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SUPPLEMENTARY NOTES ON THE NESTING BIOLOGY OF THREE SPECIES OF *SPHEX* (*ISODONTIA*) OCCURRING IN JAPAN (HYMENOPTERA, SPHECIDAE)

BY K. TSUNEKI

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SUPPLEMENTARY NOTES ON THE NESTING BIOLOGY OF THREE SPECIES OF *SPHEX* (*ISODONTIA*) OCCURRING IN JAPAN (HYMENOPTERA, SPHECIDAE)

By Katsuji TSUNEKI
(Biological Laboratory, Fukui University)

Synopsis

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New data on the nest structure, prey, provisioning and oviposition habits of *S. nigellus* Smith, *S. harmandi* Pérez and *S. maidli* Yasumatsu were described. Noteworthy is the fact that *S. nigellus* occasionally rears more than one young in one nest-chamber.

1. *SPHEX* (*ISODONTIA*) *NIGELLUS* SMITH

1. Evolution in the nest structure and the method of rearing the larvae

Since the first report in English appeared in which 30 nests of this species were dealt with I have been able to examine 35 further nests collected in Fukui Prefecture. Of these 9 belonged to natural nests and the remaining 26 to the trap-nests made of bamboo. Of the natural nests 3 were made in the cut ends of bamboo stems horizontally placed to support the fence and all the others in the abandoned beetle burrows found in logs piled up at a hill-side. Of all the material mentioned above are shown in Table 1 the length and average width of the tubes utilized by the wasps, the number of brood-chambers made in one nest, the maximum number of offsprings found in one cell and total number of offsprings in a nest. According to this table the material consists of 12 unicellular nests, 11 bicellular nests, 9 tri-cellular nests and 2 quadricellular nests.

Of the total number of 69 cells it is most interesting that *at least 7 of them contained more than one offspring*. In one instance indeed, even four cocoons are discovered in one cell (Pl. I, Fig. a); in other 6 instances all contained two offsprings. In some other nests which were classified in the table as bicellular or tricellular ones containing a single offspring in each cell, the partitioning wall between the cells successively constructed was so simple and thin that it can hardly be called a separating wall.

In general, in the multicellular nests of this species the partitioning wall between cells is markedly varied in its construction — thickness and compactness. In the well-formed instances it is about 10-15 mm in thickness, made of straws finely torn, delicately malaxated and very compactly pressed as in the compact layer of the nest closure. While in the simplest case only a few coils of masticated straws like a rough net work is placed. Such a nominal wall is most easily passed through by the larva at the time when it moves about in the chamber before spinning the cocoon. Therefore, when two cocoons are found in one brood-chamber it is strictly a doubtful fact that really two eggs were originally laid in the cell. Further, even when the partitioning wall has a considerable thickness the larva occasionally penetrates into it to appear in the neighbouring cell (See Pl. III, Fig. d). In this case, however, we can judge the real thing through the state of the disturbed wall and the adjacent cells even when two cocoons are spun in one cell. In the case difficult for judgement of the true process, however, it is not an important matter to determine whether the wall was simply present or completely not, since the two cases are close together in the development of the nest constructing technique of the wasp. At any rate various phases of structure of the cell-separating wall —— from the typical compact one through varied grades of simplification to the complete omission of it —— have been observed in nature. Moreover, even in the last mentioned case there are also two phases. In one of them the length of the cell that contains

Table 1. New data on the nests of *Sphex* (*Isodontia*) *nigellus* Smith collected in Fukui Prefecture.

Nest No.	Nest tube (mm) Length	Diameter	Numbers of cells	Length of cells (mm)	M. N. O in a cell	T. N. O.	Sex
1	150	14	2	55, 25	4C	5	♂♂♂??
2	195	13	3	30, 25, 23	1C	3	??♂
3	165	11	1	53	2C	2	♂♂
4	220	12	1	30	1C	1	?
5	380	11	3	? ? ?	1C	3	♂?♂
6	110	20	1	65	2L	2	??
7	130	19	3	45, 25, 25	2L	4	♂♂??
8	140	15	3	35, 24, 25	1L	3	♂♀♀
9	115	13	2	20, 25	2L	3	♂♂♂
10	175	13	3	35, 33, 30	1L	3	♀♀?
11	160	12	1	95	2L	2	♂♂
12	145	12	2	38, 32	1E	2	♀?
13	210	13	2	40, 70	1E	2	♀?
14	120	15	2	? ?	1C	2	♂♂
15	230	15	3	25, 23, 20	1L	3	♂♂?
16	158	12	1*	47	1L	1	♂
17	250	11	1	95	2C	2	♀♀
18	187	12	2	58, 43	1L	2	♀♀
19	100	15	1	28	1L	1	♀
20	235	11	4	35, 42, 30, 27	1L	4	♂♂♂♂
21	194	10	3	55, 28, 25	1L	3	♀♂♂
22	160	10	1	80	1L	1	♂
23	195	9	2*	85, 35	1C	1	♂
24	200	10	4	30, 35, 22, 20	1C/L	4	♂♂♂♂
25	168	8	3	32, 30, 25	1C	3	♂♂♂
26	190	9	2*	35, 70	1C/L	2	♂♂
27	205	8	1	120	1L	1	♂
28	195	10	1	30	1C	1	?
29	350	9	2	48, 43	1C	2	♂♀
30	188	10	1	45	1C	1	♂
31	140	13	2	30, 27	1L	2	??
32	192	10	2	47, 65	1C	2	♀♀
33	195	11	3	50, 33, 35	1C	3	♀♀?
34	100	12	1	?	1C	1	?
35	220	10	1	?	1C	1	?

Remarks. M. N. O. ··· Maximum numbers of offsprings. T. N. O. ··· Total numbers of offsprings.
Column of M. N. O. ··· C, cocoon. L, larva. E, egg. In cell number, * ··· incomplete.

two offsprings within is markedly large, approximately twice as large as the usual cell (Pl. IV, Fig. a); while in the other it is only slightly larger than usual. Of course there are also intermediate cases.

Among the five instances in which the presence of two offsprings was confirmed four were the cases wherein two young larvae were present, each still attaching to its own pedestal victim. The state really shows the simplest case of rearing the multiple larvae in one brood-chamber. Such a method of rearing the larvae is most highly developed, so far as is known, in *S.* (*Isodontia*) *harmandi* Pérez. But such a particular method in *nigellus*, though apparently similar, differs in the strict sense from that of *harmandi* and they can not directly be connected with each other on the developmental pedigree of the instinctive behaviour. Because in *har-*

mandi the eggs are laid, as a rule, suceessively on the first several victims and the necessary food is supplied as a mass afterwards and it can be represented, according to Iwata's method (1942), by the formula, $(HTSO)^{m}\ (HTS)^{n}$*, while in the similar case in *nigellus* the process must be shown by $[(HTSO)\ (HTS)^{n}]^{m}$. The latter can be reached comparatively easily from the multicellular nest by the simplification and the eventual omission of the septum-construction between cells, but to reach the state of the former a sudden spring (mutation in instinct) seems necessary.

Particular mention seems necessary as to the nest that contained four cocoons in one brood-chamber (Pl. I, Fig. a). It was made in the cylindric space (Table 1, No. 1) found at a cut end of a bamboo stem used for the transverse support of a rail-fence near the seashore. It was a bicellular nest, with the first cell 55 mm in length and the second 25 mm. In the first cell four cocoons were found spun leaning or attaching to each other and covered commonly with a cocoon-cover membrane, just as is the case in *S.* (*Isodontia*) *harmandi*. The second cell contained a single cocoon which was in the figure hidden under the straw packing that was pulled out of the walls and spread over the floor by the full-grown larva. (The figure is therefore the view from beneath.) The partitioning wall between the two cells was about 10 mm in thickness and very compact. Outside the cocoons in cell 1 there could be observed a few bits of straw, but they were not considered derived from the nominate walls between the cells. Probably they were also a derivative from the outer wall of cell 1 meant here. In other cells containing more than one larva that were found in nature or made artificially the cocoons finally spun showed much the same state as mentioned with respect to the above nest.

From the view point of evolution in behaviour *S. nigellus* is a particularly interesting species in affording instances of various grades of development of their nest constructing technique and the young rearing method. Judging from the recorded instances most of the wasps of this species make an unicellular nest repeatedly in their life time and rear a single larva in each cell; but a considerable part of them make a multicellular nest, of which the bicellular is the commonest and the more the number of the cells the lesser the instances. Further, the partition walls between cells of the multicellular nests are varied in structure, from the typical compact one to the rough simplest and in the extreme case they are completely omitted, turning into a cell containing multiple larvae within.

2. The inclination towards social life in larvae

As above stated it has not yet fully been developed in the instinctive behaviour of the mother wasp to rear her young completely in a social relation as observed in *S. harmandi* and, moreover, the approach to the relation hitherto attained occurs rather occasionally. It seems particularly of interest, therefore, that we can find in the larval instinct a latent character towards social life just as in the larvae of *S. harmandi*. This can easily be shown by putting several larvae in an artificial cell with the food necessary for their growth. I have repeatedly tried such a rearing always with success. They never tried to eat each other even though they moved about over and side of others to search for the food. This is a surprising fact among such carnivorous larvae.

So far tried by me this has by no means been possible among the larvae of other species of *Sphex* such as *Sphex* s. str. Among them cannibalism always occurred sooner or later,

* H, hunting; T, transportation; S, storing; O, ovipostion.

however abundant may be the food supplied in the chamber.

