially filled with pollen. This contained seven eggs which had been laid in an irregular manner. I am quite certain that these eggs were laid by workers. Many of the large larval cells plainly showed the presence of the small hole through which food was supplied them by the workers. Figure 1 shows the nest as it appeared on September 16.

On September 21, the old queen was alive and active as ever. The two young queens were still in the nest, besides fifteen males and ten workers. One worker was found dead in the nest box, but no trace of parasitism was found. Additional egg cells had been constructed and one of them contained seven eggs. The last week of September the old mother queen died. At this time there still remained in the nest about fifteen male and four queen cocoons from which the adults had not emerged. Because of the lateness of the season and cool nights, I moved the colony indoors so that other adults might emerge. From these cocoons two queens and four males emerged indoors as late as October 4. The males and queens produced by this colony were used in mating experiments (Frison, 1927a).

2. Nest 23, 1916.

At Hermon, New York, in 1916, I found a colony of *B. vagans* in the loft of a barn. The nest itself was in a cavity in a roof-joist, at a point where a side brace was joined to it. Evidently, the joint was so poorly constructed that mice had been able to enter the joist and gnaw out a cavity large enough for their nest. This place had then been found by a searching queen and adopted for her future home. The interesting feature of this nest was that a queen had been able to find this desirable location. In order for her to do so, it was necessary for her to enter the hay-loft of the barn through a small door. When once in the hay-loft, it must have required considerable searching on the part of the queen to find this nesting site, unless she was instinctively guided to the mouse nest by an olfactory sense.

When the nest was opened on August 18, it contained the old queen, twenty-eight workers, twenty males, four young queens, fifty-three cocoons containing pupae, six cocoons containing larvae, thirty-four empty cocoons, twenty-seven larvae in various stages of development, and five egg cells. Honey was stored both in large wax-pollen cells and in sixty-four renovated cocoons.

Pollen was found in four cocoons and in several of the large wax-pollen cells. One of these wax-pollen cells was three-fourths of an inch in height. The egg cells contained from six to fifteen eggs, the average number being over eleven. Two dead workers were found in the nest débris, but neither of them showed evidence of insect parasitism.

3. *Nest 1, 1920.*

This nest was found near Grand Marsh, Wisconsin, on August 21, 1920. The colony was located in a mouse nest at the base of a young cherry tree in a small orchard. The nest contained the old queen, four young queens, fourteen males, twelve workers, about fifty cocoons, nearly forty larvae in various stages of development and two egg cells. Honey was stored in empty cocoons and in special wax-pollen cells. Pollen was observed only in the renovated cocoons. No parasites or inquilines were found in this nest.

D. Biological Summary.

1. *Résumé of literature.*

The first record of the occurrence of a nest of this species of which I am aware is one by Putnam (1864), who mentions finding a nest of *B. vagans* at Warwick, Massachusetts, in the summer of 1862. This author says nothing concerning the habits of these bees or the contents of the nest, except that the nest was made in a deserted mouse nest. Packard (1864) says that the nest discovered by Putnam in 1862 contained thirty workers and that no special variation occurred among them except in the different shades of yellow.

Franklin (1913), the next to report the finding of a nest of *B. vagans,* records one situated on the surface of the ground in an open field in what apparently was originally a mouse nest. " It contained two queens, eight workers and two males and was taken in the day time of July 20, 1904. The workers of this nest were the most vicious and ready to sting of any with which I have had any experience." In the collection of the American Museum of Natural History, New York, is a nest of this species which Franklin says " was taken by Mr. Wm. Beutenmüller at Potato Knob in the Black Mountains of North Carolina (elevation 6,420 feet) about July 1, 1902. This nest was located in the hollow trunk of a standing mountain ash and it contained two queens and eight workers, but many bees escaped as it was taken in the day time."

This nest, also, was apparently originally a mouse nest and was made from dried grass.

