Biological Observations on Some Solitary Vespides.

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Preface.

My most hearty thanks are due to Dr. and Mrs. E. Tetens Nielsen for their exceptional kindness and constant readiness to help.

I am also very much indebted to Mr. E. Halager, M. A., and Mrs. Halager for their most valuable assistance by proof-reading.

I point out that all statements of time are M. E. T., one hour before Greenwich time.

I.

Anchistrocerus trifasciatus F.

Höppner (1910), Enslin (1921 b), and Tetens Nielsen (1932) have given detailed reports on this wasp. It is so rare, however, that I will give some observations on its nest.

Verhoeff (1893) has found two cocoons in galls on the root of an oak, and Enslin and Höppner have found its nest in stalks of bramble, while Tetens Nielsen and I have found it nesting in the straws of a thatched roof.

In the three nests which I have found, the inner diameters of the straws were 4.5 mm, 6.5 mm, and 6.5 mm respectively, thus a little bigger opening than Enslin has observed in stalks of *Rubus* (5 mm). The distances

from mouth to joints were 107 mm, 54 mm, and 151 mm, while the nest that Höppner found was 250 mm long. Enslin has given no measurement. I do not think that so long a nest would be found in thatch, as the distance between two joints only very rarely exceeds 200 mm.

In all three nests there were cocoons, each containing a praepupa (fig. 1), in accordance with the description of Enslin, but in several cases the grown up larvae had spun no spin-plate, which was always the case in the nests described by Höppner and Enslin.

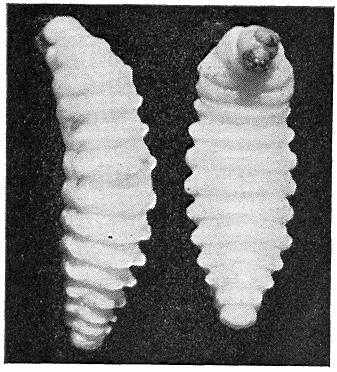


Fig. 1. *Anchistrocerus trifasciatus* F. Praepupae. The swelling on the head of the praepupa on the right is abnormal.

As distinct from the nests of *Symmorphus sinuatus* F. (see below) I have only with *A. trifasciatus* found one atrium between the main-close, which is present in all cases, and the clay-wall of the youngest chamber.

The main-closes were of somewhat different thicknesses, namely 1 mm, 3 mm, and 4 mm.

The number and sizes of the chambers may be seen from the description of the three nests.

August 14, 1940. Nest No. V.

Behind the main-close there was an atrium of 73 mm, and then there was a partition-wall of clay of 1 mm. Up against that one there was a 12 mm long cocoon, as described by Enslin. The chamber ended in a 2 mm thick clay-wall, which was spun together with the excrements, remains of the prey, and the cocoon, and formed the bottom of the next and last chamber, which was 19 mm long. Here the cocoon lay in the middle of the chamber with spaces of 2 mm at each end. Accordingly the cocoon was 15 mm long including the farthest clay-wall of 2 mm, with which it was spun very firmly.

April 9, 1941. Nest No. XI.

In this nest there was an atrium of 34 mm between the main-close and the first clay-wall of 2 mm thickness. Behind this was the only chamber of the nest, 15 mm long. The cocoon was here lying up against the joint as far back as possible. The wasp had put clay at the bottom as usual. The length of the cocoon was 10 mm. The space of 5 mm between the cocoon and the partition-wall was filled up with some remains of the prey, which showed that the larva is fed on larvae of microlepidopteres.

In none of these two nests were found spin-plates, the places of which, according to Enslin, may show whether the nest has been made by a *Symmorphus sinuatus* F. or an *A. trifasciatus* F.

April 9, 1941. Nest No. XIII.

This nest was the most interesting, as it contained several chambers.