3. Prey

The data on the prey still living in the nests in the paralyzed state can be summarized as given in Table 2.

Table 2. The species of the prey (Orthoptera, Tettigoniidae)

Species	♀	♂	Imago	Nymph	Total
Conocephalus melas de Haan	46	49	16	79	95
Conocephalus gladiatus Redtenb.	8	6	14	0	14
Hexacentrus japonicus Karny	30	49	1	78	79
Ducetia japonica Thumberg	1	5	6	0	6
4 species	85	109	37	157	194

The number distribution per one cell is shown in Table 3. The number is of course varied with the size of the prey, but most usually it ranges from 3 to 5. Exceptionally wasp No. 11 provisioned the cells of its tri-cellular nest with 10, 12 and 11 nymphs of *Conocephalus melas* respectively. In the four cells that contained two young larvae inside the number of the prey stored was respectively 10, 11, 11 and 12, the species being all *Hexacentrus japonicus* (all nymphs).

Table 3. Distribution of the number of the prey per one cell (containing a single larva)

Number	1	2	3	4	5	6	7	8	9	10	11	12	13
Frequency	–	3	8	10	8	2	–	1	1	2	2	2	–
Total	0	6	24	40	40	12	0	8	9	20	22	24	0

As reported in my previous paper (1963) the long antennae of the prey are cut off, as a rule, leaving the basal 4–6 segments intact. But sometimes the prey are found in which one or both of them are left intact. These are usually mixed among those which were provisioned toward the end of the work of the nest.

The prey are most usually placed head in and venter up, but fairly frequently some of them are laid with the side upwards.

As to the developmental stages of the prey it seems that no particular preference is made by the wasp. Early in the season, from June to early in August, the prey are all in the nymphal stage, but in September they all consisted of the adult insects. This is only parallel with the growth stages of the prey.

As for the preference of a certain species of the prey a fairly distinct inclination is observed. Some wasp that showed a tendency to hunt *Hexacentrus japonicus* stuffed its multicellular nest exclusively with the species. But the cases wherein one or two insects of *Conocephalus* or *Ducetia* are mixed are more frequent. On the other hand not the least preference was shown as to the sex and colour of the prey.

2. *SPHEX (ISODONTIA) HARMANDI* PÉREZ

In the trap nests of bamboo tubes inserted among the piled up logs at Arashi in the montane region of Fukui Prefecture I could have induced a number of wasps of this species. During the period of the activity of the wasps I frequently visited the place and observed the actual procedure of their nest construction, prey collection and oviposition which were quite inadequately touched upon in my previous paper.

1. The tubes adopted by the wasps

The tubes used for my trap nests were 100–350 mm in length and 8–25 mm in averaged inside diameter. Those adopted by the wasps were any that were more than 130 mm in length and more than 11 mm in diameter. Usually the tubes having the length of more than 160 mm were preferred by the wasps. This is probably due to the fact that a considerable space is necessary to make a large brood-chamber to rear several larvae collectively in it, together with the fact that the compact closure of leaf-moss also necessitates a fair degree of tube length.

I have observed also in the same village some wasps of this species nesting in the very broad tubes of bamboos, having the diameter of cut end of about 30–50 mm, that were used for the water passage and inserted in the concrete banks at the side of the mountain path, very dangerous material for nesting. In all the nests made in the broad tubes the space was narrowed by placing a thick, compactly pressed moss floor at the part used for the brood-chamber. This mode of improvement of the width of the nesting cavity may be the same tactics as used by the wasp when the innermost part of the tube is unfavourable for nesting, such as too narrowly attenuated or not completely light-proof. In such cases the wasp always packs moss tightly at the portion of the tube for a considerable length to obtain the proper width or to intercept the peeping light.

2. Temporary closure

The temporary closure of the nest is always made before storing the first prey. It includes two kinds in morphology and significance. One is made very roughly at the entrance of the tube as soon as it is occupied by a wasp. It consists of a few bits of the leaf-moss very loosely entangled and is considered of no use even to prevent intrusion of the parasitic fly. Probably this is an occupation mark towards other wasps, not only of its own species, but also of different species. It is retained until the end of the work of the wasp, though slightly changed in constitution as well as in situation (Pls. V, VI, Fig. a; Pl. VII, Figs. c, d). The other is made deep inside the tube, having the length of about 25-40 mm and approximates in compactness to the compact layer of the final closure. It is constructed just before the first prey is hunted and forms the outer wall of the brood-chamber. This is a true barricade of the chamber and can not be penetrated by such powerless insect as the parasitic fly. The space of the brood-chamber is determined at first; and it does not occurred that the temporary wall is moved outwards as the accumulation of the prey proceeds. Finally when the provisioning of the chamber has finished it is slightly more firmly and compactly pressed together with the additional material and turns into the compact layer of the permanent closure.

This sort of the temporary closure is so thick and compact that the wasp might have to make a considerable effort every time of her passing to and fro, if she honestly loosening and pressing the closure. During the time of most active work for provisioning to her chamber she must enter it 15–20 times a day. The work of nearly complete removal and reconstruction of so tight a wall every time of her passing is too heavy to her. In order to lessen such a toilful work she has developed an ingenious adaptive behaviour pattern. The wasp makes a narrow passage, a well pressed furrow, just as large as her body width, on the tampon along the upper tube wall (Pl. VI, Fig. e; Pl. VII, Fig. b). Whenever she enters the chamber she loosens the moss plug made at the entrance of the furrow, pulls it out a little and the passage leading to the chamber is clearly opened. Whenever she leaves the chamber she pulls together the loosened moss and presses it firmly to form a plug of about 10 mm or so in thickness.

Table 4. New data on the nests of *Sphex* (*Isodontia*) *harmandi* Pérez collected in Fukui Prefecture (No. with an asterisk is complete, others all imcomplete).

Nest No.	nest Length	tube Diameter	Cell Length	Prey	Offspring	Resulted cocoon	Sex
* 1	260 mm	16 mm	50 mm	19	2+?	-P	–
2	180	13	45	15	9	4	♀♀♀♀
3	260	16	80	16	6	-A	–
4	170	18	70	17	7	-A	–
5	275	22	80	26	9	-A	–
6	190	13	65	10	7	-P	–
* 7	190	14	110	59	6	6	♀♀♀♀♀♀
8	170	13	65	?	?	3	♂♂♂
9	270	17	75	46	6	6	♀♀D
10	275	22	50	10	6	1	D
11	180	22	80	16	1	1	♂
12	180	18	70	39	12	7*	♂♂♂♂♂♂D
*13a	375	24	80	?	?	6	♂♂♂♂DD
13b	375	24	45	17	5	3	♂♂♂
*14a	350	14	105	?	?	4	♂♂♂♂
14b	350	14	70	38	6	4	♂♀DD
*15	210	14	95	37	?	1P	♂
16	190	14	45	4	4	-P	–
*17	195	14	90	42	6	5	♂♂♂♂♂
*18	200	13	105	27	5	4	♂♂♂♂
*19	160	11	60	20	4	4	♂♂♂♂
*20	120	12	70	27	5	5	♂♂♂♂♂
21	270	16	40	9	5	-P	–
22	270	20	45	11	5	1	♀
23	195	11	80	?	?	2	♂♂
24	180	12	70	13	8 (5)	1*	D
25	256	12	80	(23)	?	4	♂♂♂♂
26	168	20	50	18	8	4	♂♂♂♂
27	350	13	80	18	9	3	♂♂♂
28	210	13	70	10	6	2	♂♂
29	190	15	50	16	9 (5)	2	♂♂
30	190	13	80	18	7	3	♂♂♂
*31	267	17	60	37	6 (4)	4	♂♂♂♂
32	180	11	70	1	1	–	–
33	285	18	75	3	3	–	–
*34	180	18	50	25	?	-P	–
35	190	15	100	9	8	1	D
36	200	12	75	14	6	2	♂♂
37	160	12	50	11	4	2	♂♂
38	235	13	40	27	?	-P	–
39	245	13	75	20	6	3	♂♂♂
*40a	210	11	70	25	?	-P	–
40b	210	11	40	11	3 (2)	2*	DD
41	290	19	40	6	5	3*	♀♀♀
*42	218	12	32	8	2 (1)	1	♂
43	280	11	60	11	7	6*	♂♂DDDD
44	350	14	150	9	6	-P	–
*45a	210	14	78	26	6	5	♂♂♂♂♂
45b	210	14	30	5	4	1*	♂
*46	235	12	45	12	?	-P	–
47	240	15	50	7	4	-P	–
48	187	14	50	26	6	3*	♀♀♀
49	165	13	25	5	3 (2)	1	♂
50	213	11	40	3	3 (1)	1*	D
51	230	13	55	15	5 (2)	2	♂D
52	265	21	100	–	–	–	–
53	215	18	55	2	–	–	–
54	290	19	80	6	5	3*	♀♀♀
55	193	15	60	4	4	3*	♂♂D
*56	210	12	93	35	(7) ?	-P	–
57	178	22	30	16	4	3	♂♂D
58	205	13	30	5	?	-P	–
*59	185	13	90	45	5	5	♀♀♀♀♀
60	178	18	25	0	–	-P	–
61	170	20	40	0	–	–	–
62	220	12	160	0	–	–	–
63	215	13	85	36	6 (0)	-M	–

*64	127	14	60	24	(5) ?	– P	–
*65	270	19	43	32	?	– P	–
66	154	14	50	6	6 (4)	1*	♀
67	185	12	45	33	–	–	–
68	243	12	70	4	3	2	♂ D
69	245	13	80	15	?	– P	–
*70	113	13	60	(25)	?	3	♂♂♀
71	190	15	50	17	6 (1)	1	♂

Remarks. Column of Prey: Numerals parenthesized are counted from the remains. Column of cocoon: Numerals with an asterisk show that the larvae were reared with additional prey. P, parasitic fly; A, accident; M, mite. Column of Sex: D, pupa or prepupa died in the cocoon.