The next reference of a biological nature concerning this species is by Jackson (1920), who gives data regarding the time of appearance of the various castes in the vicinity of Washington, D. C., and plants they were observed to visit. Beginning in 1922, Plath has published several papers of special importance. In the first of these (1922a), this writer records the finding of nests of *B. vagans* near Boston. " Two of these were surface nests, while the remaining four were subterrean." This same author says the largest nest that he examined contained the old queen, over seventy workers and many brood cells. Another colony contained the " old queen, about fifty workers, and several males " and a queen of *Psithyrus laboriosus.* Shortly after this (1922b) the presence of the social parasite, *Psithyrus laboriosus* (Fabr.) in the nests of *B. vagans* is mentioned again in greater detail and the behavior of its host under such conditions discussed.

In a third paper (1923), the successful rearing of the colonies of this species in artificial nests is recorded. The fact that queens of *B. vagans* do not enter hibernating quarters until August is mentioned by Plath (1924). At a later date (1925), the same author presents some evidence in support of the fact that the variety *citrinus* (F. Sm.) of *Psithyrus laboriosus* (Fabr.) is partial to the nests of *B. vagans* rather than the typical form of this social parasite. In two still more recent papers *B. vagans* is recorded as a non-pocket maker (1927a) and that the queens are the latest of the *Pratorum* group (=*Pratobombus*) of species to appear in spring in New England (1927b).

In several papers the writer has published facts regarding the biology of *B. vagans.* In one paper (1927a) was recorded the fact that queens and males of this species would mate under controlled conditions, in a second paper (1927b) reference was made to the variation in size of bumblebees of this species and explained upon the basis of trophogeny, and in a third paper (1927c) evidence was presented to show that *B. vagans* could be readily semi-domesticated.

2. *Anthophilous habits.*

This bumblebee has been recorded as frequenting a large number of flowers and like all others thus far studied is polytropic. Most of the records of the flowers visited by this bumblebee have

been listed by Lutz and Cockerell (1920), with the exception of those of Jackson (1920) which are as follows: *Pentstemon hirsuta, Arctium minus, Monarda fistulosa* and *Brassica juncea.*

3. *Duration of the developmental stadia.*

These deductions concerning the developmental stadia are based upon a tabulated record of forty-two detailed examinations of the comb in Experiment 19, 1919, between June 22 and October 4. The data were secured by methods described in a previous article (Frison, 1928). It should be mentioned here that my conclusions regarding the length of time required for the three developmental stadia are essentially in agreement with data presented for other species (*B. bimaculatus, B. impatiens* and *B. americanorum*).

The egg stage was found to be the shortest of the three developmental stadia and lasts approximately four and one-half days for queens, workers or males. The larval stage is variable within certain limits even in the same caste. Larvae which produced workers required between fourteen and nineteen days to complete their development. The workers produced the latter part of August required more time in the larval stage than those produced in July and correlated with this lengthening of this stage of development was an increase in the size of the workers. Queen larvae required a longer time to complete their development than did worker larvae and the males required at least as long a time as the workers and sometimes longer.

The pupal period of the workers varied between six and eight days. That of the queens was at least this long and there were some data indicating it might be longer. The male pupal period was not accurately determined, but available data show that it could not have been less than that of the workers and in all probability was longer.

My data show that the first workers which emerged in Experiment 19, 1919, required between nineteen and twenty-two days to complete their development. Workers which emerged in August required more than this amount of time and most of the records indicate a period of about thirty days. The queens certainly required a month or possibly more. The males required less time than did the queens to complete their immature development. Although my records for this species are much less complete than for *B. bimaculatus* (Frison, 1928), they are sufficient, however, to permit of the above approximations and clearly show that *B.*

vagans does not present any great deviation in regard to the duration of the developmental stages from *impatiens, bimaculatus,* and *americanorum.*

4. *Seasonal appearance of the castes.*

B. vagans is not sufficiently common in the vicinity of Urbana, Illinois, to permit of a close study of the appearance of the over-wintering queens in spring. The species, however, appears much later than either *B. bimaculatus* or *B. impatiens.* At Antioch, in northern Illinois, on June 3, 1919, queens of this species were very abundant.