Main-close	4 mm
Atrium	70 mm
Clay-wall	1 mm
Chamber a	15 mm
Partition-wall	2 mm
Chamber b	10 mm
Partition-wall	1 mm
Chamber c	9 mm
Partition-wall	1 mm
Chamber d	18 mm
Partition-wall	1 mm
Chamber e	10 mm

a) contained a brown Chrysis-cocoon, from which, on the 20th of May, I took a pupa, which was still quite bright, the eyes were dark-brown, and the abdomen had a faintly green gleam.

b) was filled up with a cocoon *(A. trifasciatus)* and a spin-plate.

c) as b.

d) contained a cocoon in the middle of the chamber and close to this a spin-plate, made by the larva. 1 mm from this spin-plate there was another older one with a hole in the middle, which shows that the straw had been used once before. Perhaps it was because of this spin-plate that this chamber was so unusually big.

e) also contained a cocoon, which, however, was destroyed, and only contained a mouldy mass. There was a spin-plate between the cocoon and the bottom of the chamber. Between the farthest partition-wall, and the bottom of the straw there was a space of 2 mm.

On the 20th of May the cocoons were opened, and they all contained pupae, which might have been a week or so old. The eyes had become brown and the wings were somewhat darkened.

Though the cocoons are free cocoons, they fill up the straws in all cases, and thus they may differ in cross sections according to the width of the straws.

On the whole, it may be said that *A. trifasciatus* is somewhat coarser than the *Symmorphus* species. It uses wider straws, and the clay-walls and main-closes are somewhat clumsier in construction, but still finer than with *A. callosus*.

II.

Symmorphus sinuatus F.

The life history of this species has been specially described by Enslin (1921 a), who found it nesting in straws of bramble; further contributions may be seen in Alfken (1914), and Tetens Nielsen (1932), who found the nests in thatches.

Tetens Nielsen writes p. 109, "Sans doute, *O. sinuatus* est l'espèce de *Symmorphus* la plus commune en Danemark. Pourtant je ne l'ai pris qu'une fois en 1927, mais en 1931, j'ai trouvé l'Hyménoptère et ses nids plusieurs fois dans les toits de chaume aux environs de Pilehuset."

Mr. Tetens Nielsen informs me that in the following one or two years *S. suecicus,* which had been there for several years, was totally displaced by *S. sinuatus*. I have had the opportunity of making a hasty examination of the roof of the laboratory in 1939 and 1940, and a more thorough one in 1941, and have not been able to find other *Symmorphus* than *sinuatus*.

On this well-known wasp I have made observations, which will be reported in the following.

1. Swarming period.

The males appear at the end of June and the swarming period of the females goes on in the first week of July; this year (1941) on the 5th and 6th of July.

I have noticed the copulation in a single case, on the 7th of July at 2:00 p. m. Some females were out looking for nesting-places; the wasps were swarming before the eaves and now and then they entered a straw to see if it was a suitable one for the nest. The copulation took place without any ceremonial. A female was sitting on a straw when a male arrived and sat down upon her, keeping the balance by whirling his wings. Then he bent his abdomen beneath the end of hers, in which position the copulation was completed. When the copulation was finished the male flew away, while the female went on with her searching. The males are to be found in the garden outside the house, and their number is decreasing fast.

After the copulation the females begin building the first nest in a straw of the roof.

2. The nest (nesting habits).

As to the number and largeness of the chambers Enslin says: „Die Zahl der Zellen schwankt zwischen vier und acht, ihre Länge von 9—13 mm und ihr Durchmesser von 3—4 mm."

I have, in 25 nests, found the distribution mentioned below:

The number of chambers	1	2	3	4	5	6	7	8
Number of nests with the corresponding number of chambers ...	13	7	1	1	2	1	0	0

This table shows that in the thatch the number of chambers in each nest is considerably smaller than in bramble.

The smallest chambers I have found were 10 mm long, and they are to be found in all sizes up to 18 mm. Sometimes there is no clay-wall, so that the nest is one big chamber (fig. 2).