Apparently the outer surface of the temporary closure comes to be uniform in structure; therefore it is completely impossible to the insects unknown of the furrow to find out such a particular entrance passage concealed. The location of the furrow is always determined to the upper centre of the nest tube horizontally laid. When the chamber is filled with the prey accumulated the inner portion of the furrow is also partly utilized to receive some of them. But usually when the temporary closure is turned into the compact layer of the permanent closure the portion of the furrow is also compactly and thoroughly stuffed with moss.

3. Prey

The long-horned grasshoppers captured by the wasps of this species as food for their young belong to about 98 % to *Conocephalus* spp., the greater part being *C. melas* de Haan. The remainder is *Xiphidiopsis japonicus* Matsumura and Shiraki. Only very exceptionally I found few specimens of *Mecopoda elongata* Linné. As to the developmental stage the nymph occupies the greater part and it is only late in the activity period of the wasp that the imago is mixed. In this species, different from *S. nigellus* or *S. flammitrichus*, it seems that the capture of the nymph depends chiefly upon the preference of the wasp, since even in the middle of September the ratio of the nymph to the imago is overwhelmingly large. But *Xiphidiopsis* forms an exception in regard to this general rule. Probably this is due to the soft texture of the adult insect of the species. As to the sex of the prey the female is more abundantly captured than the male (Table 5). But it is not considered that the fact depends upon the selection.

The prey are stuffed in the chamber from the interior outwards, always obliquely laid, with the heads inwards and slightly high. When the chamber is broad they are laid in two, three or even four rows and in two layers. In order to determine the stored order of the prey in such a chamber a particular care must be taken as to the state of their piling, especially of the legs. As a rule, they are laid venter up, but sometimes, especially towards the time when the provisioning is most actively carried out they are placed not unfrequently dorsum up or side up, and occasionally even head out. The antennae of the prey are always left intact, not cut off as in *S. nigellus*.

According to the examination of the nests that have just been accomplished (Table 5) the number of the prey stored per one larva is as follows:

In the case of 2 larvae: 4; of 5 larvae: 4, 5, 5, 5; of 6 larvae: 4, 4, 6, 6, 6, 7, 10; of 7 larvae: 5.

It shows that usual number of prey supplied to one larvae is 4-7. But in the case of 4 prey, judging from the observation under rearing, probably cannibalism among larvae occurs, since 5 prey at least of moderate size are needed for the growth of one larva.

Table 5. Location of the eggs in the brood-chamber and the sex of egg-bearing prey

Nest No.	Provisioned order of egg-bearing prey	Number of egg	Egg-bearing prey ♀	Egg-bearing prey ♂	Total prey ♀	Total prey ♂	Total prey Total
2	1, 2, 3, 4, 5, 7, 9, 10, 14	9	6	3	11	4	15*
3	1, 2, 3, 4, 5, 9	6	4	2	10	6	16*
4	1, 2, 3, 4, 5, 6, 9, 13	8	6	2	11	6	17*
5	1, 2, 3, 4, 5, 9, 12, 15, 26	9	9	0	22	4	26*
6	1, 2, 3, 4, 5, 7, 10	7	4	3	7	3	10*
7	1, 2, 3, 4, 7, 11	6	5	1	44	15	59
9	1, 2, 3, 7, 8, 11, 14, 27	8	5	3	25	21	46*
10	1, 2, 3, 5, 8, 9	6	5	1	7	3	10*
11	1	1	–	1	9	7	16*
12	1, 2, 3, 4, 5, 6, 7, 8, 10, 13, 18, 25	12	8	6	19	20	39*
13b	1, 2, 3, 4, 5, 6	5	5	–	11	6	17*
14b	1, 2, 3, 4, 5, 13	6	2	4	17	21	38
15	1, 2, 3, 4, 5, 6	6	2	4	21	16	37
16	1, 2, 3, 4	4	4	–	4	–	4*
17	? ? ? ? ? ?	6	?	?	37	7	44
18	1, 2, 4, 5, 7	5	4	1	24	3	27
19	1, 4, 6, 7, 10	5	4	1	16	4	20
20	1, 2, 3, 4, 5	5	5	–	26	1	27
21	1, 2, 3, 4, 7	5	3	2	6	3	9*
22	1, 2, 3, 4, 5, 6, 8	7	4	3	7	4	11*
24	1, 2, 3, 4, 5, 6, 7, 9	8	7	1	8	5	13*
26	1, 2, 3, 4, 5, 6, 10, 18	8	6	2	13	4	17*
27	1, 2, 3, 4, 5, 6, 7, 8, 17	9	6	3	11	7	18*
28	1, 4, 5, 6, 7, 9	6	4	2	7	3	10*
29	1, 2, 3, 4, 5, 6, 7, 8, 14	9	7	2	9	7	16*
30	1, 2, 3, 4, 5, 6, 7	7	1	6	7	11	18*
31	1, 2, 3, 4, 5, 8	6	4	2	20	17	37
32	1	1	1	–	1	–	1*
33	1, 2, 3	3	1	2	1	2	3*
34	1, 2, 3, 4, 5, 7	6	3	3	13	12	25
35	1, 2, 3, 4, 5, 6, 7, 8	8	8	–	9	–	9*
36	1, 2, 3, 4, 5	6	2	3	7	7	14*
37	1, 2, 3, 4	4	1	3	6	5	11*
39	1, 2, 3, 4, 5, 8	6	2	4	13	7	20*
40a	? ? ? ? ?	5 ?	?	?	14	11	25
40b	1, 2, 3	3	1	2	8	3	11*
41	1, 2, 3, 4	4	1	3	3	3	6*
42	1, 2	2	1	1	4	4	8
43	1, 2, 3, 4, 5, 6, 7	7	6	1	10	1	11*
44	1, 2, 3, 4, 5, 8	6	5	1	9	1	10*
45a	1, 2, 3, 4, 5, 10	6	5	1	20	6	26
45b	1, 2, 3, 4, 5	5	3	2	3	2	5*
46	?	?	?	?	7	5	12
47	1, 2, 3, 4	4	–	4	3	4	7*
48	1, 2, 3, 5, 7, 8	6	1	5	11	15	26*
49	1, 2, 3	3	3	–	3	2	5*
50	1, 2 3	3	3	–	3	–	3*
51	1, 2, 3, 4, 7	5	5	–	10	5	15*
54	1, 2, 3, 4, 6	5	2	3	2	4	6*
55	1, 2, 3, 4	4	4	–	4	–	4*
56	?	(7) ?	?	?	17	18	35
57	2, 3, 4, 5	4	–	4	6	10	16*
59	(1, 2, 3, 4)?, 34	5 (?)	?	?	35	10	45
63	1, 2, 3, 4, 6, 7	6	6	–	28	8	36*
64	?	?	?	?	17	7	24
65	?	?	?	?	16	16	32
66	1, 2, 3, 4, 5, 6	6	2	4	2	4	6*
68	1, 2, 3	3	2	1	3	1	4*
71	1, 2, 3, 4, 5, 9	6	5	1	11	6	17*

* in the column of Total prey shows that the nest is incomplete.

4. Method of oviposition

In order to reconfirm the real feature of oviposition I examined as many nests as possible that were in the course of provisioning by frequently visiting the village where the trap-nests were set. The results obtained with respect to whether the eggs are successively laid to the first several prey only, or to some others in addition were summarized in Table 5.

It was again confirmed that the eggs of a wasp were laid successively to the first 5–7 prey, one on each insect, but from towards the time later, one to three prey are inserted without oviposition between the two egg-deposited prey. The maximum number of sucessive oviposition without interruption was 8, four instances appeared in nest Nos. 12, 27, 29, 35 and the next maximum was 7, three instances (Nos. 24, 30, 43). Fairly frequently one to three of the eggs are laid far apart from the main egg-group towards the middle or at the end of the provisioning. Such a later laid egg or a young larva hatched therefrom is usually devoured by other early hatched larvae together with its pedestal insect when they eat actively the collected food. But at the time when the eggs laid earlier are destroyed by a comparatively small number of the parasitic fly maggots it has a chance of survival and becomes an important successor of the parental generation.

According to the comparative observations of hatching of the eggs or the growth degrees of the larvae found in a nest the number of the eggs laid the first day is usually from one to three, rarely four or five, while those from the second day onwards are usually from two to four, rarely 5. In nest No. 2, observed on the 8th of August, 9 out of 15 prey collected in the cell carried a wasp's offspring respectively, and all of them were still in the state of the egg, showing no sign of hatching. It shows therefore that the 9 eggs must be laid within 30 hours or so, the time needed for hartching. According to Iwata (1957, 60) this species has 3 pair of ovarioles. They probably enable the wasp to lay 6 eggs successively. In the above instance, therefore, three further eggs at least must be penultimate eggs in the ovarioles. Accordingly it can be presumed that the penultimate egg in a ovariole can be maturated within about 30 hours after the ultimate egg is laid. With regard to the additional prey on which the egg is not laid there is much evidence that they are collected quite promptly, usually 15–20 in number a day.