Data on pinned queens in various collections corroborates a late appearance of the queens in spring in all parts of their range. Most of the queens from New Jersey and Pennsylvania in the collection of the Academy of Natural Sciences of Philadelphia and of the American Entomological Society were collected in the months of May and June. I have seen many queens in the same collection, collected in Northern Michigan (Barago County) by Mr. Morgan Hebard, which were captured from July 4 to July 20. I am certain, too, that these latter queens were ones that had over-wintered. There are a large number of queens of this species in the Nason Collection belonging to the Illinois State Natural History Survey which were collected at Algonquin, Illinois, in May and June. In Champaign County, Illinois, I have captured the queens in the latter part of June. The earliest record I have seen for a queen of this species is May 1, 1915. This specimen was collected by Mr. C. A. Frost at Sherborn, Massachusetts. No doubt in certain years the queens appear earlier than these records indicate, but it is quite evident that as a rule the queens appear considerably later than most, if not all, other queens of *Pratobombus* in central and eastern North America. Data by Plath (1927b) and Jackson (1920) confirm my conclusions about the seasonal adjustments of the queens of this species.

Because of the late appearance of the queens, the workers are encountered much later than those of certain other species. In Experiment 19, 1919, the first workers emerged on July 1. In the collection of the Illinois State Natural History Survey are two workers captured on July 9 and 13 at Urbana, Illinois. A study of a large series of specimens of this caste from various parts of its range shows that the workers are most commonly collected from the middle of July to the middle of September. I have seen

workers collected in Maryland as late as October 6. Of course the appearance of the workers varies somewhat according to the lateness or earliness of the season and according to locality, but it is most influenced by the late appearance of the queens in spring.

The first males to appear in Experiment 19, 1919, emerged between the last of August and first of September. Males continued to emerge in this nest until the first part of October. The data obtained from the study of a very large series of males from various parts of the country show that the males are captured as a rule in August and September. Males occur much earlier than this, however, and I have taken them in 1920 as early as July 11, at New London, Wisconsin. Such early males may be the product of worker eggs in a nest which has lost its queen.

5. *Caste ratio.*

According to my studies and the figures given by Franklin and Plath, the workers outnumbered the young queens anywhere from three or seven to one. Apparently, as a rule, more males are produced than queens. In Experiment 19, 1919, nearly seven males were produced for every queen, and nearly as many males as workers. There are so many factors governing the numerical abundance of the various castes, that at the best these figures are but indications of what is generally encountered.

6. *Size of colonies.*

Judging by the records just given the colonies of this species never attain very large size compared with species such as *B. impatiens* or *B. americanorum.* Nest 23, 1916, is undoubtedly a good example of the colony of this species. Only seventy-three adults were found in the nest. Adding to this figure the number of workers probably foraging in the field when this nest was removed, and the adults that might have emerged later in the season (as indicated by cocoons and larvae), the colony could probably not have produced more than one hundred and seventy-five adults. If the colonies studied by Plath, Franklin and myself are truly representative, few colonies of *B. vagans* produce over one hundred and fifty adults.

7. *Variation.*

Franklin (1913) gives a table showing the variation in the length of the malar space of this species which represents con-

siderable variation. In a recent paper (1929a) I have shown that the *vagans* and subspecies *sandersoni* of Franklin was a mixture of two species; *vagans* with a comparative long malar space and *frigidus* with a shorter malar space. Polymorphism in size, particularly in the females, is considerable and is due to trophogeny (Frison, 1927b). Although this species is fairly constant in color characters there are variations which merit recognition. Males were produced in Experiment 19, 1919, which had some ferruginous pubescence at the apex of the abdomen and specimens about like these have been named by Bequaert and Plath (1925) as variety *coctus*. Specimens with the apical abdominal segments yellowish instead of black are common and have been assigned the varietal name of *helenae* by the writer (1929). Both the varieties *coctus* and *helenae* occur in the same nest with typical specimens of *vagans* and hence are merely color varieties. Recently the writer (1929a) has reduced the form *bolsteri* Franklin from specific rank to the status of a subspecies of *vagans*. This is because no structural characters exist for the separation of *bolsteri* from *vagans* and it seems that *bolsteri* is a color form of *vagans* " farther along nature's path to species than a form differing but slightly in color characters from the typical species." *Bolsteri* seems to be endemic to Newfoundland where typical *vagans* is not known to occur.