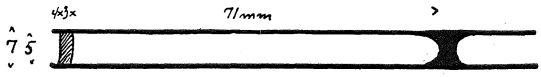


Fig. 2. Diagram of a nest of *Symmorphus sinuatus* F.

April 9, 1940. Nest No. VIII.
Outer diameter of the nest..... 6 mm
Inner diameter of the nest..... 4 mm
5 mm from the outlet there was a three mm thick main-close. 89 mm inside there was a brown spin-plate, spun by the larva and behind this the cocoon was lying.

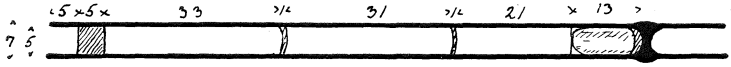


Fig. 3. Diagram of a nest of *Symmorphus sinuatus* F.

Another example will be given on p. 310. On fig. 3 is shown another nest. Here the chamber is also unusually big, but yet there is a partition-wall, and besides this another clay-wall that divides the tube into two rooms. Such a wall is often found, as is already mentioned by Enslin. On the whole, there seem to be very great individual differences among the *S. sinuatus* as to the nestbuilding.

A straw of 178 mm was arranged as follows: 6 mm from the outlet there was a main-close of only 1 mm in thickness, then an atrium 16 mm, and a 1 mm thick clay-wall. The first chamber consisted of a space of 12 mm, ending in a spin-plate, followed by an empty space of 21 mm up to the cocoon, which measured 12 mm including a thin partition-wall, to which the cocoon was spun, and finally an empty space of 8 mm.

The main-close was missing only in a single case.

Several times I have seen a wasp building the main-close. It is done as described for *Symmorphus connexus* Curt., see p. 316.

With *S. sinuatus* I have made observations on the duration of the nest construction in the way described by Tetens Nielsen (1933). By means of a grass straw and a concave mirror the straw is examined at suitable intervals; when the nest is finished, the straw is split up lengthways, and the contents measured in order to verify the readings made by means of the straw.

However, it appeared that the nests which I tried only contained a single chamber. One example only will be given.

July 8, 1941, at 6:51 p. m.
When the distance from the mouth to the first joint is measured, one finds that this is the depth of the nest. Nest 81 mm deep.

July 9, at 12:11 p. m.
Nest 66 mm deep.
The same day, at 4:50 p. m. No change.

July 11, at 12:30 p. m.
A new close.

The diameters of the straws used by *S. sinuatus* F. are from 3 to 6 mm, a little more than Enslin has observed in stalks of bramble, namely 3 to 4 mm.

3. The prey.

As food for the offspring this wasp uses larvae of Chrysomelides, the ordinary prey for the species of the sub-genus *Symmorphus*.

Enslin reports to have found larvae of microlepidopteres in the nests of *S. sinuatus* F., but this rather curious information I am not able to confirm.

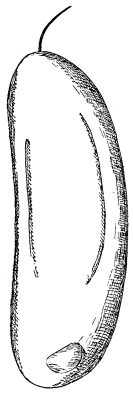
The prey is carried abdomen to abdomen, the female takes hold in the throat of the prey-larva with her mandibles, and holds it firm with her second pair of legs.

Thus the larva is not hanging down as will be described with *Symmorphus connexus* Curt. p. 322.

This wasp uses the leaves of the birches in front of the nests as intermediate landing places, when she is bringing home her prey. Having alighted on the leaf, the motherwasp puts down the larva, and breathes very energetically. Before starting again she arranges the larva with her legs, and takes hold of it, and steers towards the nest, where she takes hold of the straw with all her legs and pushes in the larva. In each chamber I have found from 10 to 17 prey-larvae.

A few days after the prey-larvae had been brought in, I observed that a few of them had pupated. This, I believe, is very rare. The prey-larva is not quite paralysed, and can move its legs and body a little. Nevertheless, it is seldom that it has so much vital power that it can pupate. I have found no prey-pupae in 30 nests which were opened after the larvae had spun their cocoons.