Table 6. Egg attaching side on the sternum of the thorax

Nest No.	Egg attaching side	Total D	Total S
6	D D D D D – D – – D	7	–
7	S S D S – – S – – – D	2	4
9	? ? ? – – – D D . . . D . . . D . . . . D	5	–
10	D S D – D – – D – – D D	5	1
12	????? D D D ? S ? D . . S . . . S	4	2
13	S D – S D D	3	2
14	D D D D D . . . . . D	6	–
18	D S – S S – D	2	3
20	D D D D D	5	–
21	S ? D ? – – D	2	1
22	D D S D S S D	4	3
24	D D D ? S D ? – ?	4	1
26	D D S D S S – – – S . . . . D	4	4
27	D D S D S S D S . . . . . . D	5	4
28	S – – D D D D – S	4	2
29	D D D ? ? D S S . . . . . . S	4	3
30	D S S S S S S	1	6
31	? ? ? D D – – S	2	1
32	D	1	–
33	S D S	1	2
35	S S S S S S S S	–	8
36	D S S D D	3	2
37	S S S S	–	4
39	S D D S S – – S	2	4
41	D D D D	4	–
43	S S S D S S S	1	6
44	S D S S D – S	2	4
45a	S S D S D	2	3
47	S S S S	–	4
48	D S S – D – D S	3	3
49	D S S	1	2
50	D S D	2	1
51	S S S S – D	1	4
54	S D D S – S	2	3
55	S S D S	1	3
57	– S D D D	3	1
63	S S S S – S S	–	6
66	D D D D S S	4	2
68	D S D	2	1
71	D D D D D	5	–

Remarks. D, dextral side. S, sinistral side.

The manner of attachment of the egg is the same as observed in other species of *Sphex*, belonging to the sterno-ovipositing group (Pl. VIII, Fig. a).

I have examined the egg-carrying prey of a considerable number of the nests to ascertain whether or not there is a rule or a individual tendency with respect to the selection of a certain side to attach the egg. The results were as given in Table 6 (S, sinistral side, D, dextral side). According to this in 10 instances (about 25 % of the number observed) a certain side is exclusively selected (D only was 6 and S only 4) and in 7 instances a certain side is overwhelmingly largely preferred. In the remaining 22 instances selection of either side is mixed in more or less varied degrees. It seems to me that some individuals have a natural tendency to select a certain side of the prey to deposite her eggs, in other words, to take a certain fixed posture against the pedestal prey at the time of oviposition.

5. Relation between hatching of the eggs and provisioning of the mother wasp

As related elsewhere in this paper the eggs laid by a wasp in a brood-chamber were deposited during the period of a few days. In the case when about 10 eggs are laid and the work of the wasp is favoured by good weather it takes the wasp usually 3 days. As the time required by the egg for hatching is about 30 hours or so in August in our region the eggs laid earlier must hatch out before the later laid eggs appear in the chamber. Towards the end of mass provisioning, therefore, the greater part of the eggs laid must turn into the larvae. Indeed, it is a usual fact that we observe several larvae eating the prey at the interior of the brood-chamber to which the mother wasp still continues to carry the additional prey.

Of course, however, this does not represent a state of the so-called progressive provisioning. The manner of collecting the prey is distinctly massive in this species. The wasp of this species has no contact whatever with the hatching larvae. The presence of the larvae in the cell to which provisioning of the wasp is still going on is only an inevitable result due to the long duration needed to complete such a particular nest. Thus, in this species there is no development of social relation between the mother and her young. It is interesting, therefore, that there has developed a high degree of sociality among the carnivorous larvae that are laid gregariously in one brood-cell.

6. Socialization of the larvae and cannibalism

As mentioned in the previous paper the larvae of the same brood-chamber do not try, as a rule, to eat the brothers or sisters lying side by side, as far as the prey insects are accumulated in the chamber. According to the different time of oviposition they naturally differ in body size and usually they are divided into 3 or 4 classes. Apparently the state is dangerous to the smaller grubs among such greedy carnivorous insects. In reality, however, there is no danger at all, as far as the food is abundantly found in the nest, excepting to the very smaller one which is laid towards the end of provisioning, far apart from the group of the early laid eggs. Such a very small larva (or sometimes an egg) is eaten by the large one at the time when the latter eats its pedestal insect, probably without being taken notice as to its existence.

The group of the larvae, after eating each own pedestal prey, begin to move towards the outer portion of the cell where fresh prey are piled and stuffed by the mother wasp. They come to move in close contact, sometimes crawling on others, sometimes penetrating between two.

In connection with this, nest No. 12 gave us an interesting instance. In this nest the innermost 5 prey had largely been eaten and there 3 about 13 mm larvae were still eating the remains. The next 3 prey (namely the 6th, 7th and 8th) and the 10th each carried a larva of about 8 mm in body length. The 9th and 11th prey were being eaten by a 13 mm larva respectively. Further, the 13th and 18th prey were each attached by a 6 mm and a 4 mm larva respectively, and on the 25th prey was found an egg. According to the growth degrees the offsprings can be divided into 5 classes, indicating that 5 eggs were laid the 1st day, 4 eggs the 2nd day and 1 egg each on the 3rd, 4th and 5th day. Probably the inner 5 prey each carried an egg and the three 13 mm larvae found inside and the 2 of the same growth degree, each on the 9th and 11th prey, represent the delivatives from those 5 eggs. The larvae on the 9th and 11th prey were interesting in that they had to pass the side of 3 or 4 prey each carrying a slightly little brother, without trying to eat their pedestal-prey. Moreover, on the prey that they were eating (9th and 11th prey) there was no sign of carrying the egg, since when examined the insects were just touched by the larva and the thorax region remained still intact. The two larvae, therefore, might avoid to eat the brother-carrying prey and select the ones free from the young of the mother wasp.

I put the contents of all the collected nests that contained the larvae or eggs in a glass tube of the favourable size respectively and observed the procedure of their growth. A considerable number of the eggs or the young larvae died through the disturbance given during the most delicate period of development. Cannibalism also occurred, but it occurred only in such bottles as were furnished with quite insufficient food and only when the food stored was completely consumed.

Usually in nature in most of the nests that were examined soon after completion of provisioning the number of the prey collected in the chamber was well balanced with that of the eggs or the larvae in it. It seems, therefore, that the wasp actively equilibrates the amount of food with the number of the eggs she laid, just as observed in most solitary wasps and bees when they prepare the proper amount of food to their eggs destined either to the small male or the large female.

However, as mentioned in foregoing pages in relation to the prey, sometimes the food furnished by the mother wasps is considered insufficient, for instance 4 prey per one larva. In such a case cannibalism must occur even in nature. Judging by the method of oviposition of this species those nests which contain only 2 or 3 cocoons within are considered worth suspicion.

Cannibalism usually occurs at the final phase of larval growth when the larvae become most voracious and the food becomes most scarce to the contrary. Those that drop to the victims are always the smaller larvae. But it is a surprizing fact that the victim is eaten by other companion or companions quite calmly, without showing the least resistance nor struggle.

7. Sex distribution of offsprings in one chamber

In my previous paper I reported that the adult wasps emerged from the same brood-chamber belonged always all to the same sex. From the new observations of the 32 brood-chambers from which more than two adult wasps emerged I reconfirmed the same fact, but this time with two exceptions (Table 4). The exceptions were brought about by nest Nos. 14a and 70. In the former the emerged wasps were 1 ♂ 1 ♀ with 2 dead prepupae, while in the latter 2 ♂♂ and 1 ♀. From the results it was made out that this species very rarely mixes both sexes of offsprings in one chamber, but it is quite exceptional.

8. Some abnormal events in the nests and the wasp's behaviour

Intrusion of the parasites It was not rare to find the nest in which the wasp's eggs had already been destroyed by the parasitic fly maggots and to which the wasp was still continuing the provisioning activity. But it is rather rare that the wasp actively provisions the chamber which is filled with the nasty smeil due to rottening of the prey which is brought about by the random eating of the fly maggots. Such a rare instance was furnished by nest No. 69 in which 10 prey together with some unknown number of the eggs on them were already decomposed and emitting a putrefying smell, yet the wasp was collecting the prey. When examined at 10 o'clock in the morning 5 fresh victims had already been accumulated in the cell and the wasp further brought a victim during examination. Usually under such a condition the wasp abandons the nest. However, in the nest to which the wasp has just completed the final closure we frequently find the ravage of the parasitic fly maggots that have finished a considerable growth. This seems to show that towards the end of provisioning the blind work obeying the internal drive only occupies a considerable weight in the activity of the wasp. This is also shown by the fact that the prey broght in later are random in the orientation of their venters, not regularly laid venter up. The wasp must work only to collect the necessary amount of the prey and neglect the refined manner of packing them, a behavioural character which must be secondarily acquired.

Examination of the nest contents The bamboo tubes that I used as the trap nests were split in two and combined again by means of vinyl-tapes prior to setting. To examine the nest contents it was only needed to untie and open. But to take records with regard to the egg position, prey species and their sex and developmental degrees the prey had to be taken out one by one. After examination I replaced the contents as naturally as possible. It was, however, hardly possible to arrange the long antennae still slowly moving properly within the chamber. I don't think this to be the main cause of the change occurred upon the behaviour of the wasp. At any rate, such a *disturbed* nest was abandoned by the wasp, usually after being provisioned with one or two more prey. Of course I handled the material with the pincettes and there is no question as to the introduction of different smell in the nest. In spite of her not deeply entering the brood-chamber the wasp must feel the change in the state of the nest contents and this makes her stop the succeeding work of the nest.