8. *Cocoons and food storage.*

It was found that both pollen and honey were stored in cocoons from which the adults have emerged. Special wax-pollen cells are also constructed, usually on the edge of the comb, for the storage of honey and pollen and in Experiment 19, 1919, most of the honey was stored in these wax-pollen cells. In Nest 23, 1916, however, which contained a large honey surplus, it was mostly stored in renovated cocoons. Several wax-pollen storage pots in Experiment 19, 1919, were fifteen millimeters in height by seven millimeters in breadth. The cocoons when freed of wax and pollen usually have a pale yellow appearance and are thin in comparison with those of certain other species such as *B. americanorum*. One worker cocoon was ten millimeters in height and eight millimeters at its greatest diameter.

In agreement with *B. bimaculatus* and *B. impatiens*, both members of the subgenus *Pratobombus*, this species belongs to the " Pollen-storer " section in the terminology of Sladen (1912)

which is equivalent to the *Anodontobombus* Krüger as now restricted.

9. *Mating.*

There are no records in the literature concerning the mating habits of this species. Young queens produced in Experiment 19, 1919, readily mated with males from the same colony under controlled conditions during the last of September and early part of October (Frison, 1927a). Undoubtedly under natural conditions copulation takes place in late summer and fall.

10. *Nest situations.*

The queens of *B. vagans* will apparently nest almost any place where a suitable protected situation can be found, either below or above the surface of the ground. The nests of mice offer both desirable nesting materials and favorable nesting sites and hence are usually utilized by the queens in spring. Reference has already been made in this article under a heading of "Résumé of literature" to locations of nests reported by Franklin, Putnam and Plath and will not be repeated here.

11. *Miscellaneous.*

The workers of this species are aggressive and this species must be listed as vicious compared with such a docile species as *B. auricomus* (Frison, 1918).

Records have already been published by the writer (1926) showing that the larvae of *B. vagans* are subject to the attacks of *Brachycoma sarcophagina* (Townsend), that the adult queens are sometimes infested with the nematode *Spherularia bombi* Dufour, the nest damaged by larvae of *Vitula edmandsii* (Packard), and that various scavengers may lodge within the nests. No doubt other parasites, such as *Physocephala* will be found to attack *B. vagans.* Among the social-parasites, or *Psithyrus,* Plath (1922b) has found that *B. vagans* is victimized by *P. laboriosus.*

12. *Domestication.*

Experiments of Plath (1923) and those of my own performed in 1919 demonstrate that queens of this species may be readily induced to start colonies under controlled conditions. Since the males and females mate under controlled conditions (Frison, 1927a), this species may be semi-domesticated. Because *vagans*

has a wide distribution, a long malar space permitting the workers legitimate access to many flowers, a fairly long seasonal adjustment, and may be semi-domesticated, this species opens up possibilities to the laboratory worker and is a fit subject for economic exploitation.