4. The development. (Egg).



At the joint of the selected straw the wasp puts some clay, which continues a little way down the sides. From this layer of clay the female suspends an egg in the usual thread, which is about $^1/_7$ of the length of the egg, which, again, is about $2\frac{1}{4}$ mm long (fig. 4).

The egg is a little curved in shape, and narrower at the top end than at the bottom.

The hatching time of the egg may be supposed to be 2 or 3 days.

Fig. 4. Egg of *Symmorphus sinuatus* F. with the thread by which the egg was suspended.

July 7, 1941.

A *S. sinuatus* was carrying in a prey-larva. On a closer inspection it appeared to be the fifth, as there were another four already lying close to the egg (fig. 5). The egg looked quite new and had, undoubtedly, been laid on the night before the 7th. On the 9th at 5:05 p. m. the egg was newly hatched.

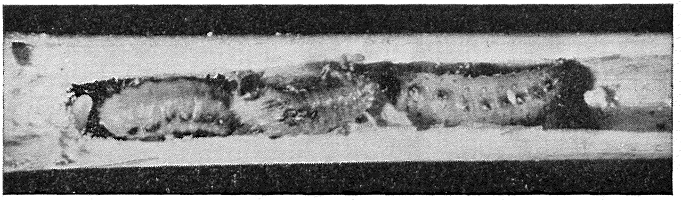


Fig. 5. Chamber in a nest of *Symmorphus sinuatus* F. with an egg and 3 prey-larvae.

The development. (Larva).

The newly hatched larva (fig. 6) is pale pink, its mouth parts are still almost transparent all over, and with the exception of the ends of the mandibles, they are still weak and soft. The segments are difficult to distinguish, as the cuticle is all stretched. The position of the stigmas can only be observed with difficulty. There are stigmas near the caudal end of the first and second, and near the cranial end of the fourth to eleventh segments. Thus there is no stigma on the third segment, just as Enslin has observed for the praepupa.

The newly hatched larva at once begins eating the nearest prey-larva, biting a hole with its mandibles and sucking out the contents of it. The larva grows fast, and in a week it has devoured all the prey. Different examples are given to show the time of development of the larva.

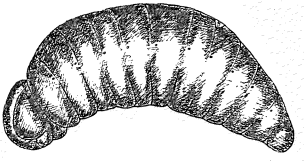


Fig. 6. One day old larva of *Symmorphus sinuatus* F.

July 10, 1941. Nest marked d.
Egg hatched.
July 14.
The larva eats well, but the prey is somewhat shrunk.
July 17.
Everything is eaten.

July 10. Nest marked e.
Egg hatched. Two of the prey-larvae show signs of pupating.
July 14.
The larva eats well.
July 17.
Everything eaten, except two pupae. These may be so hard that the larva cannot pierce them with its mandibles.

In most cases I have found, like Enslin, that the so-called spin-plate spun by the grown-up larva (fig. 7), has been placed close to the cocoon, but often away from the partition-wall. An example has been given where the distance between the spin-plate and the cocoon was 21 mm.

Enslin's description of the free cocoon (fig. 8) and praepupa (fig. 9) I can confirm in all details.

Fig. 7. Grown-up larvae of *Symmorphus sinuatus* F.

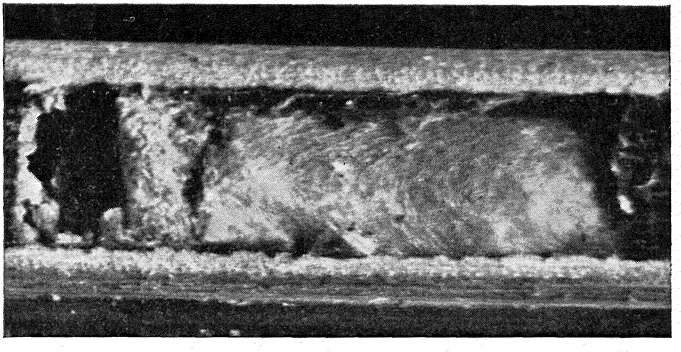


Fig. 8. Cocoon spun by a *Symmorphus sinuatus* F. larva. Note the spin-plate.