In nest No. 2 in which 9 eggs were laid on 9 of the 15 prey accumulated and to which the wasp was still adding the grass-hoppers, only 4 cocoons (♀♀) were found in the cell when it was examined after completion. In this instance it seems most probable that the wasp stopped provisioning and abandoned the nest and the insufficient food induced the cannibalism among the wasplings. All the nests that I examined were always abandoned by the wasp, however carefully the contents were handled and replaced. Similarly and more obviously the emptied nest was abandoned by the wasp, even when the temporary closure is left alone.

* * *

The following are only the abnormal events, not accompanying the wasp's behaviour, but they seem worth recording:

Two eggs on a single prey In nest No. 36 which was in the course of provisioning contained 14 prey, the inner 5 of which carried the wasp's eggs. On each prey except the third from the interior an egg of the wasp was laid normally. But on the third an additional egg was found attached with its anterior end to the tip of the first egg normally laid. The procedure of this abnormal oviposition was of course unknown. But the fact shows that in this species two eggs at least in the ovarioles are in the state to be laid at a time.

A single egg supplied with 16 prey In this nest (nest No. 11) also provisioning was still going on. A single brood-chamber was a cavity, 80 mm in length and 22 mm in diameter. It contained 7 male- and 9 female-grasshoppers irregularly mixed. Outer 9 of the prey except 1 were laid dorsum up and the innermost one carried an egg of the wasp normally. I carefully examined the prey by taking them out one by one, but no other egg was discovered on any of them. On the other hand, no trace of intrusion of the parasitic fly maggot was there. Apparently the state was brought about by the automatic continuation of the activity of some wasp that had been deprived of the contents of its own nest at the early time of provisioning. But actually there was no such a nest tube at the same place previously and the temporary closure of the nest was made by the wasp itself.

This nest may represent an instance of instinctive atavism.

III. *SPHEX (ISODONTIA) MAIDLI* YASUMATSU

In the addenda of my previous paper the description of a tricellular nest of this species made in a bamboo tube was recorded. In Pl. IV, Fig. e of this paper I gave the photograph of the nest. The trap nest was one of those placed among logs in the village of Koike, Fukui Prefecture, about 800 m above the sea level.

The structure of the nest The space of the bamboo tube: 182×13 mm, the inner node was lined with simple packing of moss. Cell length from inside: 35, 30 and 28 mm. The length of the partition walls from cell 1: 17 and 17. Permanent closure: Rough layer 10, compact layer 10 and again rough layer 10 mm, then the entrance rough tampon up to the exterior.

Prey Counted from the remains (head capsule, pronotum, wings, genital organs are taken into account). Cell 1: 3 ♀♀ 2 ♂♂, 1 imago and 4 nymphs. Cell 2: 5 ♀♀ 0 ♂, 1 imago and 4 nymphs. Cell 3: 3 ♀♀ 1 ♂, 1 imago and 3 nymphs. All *Conocephalus melas*.

Cocoon Dimesions from that of cell 1: 22×7, 23×7 and 24×7 mm. Similar in colour and structure to that of *S.* (*Isodontia*) *harmandi*, but paler in colour, reddish brown with a whitsh band at the equatorial zone, covered with a thin semitransparent cocoon-cover as in other species.

Sex of the adult wasps emerged All males, came out of the cocoons on June 15. 1964.

Reference

Tsuneki, K. 1963. Comparative studies on the nesting biology of the genus *Sphex* (s. l.) in East Asia (Hymenoptera, Sphecidae). Mem. Fac. Lib. Arts, Fukui Univ., Ser. II, Nat. Sci., No. 13, Pt. 2, pp. 13-78.

Explanation of the Plates

Plate I. Nests of *Sphex (Isodontia) nigellus* Smith.

Fig. a. Four cocoons are included in one brood-chamber, one of which has the cocoon-cover tone off.

Figs. b, c and d. The nests made in the abandoned beetle burrows in logs, each including some cells with a cocoon.

Plate II. *Sphex (Isodontia) nigellus* Smith.

Figs. a, b and c.. Successive phases of rearing of the larvae in one glass cell.

Fig. d. An accomplished nest with two brood-cells.

Fig. e. A nest made in a log, with two cells from which the adult wasps already emerged.

Plate III. Figs. a-d and f: Nests of *Sphex (Isodontia) nigellus* Smith made in the bamboo tubes.

Figs. a, b and d. Bicellular nests; in b there is a simple packing before the innermost node; the 2nd cell is still being provisioned and the partitioning wall between cells is very simple.

Figs. c and f. Tricellular nests. The larva in inner cell folds over its anterior body over the abdomen to turn over; the 1st wall is simple and the 2nd somewhat thicker; in Fig. f a cocoon in each chamber.

Fig. e: A nest of *Sphex (Isodontia) harmandi* Pérez for comparison. Closing material: Leaf moss.

Plate IV. Figs. a–d: Nests of *Sphex (Isodontia) nigellus* Smith.

Fig. a. A tricellular nest, with two larvae of the wasp in the inner cell.

Fig. b. The cell is in the course of provisioning; the closure is temporary and is not compactly pressed.

Figs. c and d. Quadricelluar nests; in d innermost cell has been ravaged by the parasite.

Fig. e. A tricellular nest of *Sphex (Isodontia) maidli* Yasumatsu, including cocoons.

Plate V. Nests of *Sphex (Isodontia) harmandi* Pérez.

Fig. a. A nest in the course of provisioning. Two kinds of temporary closure are seen.

Figs. b and c. Accomplished unicellular nests; in c the inner portion of the tube is stuffed with a tampon of moss.

Fig. d. A bicellular nest, the inner cell including four cocoons.

Fig. e. Nest No. 2. The nest was abandoned by the wasp in the middle of her provisioning work and 4 cocoons were resulted from the 9 eggs laid.

Plate VI. Nests of *Sphex (Isodontia) harmandi* Pérez.

Figs. a and e. Incomplete nests, with two kinds of temporary closure; in e the particular passage closed at the entrance of the closure is seen.

Figs. b, c and d. The accomplished unicellular nests.

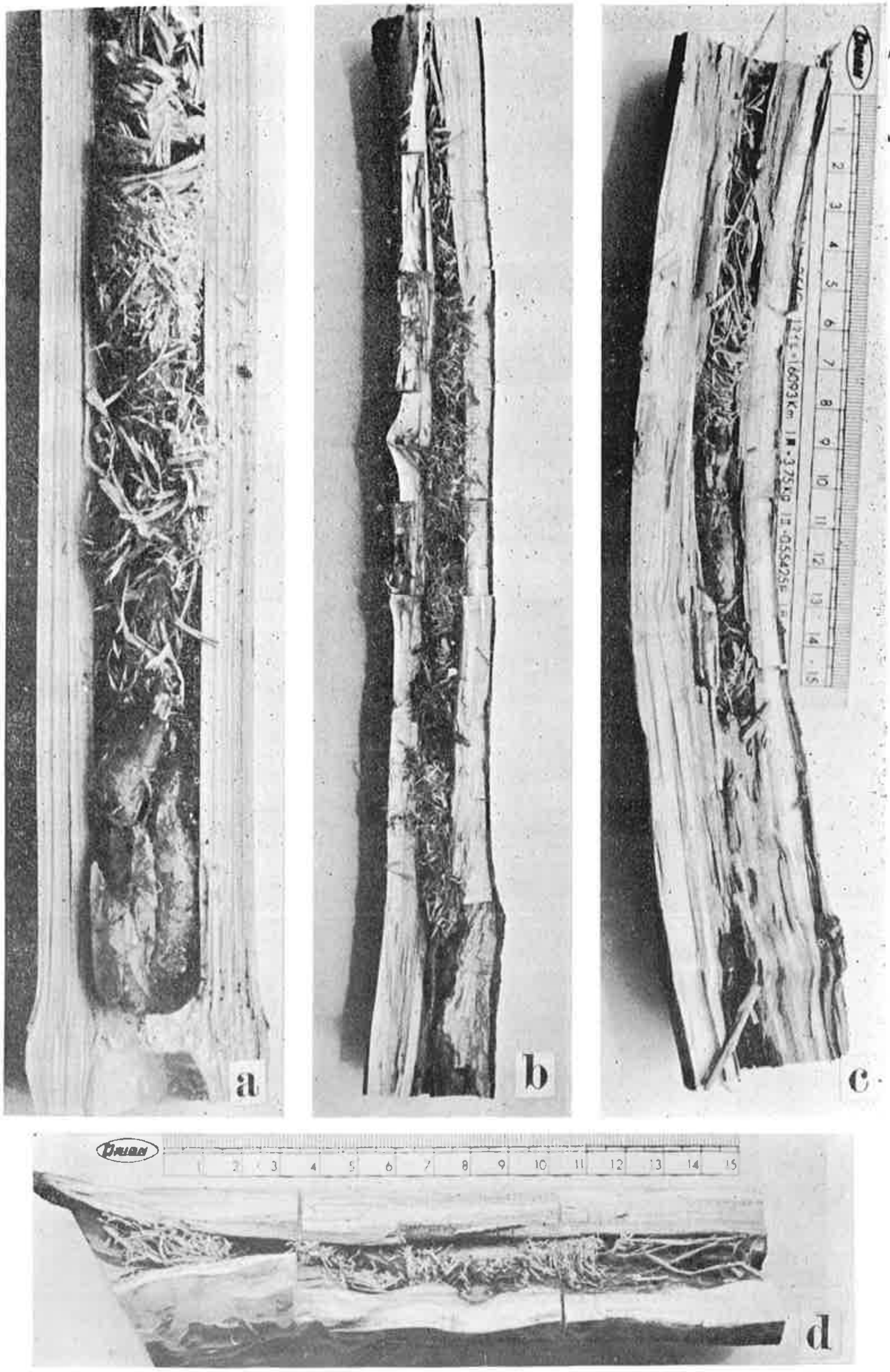
Plate VII. Nests of *Sphex (Isodontia) harmandi* Pérez

Figs. b, c, d and e. Incomplete nests; the passage in temporary closure is visible.