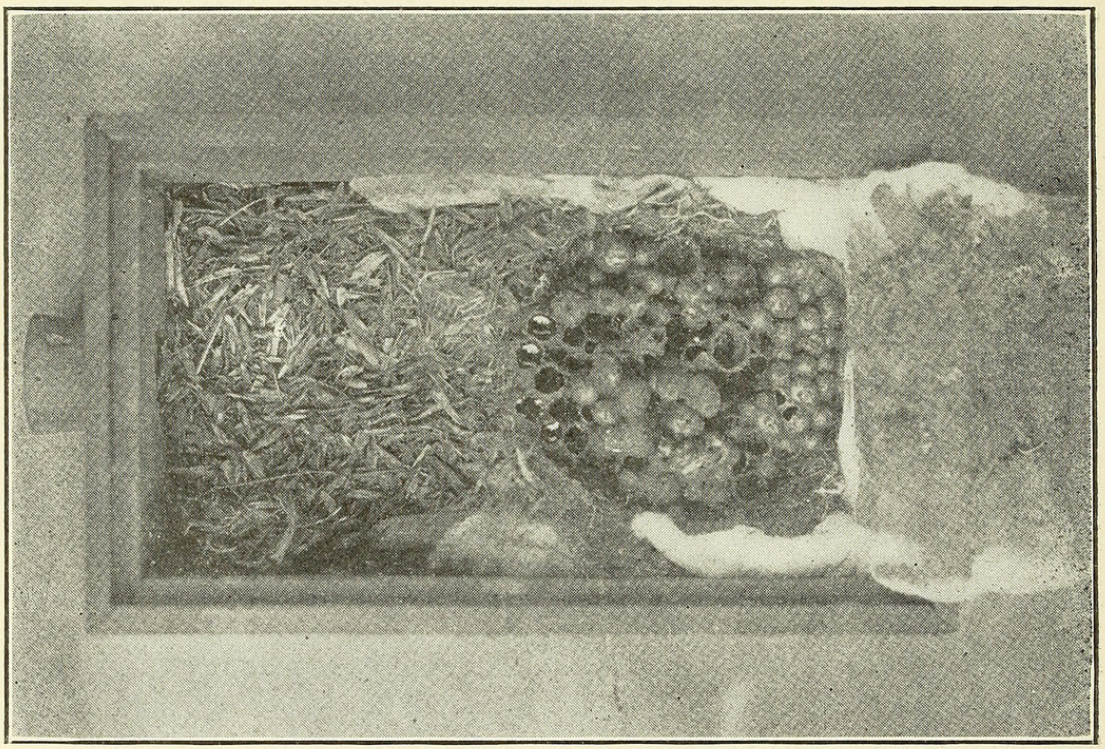

FIGURE 1. Comb of *Bremus vagans* in a small observation box, showing chaff "carded" into box by the adults in order to cover comb, and mother queen. September 16.

E. BIBLIOGRAPHY.

In order to conserve space, references in this article identical with those cited in my paper relating to *Bremus impatiens,* published in a recent number of this same journal, are not repeated and readers interested are referred to this recent paper for additional bibliographic material.

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Nesting habits of Isodontia, a subgenus of Chlorion (Hymenoptera).—In the December, 1928, issue of this Bulletin, Mr. Geo. P. Engelhardt has an interesting account of the breeding habits of *Chlorion harrisi* Fernald, which he observed in Texas with Mr. H. B. Parks. Their observations show that the nesting of this wasp is unlike that of the majority of *Chlorion,* which dig their own burrows in the soil. It is, however, similar to that of *Chlorion auripes* Fernald (*tibialis* Lepeletier), as observed in the eastern United States by Angus and, more recently, by Phil and Nellie Rau; to that of *Chlorion elegans* (Smith), as described by Davidson in California, by C. N. Ainslie in North Dakota, and by S. A. Johnson in Colorado; and to that of the European *Chlorion splendidulum* (Costa), according to P. Marchal and H. Nicolas. These four species all agree in selecting pre-existing cavities for the storing of their prey, which consists of tree-crickets or katydids. The cavities may be old galleries made by carpenter-bees in wood, abandoned burrows of *Anthophora* in adobe, hollow reeds or plant stalks, or rolled up dry leaves. Inside the hollow, the several cells are separated by plugs of dry grass or other plant material. *Chlorion harrisi* has also been recorded by H. G. Hubbard and by F. M. Jones (under the name *Isodontia philadelphica*) as nesting in the pitchers of *Sarracenia flava.* Moreover, the four species mentioned belong, within the genus *Chlorion,* to a peculiar group, or subgenus, *Isodontia,* characterized *inter alia* by the absence of a tarsal comb of long spines on the fore legs of the female. The lack of a comb is evidently correlated with the aberrant nesting habits; for in the other groups of *Chlorion,* which dig burrows in the soil, the comb is strongly developed in the female.

From these considerations one is naturally led to the conclusion that all the fossorial wasps of the subgenus *Isodontia* will prove