The development. (Pupa).

In the cases where I have taken the nests home for hatching, the change from praepupa to pupa has taken place from 15th to 20th of May the year after. This time is definitely earlier than in nature. This and other anomalies (the individuals were all very small, and some of them died) were caused by unnatural conditions during the winter, where the wasps were kept indoors at a higher temperature and a lower humidity than out of doors.

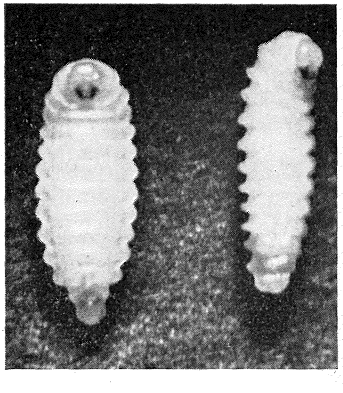


Fig. 9. Praepupae of *Symmorphus sinuatus* F.

5. Parasites.

As parasites I have several times found *Melittobia accaste* W., besides *Chrysis ignita* and *C. viridula,* and finally a parasitic fly. I quote an observation from my journal:

July 9, 1941.

At 11:45 a. m. I saw a female enter with prey. The depth of the nest was 75 mm, which was measured with a stalk of grass. At 4:50 p. m. the nest was shut up. I took it with me and opened it in the laboratory.

It appeared that the nest was 75 mm deep from outlet to joint. Thus the prey must have been fetched the very same day. The nest showed an interesting feature. There was no partition-wall to divide the chamber from the atrium, and no clay at the joint. There an egg was suspended in the thread, and 11 prey-larvae were stored up close to it. 20 mm from the joint there was an egg of a Chrysis, and 35 mm from the joint there was another prey-larva. Possibly these had fallen down from the other prey-larvae, while the nest was being carried home.

The wasp's egg was hatched on the 11th of July, while the egg of the Chrysis was not hatched at all. During the observation of this nest I remarked a custom of the Chrysises, which, to my knowledge, has not been observed before.

Near this nest a Chrysis sat and whenever another Chrysis came into the neighbourhood of it, she rushed forward and drove her off. They did not try to sting each other, but only engaged in a wrestling-match. When she had driven her rival away, she again took up her usual place. I therefore think that every female Chrysis has a hunting district, which she wants to keep to herself.

Once when *S. sinuatus* had flown away the Chrysis crept backwards into the nest and stayed there for some minutes. Thus I know that it was an egg of a Chrysis that lay in the nest, although it was not hatched.

It is very interesting, as already mentioned by Adlerz (1905), that Chrysises are able to lay eggs so quickly as opposed to the solitary Vespides, which, as far as is known, spend a whole night over it. It is very practical for them, because they have to accomplish it between two visits of the wasp.

It is unknown, of course, if it is the actual egg-laying which takes such a long time for a Vespide wasp, most probably it is the arranging of the egg, hanging in the thread which takes most of the time.

III.

Symmorphus connexus Curtis.

In the neighbourhood of the laboratory I found, this summer (1941), a wasp hitherto unknown in Denmark.

Herr Oberlandesgerichtsrat Blüthgen, Naumburg, (Saale), has most kindly examined two specimens, and he informs me that it is *Odynerus (Symmorphus) connexus* Curtis. This species has so far only been recorded from Germany, where it is very rare.

My hearty thanks are due to Mr. Blüthgen for his most valuable assistance.

In the following a description of the female will be given.

1. Description of the female wasp.

The head is coarsely punctured, black, and faintly hairy. Clypeus is black and less punctured than the remaining part of the head, with the lower edge cut straight across without any incision. It is covered with grey hairs, especially towards the edge. There is a small pale spot behind each eye. There are two almost white spots between the bases of the antennae. The scapus and the first segments of the flagellum are black, the rest of the antenna lighter and somewhat greyish brown. The mandibles are black, almost hidden behind clypeus.