Plate VIII. Rearing of larvae of *Sphex (Isodontia) harmandi* Pérez.

Fig. a. The first five prey, each carrying a wasp's egg.

Figs. b, c, d and e. Succssive phases of rearing of the larvae in a tube bottle. No cannibalism occurred among the six larvae; they spun the cocoons leaning to one another.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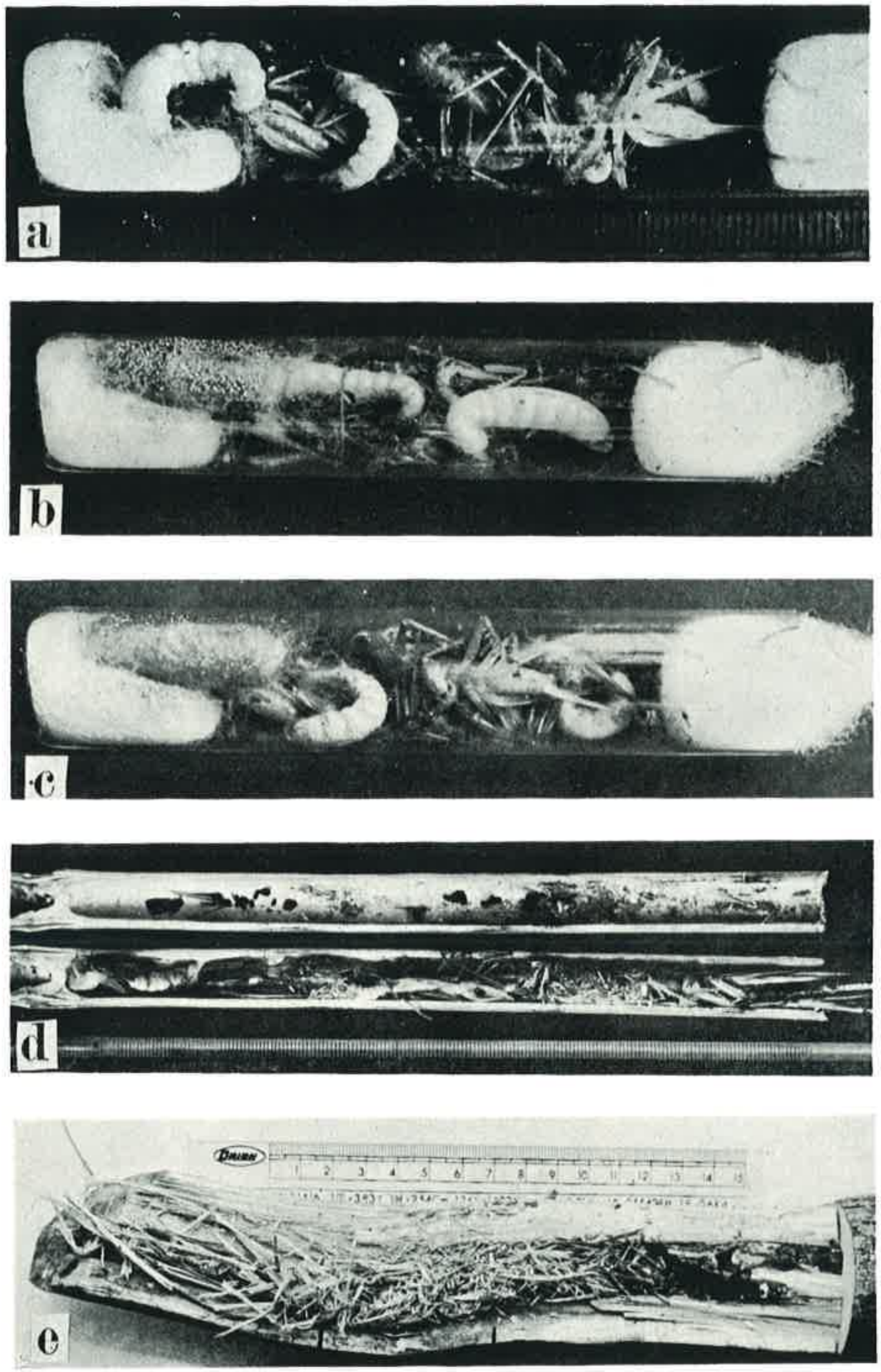