The thorax is coarsely punctured, too, and black. The edges of pronotum are drawn a little forward into small points. Scutellum and postscutellum are black, almost shiny, and more finely punctured than the rest of the thorax. Tegulae look like scutellum.

The legs are black and faintly hairy. The bases of the tibiae are reddish yellow, almost orange.

The radial-cell has the end inside the front edge of the wing. There are 3 cubital cells, with both returning veins debouching into the second.

The abdomen is faintly punctured. The first, second, and third segments have yellow edges. The yellow edge of the first segment has an incision in the middle, where the long-wrinkle begins. The first segment has a sharply marked edge about the middle. The long-wrinkle is not very deep. There are yellow edges on the underside of the second segment. The third, fourth, and fifth segment have faintly brown edges on the underside.

I have not been able to find any information regarding the life-history of this species and my observations will therefore be rather detailed.

2. Locality.

The nests were found near the edge of a wood about 150 m to the north of the road from Helsingør to Frederiksværk towards Tibirke and Tisvilde.

East of the road, just inside the wood is the so-called Wesenberg-Lund's Wall (Tetens Nielsen 1932 p. 25). As may be seen on the photograph (fig. 10), the wall consists of a clay-wall about ¾ m high and covered by a thatched roof made of *Phragmites*. The edge of the wood faces south and is sheltered from all winds, except the south wind. In and around the wall many Hymenopteres are busy. In the clay *Hoplopus spinipes* and *H. reniformis* are nesting, and in several cases *Anchistrocerus* and *Lionotus* species have been observed, coming to fetch clay for their nestbuilding. In the roof *Anchistrocerus callosus* and *Symmorphus connexus* have their nests among several other aculeate Hymenopteres. It is remarkable that, although this place has been very carefully examined formerly by Tetens Nielsen, this species

was never found. It must have invaded the W.-L. Wall after 1935, Mr. Tetens Nielsen informs me.

At the spot where I made the discovery, I think there were about 20 of these wasps, that is to say I have only seen females.

Fig. 10. The Wesenberg-Lund Wall with the thatched roof in which *Symmorphus connexus* nests.

3. Swarming period.

The first time I discovered that there were some new wasps was on the 9th of July, 1941. In the afternoon on a trip to the W.-L. Wall I suddenly saw some extraordinarily small wasps flying about along the eaves.

The swarming had taken place about July 5th or 6th. On the second of July I was by the wall, and then there were no *S. connexus*, whereas several were seen

on the 9th. On the 10th I saw several females flying with prey-larvae, so the nestbuilding had apparently begun about the 8th or 9th of July. It is remarkable that these are exactly the same dates as for the swarming period of *Symmorphus sinuatus* F.

4. Nesting habits.

As already mentioned the nests were in straws of the thatch. The number of chambers in each nest varied a good deal, as may be seen from this diagram.

Number of chambers.....	1	2	3	4	5	6	7	8
Number of nests with the corresponding number of chambers...	0	2	1	1	0	1	0	1

When the straw is a long one, the inmost chamber does not reach back to the first joint; but the wasp separates, by means of a clay-wall, an atrium, the length of which differs according to the length of the straw.

Descriptions of some nests will show the lengths of atriums, chambers etc.

July 23, 1941. Nest No. 7.
Outer and inner diameter of the straw: 4 mm and 3 mm
Main-close ..... 7 mm
Atrium ..... 33 mm
Clay-wall ..... 2 mm
Chamber a ..... 8 mm
Clay-wall ..... 1 mm
Chamber b ..... 12½ mm
Clay-wall ..... 1 mm
Chamber c ..... 13 mm
Clay-wall ..... 2 mm
Chamber d ..... 13 mm
Clay-wall ..... 2 mm
Atrium ..... 17 mm

August 5, 1941. Nest No. 6.
Outer and inner diameter of the straw: 4 mm and 3 mm
Main-close ..... 3 mm
Atrium ..... 32 mm
Clay-wall ..... 2 mm

Chamber a	10 mm
Clay-wall	2 mm
Chamber b	10 mm
Clay-wall	2 mm
Chamber c	9 mm
Clay-wall	2 mm
Chamber d	8 mm
Clay-wall	2 mm
Chamber e	10 mm
Clay-wall	2 mm
Chamber f	9 mm
Clay-wall	2 mm
Chamber g	9 mm
Clay-wall	2 mm
Chamber h	16 mm
Clay-wall	2 mm
Atrium	52 mm

July 14, 1941. Nest No. 2.

Outer and inner diameter of the straw: 5 mm and 3 mm

Empty space of	4 mm
Main-close	3 mm
Atrium	21 mm
Clay-wall	2 mm
Chamber a	8 mm
Clay-wall	3 mm
Chamber b	8 mm
Clay-wall	2 mm
Chamber c	10 mm
Clay-wall	2 mm
Atrium	48 mm

The regular decrease in the size of the chambers observed by Tetens Nielsen (1932, p. 103 ff.) in the nests of *O. (S.) suecicus* Sauss. has been observed in some cases (nest No. 7 and 8) but not in all.

It is, indeed, very curious, that it is so seldom one finds more than 4 chambers in a straw, as there are many straws which might hold about 10 chambers. The wasps obviously prefer to build in different straws. Perhaps it might be explained in the following manner. If the offspring of *Symmorphus connexus* Curt. was to be

hatched from, say, two straws, and there were bad conditions in one of them, a comparatively large part might be destroyed. On the other hand there is little probability that the wasps in more than one of, say, 8 straws will be destroyed. There may be other conditions that decide the division, or possibly there are no conditions at all, and the number of the chambers may be quite accidental.

At any rate it is certain that it is harder work for the wasp to found 6 nests with an average of 3 chambers, than to found two nests with 9 chambers in each.

In some cases the atrium is divided in two by a clay-wall, and in other cases the atrium is undivided. Both cases are found with equal frequency.

When the wasp has provided all the food for a larva, which may be done in 1 or 2 days if the weather is good, she builds a partition-wall of clay, and thus creates a chamber in the straw. In case of bad weather it takes much longer to provide the food (see below). The partition-wall is made of sandy clay. I do not know where the wasps fetch the liquid for softening the clay, but the clay itself is fetched from the clay-wall under the roof. The wasp only fetches clay three times to build up a partition-wall. She carries a ball of clay as large as her own head in her mandibles from the wall to the workplace, and she can fetch the three balls needed, and finish the wall in ten minutes. The thickness of the partition-walls ranges from 1 to $3\frac{1}{2}$ mm, a little concave in the middle and somewhat thinner there; sometimes they may be double, and then the two parts are to be seen very clearly. The partition-walls are both bottom of one chamber and ceiling of the next.

In order to see how quickly *Symmorphus connexus* Curt. works, I measured with a grass straw (see p. 305) the depth of some nests every day.

Fig. 11 shows the nest of No. 4 on the 13th of July

before she has done anything but clean the straw. In the afternoon she had put clay at the joint (fig. 12). During the afternoon of the 14th she built the first partition-wall of 2 mm, so that the depth of the nest was now 53 mm (fig. 13). For the further development of this nest see chapter 7 p. 328 (Involuntary progressive feeding of the larvae).

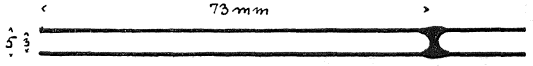


Fig. 11. Diagram of a straw after the wasp has cleaned out the future nest. July 13th, morning.

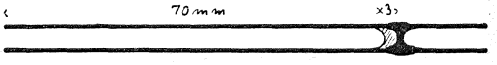


Fig. 12. The same nest on July 13th, afternoon. Clay has been put at the top of the straw.