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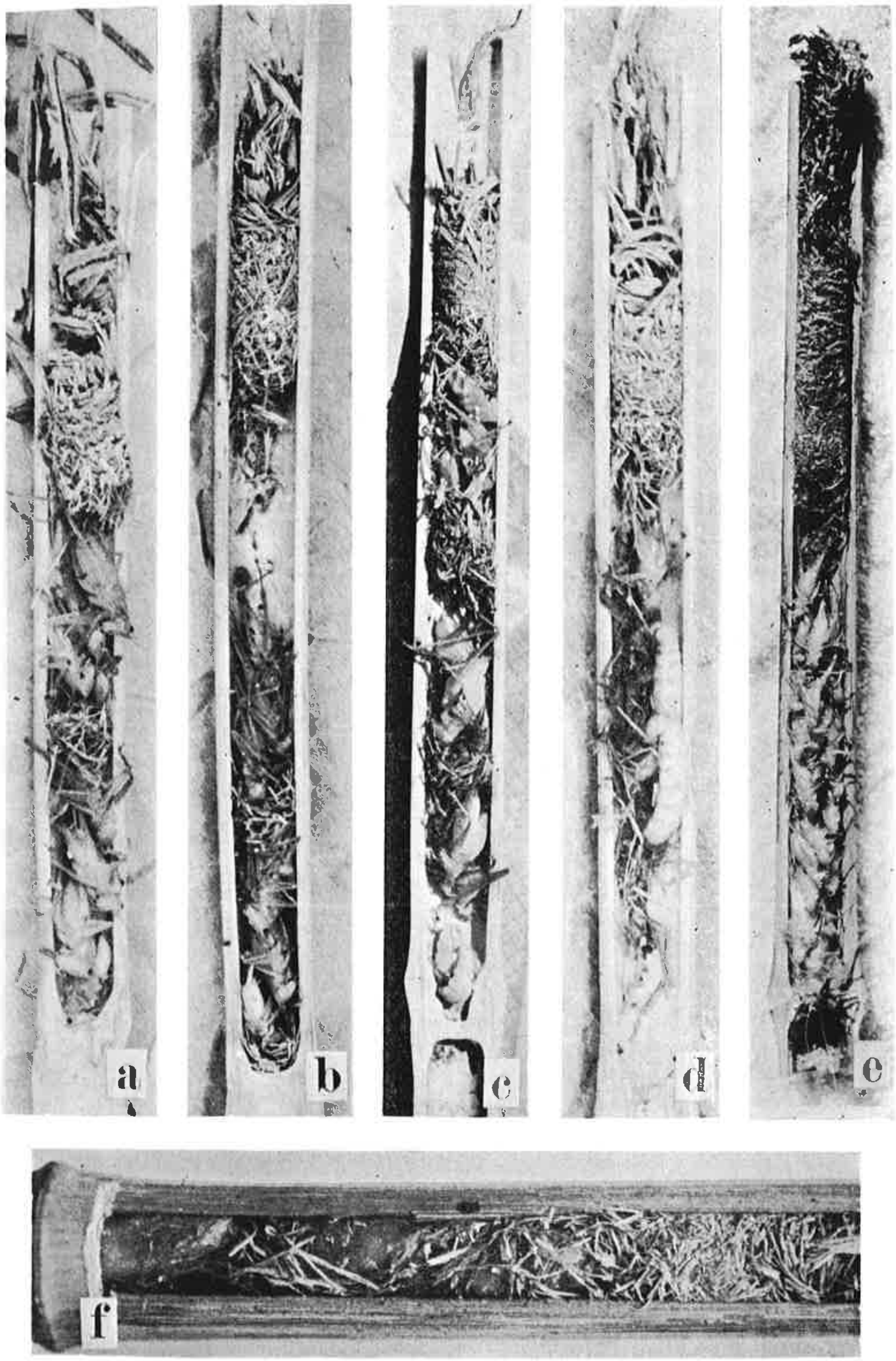
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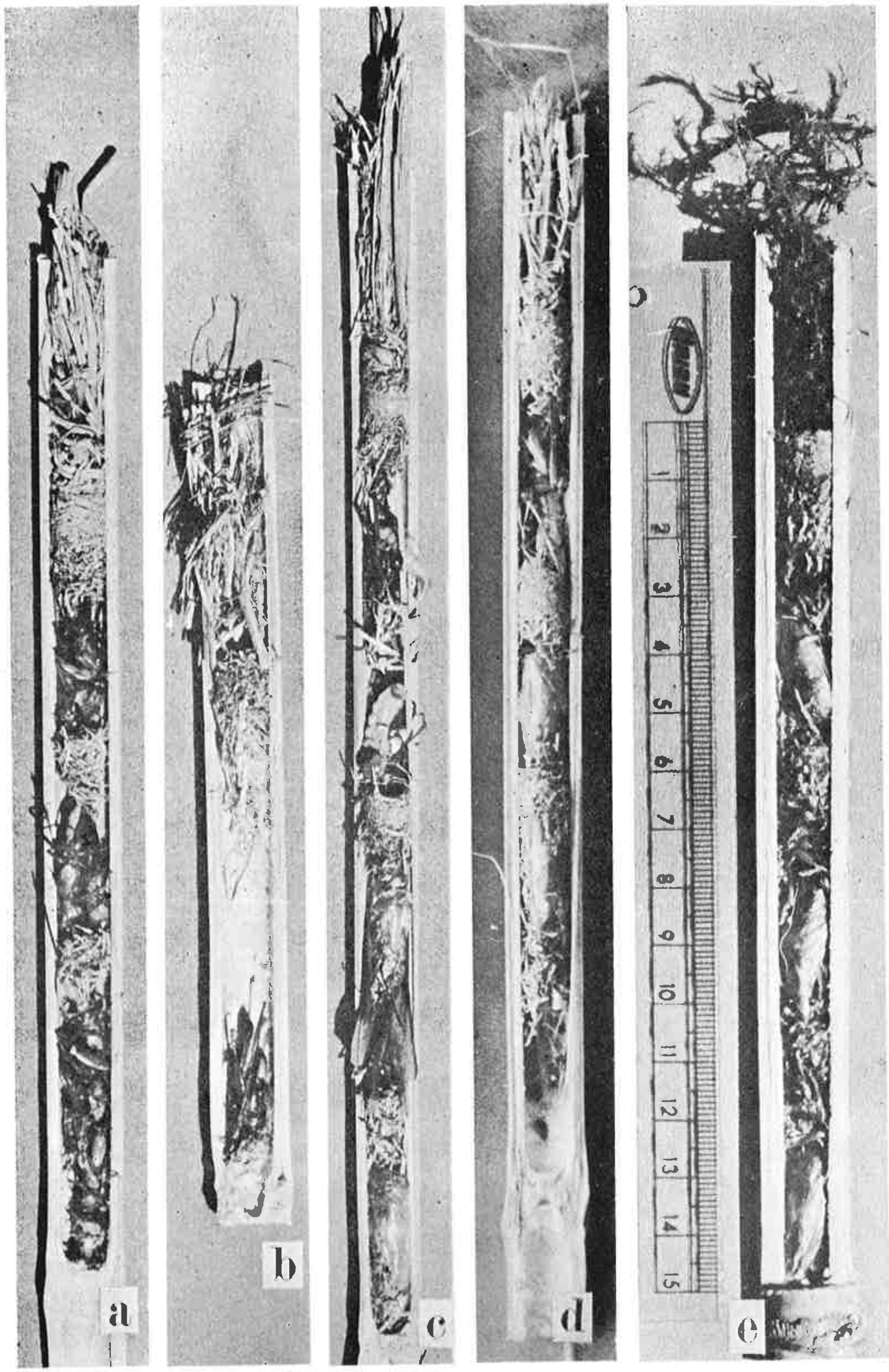
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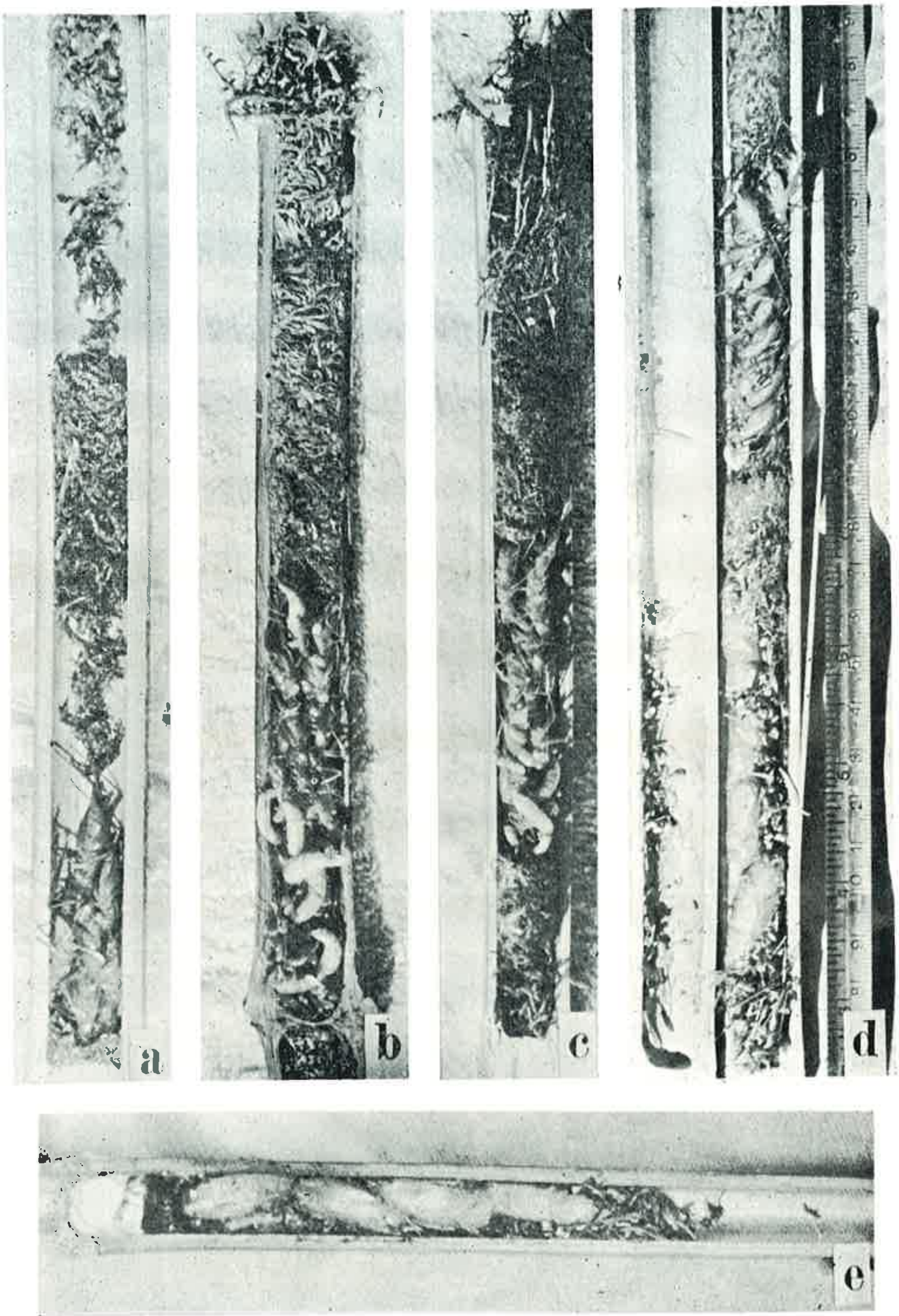
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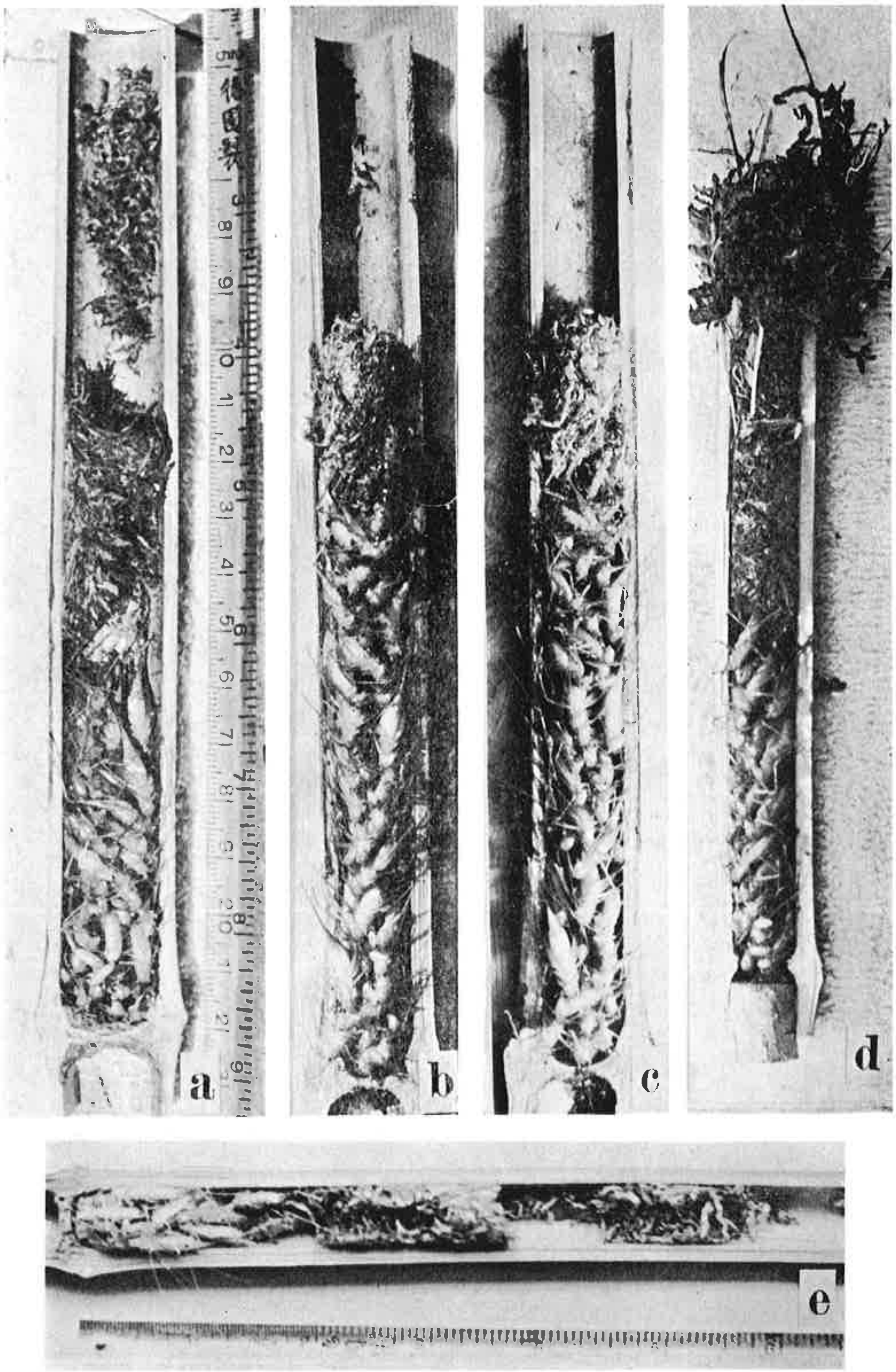

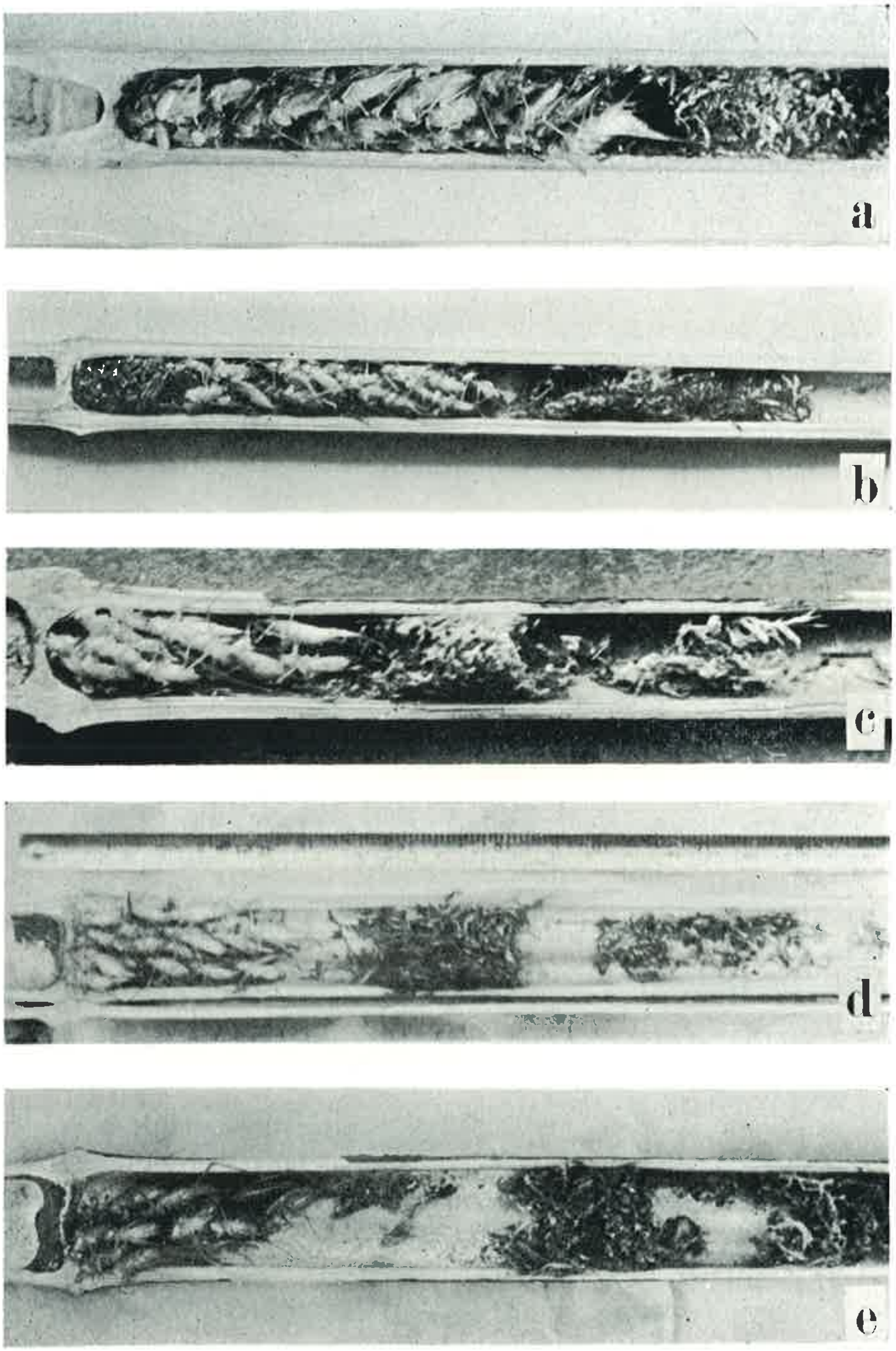
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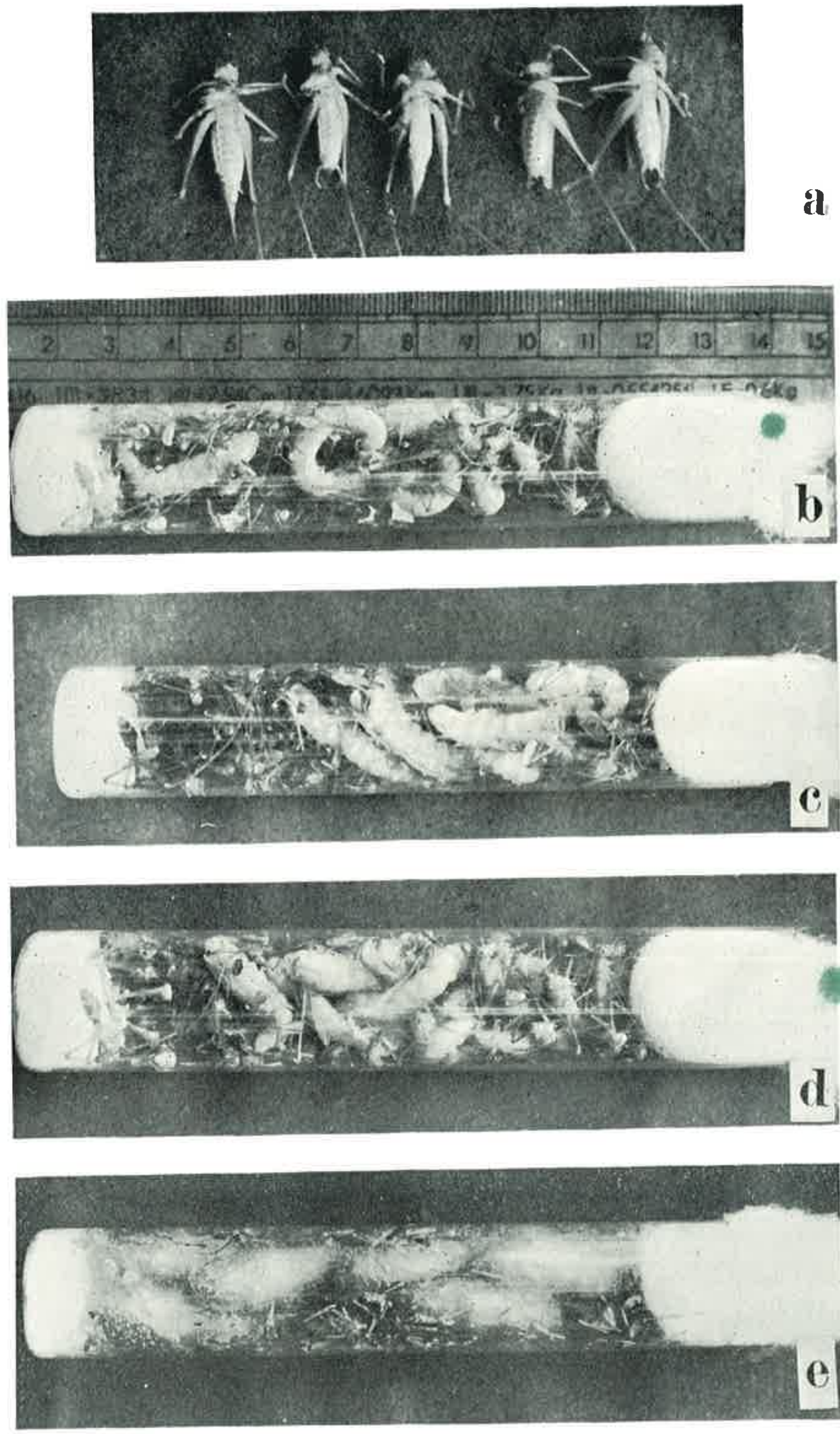
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