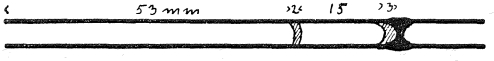


Fig. 13. The nest on July 14th. The wasp has finished the first chamber and built the first partition-wall.

This wasp (No. 4) closed up a nest on the 13th of July at 9:57 a. m., and at 3:18 p. m. she was out looking for a new straw which could be used for another nest. This one was finished on the 22nd of July. I cut the straw above the joint to procure the nest, and the same evening I noticed that she used the very same straw again. A rest pause of longer duration is never made between two nestbuildings.

It used to be taken for granted that when bees and wasps go backwards into their nests it is for the purpose of egglaying. With *Symmorphus connexus* Curt. this is not always the case. Several times I have studied females of this wasp carrying in their prey, then suddenly one of them arrived without anything, went into the chamber,

came out again soon, turned round, and crept in backwards. Sometimes she crept in backwards as far as she was able, but I have seen, in several cases, that the wasp has remained near the outlet till she went out again.

These observations I have been able to make with the aid of a concave mirror which reflected the sunlight into the straw; then it could be seen where the wasp remained and what she was doing. Sometimes a female hurried out suddenly when I reflected the sunlight on her, but I do not know whether it is the strong light or the effect of heat that is the cause. The insect has to be almost in the focus in order to be seen clearly, and is therefore exposed to a combined effect of light and heat.

On several other occasions, however, I have, by means of this method, been able to observe the wasp lying quite still in its nest, only moving its antennae.

As an example some notes from my journal are given.

July 13, 1941. Nest No. 5.
10:07 a. m. The wasp enters forwards.
10:09 a. m. The wasp enters forwards.
10:27 a. m. The wasp enters forwards.
10:57 a. m. The wasp enters backwards, and remains near the outlet.
11:03 a. m. Out, when I reflected the sunlight on her.
12:23 p. m. Out forwards.
12:24 p. m. In forwards, out, and in backwards.
12:30 p. m. In forwards.
2:14 p. m. In forwards, out, and in backwards.
2:40 p. m. In forwards.
2:48 p. m. Enters with a prey-larva,
etc.

July 14, 1941.
11:10 a. m. Wasp looks out from nest and flies away.
2:20 p. m. In forwards, out, and in backwards.
3:04 p. m. Enters with a prey-larva.

These notes give various information as to when the insects remain in the straws.

1) In the evening the wasps creep into the nests backwards to sleep, and remain there all night.

On the 14th of July I was at the nests at 9:15 a. m., but no wasps were to be seen till 10:15 a. m.

No. 5 could scarcely have escaped my notice, if she had gone out; undoubtly she came from her night-sleep at 11:10 a. m.

2) From these and other observations it may be concluded that when they rest after having done a certain amount of work they first creep in forwards, apparently to see if everything is in order, then they creep out again, turn round and creep in backwards. The resting period is from 5 or 6 minutes to about 1 hour.

3) The wasps may remain in their nests in case of bad weather. On the 14th of July No. 5 did not work in the morning. Towards 2:00 p. m. the sky was quite covered with clouds and the insect crept in backwards to wait for better weather. It is improbable that the wasp needed rest, because she had done no work at all for a long period.

I have observed something similar with *Symmorphus sinuatus* F.

It is often very difficult for the wasps to creep backwards into the narrow straws because of their wings. One day I observed a *Symmorphus connexus* Curt. which tried several times, in vain, to creep backwards into her nest. I tried to help her by pushing her wings inside the straw with my pencil, which she did not mind in the least. However, she did not get in with my help, but after I had stopped trying to help her, she succeeded in getting in herself.

Enslin and Höppner have often found nests of *Symmorphus sinuatus* F. and *Anchistrocerus trifasciatus* F. without main-closes in the stalks of bramble. I have only once found a wasp's nest without a main-close. *Symmorphus connexus* Curt. makes it, too. They are very

solid indeed, in many cases. The smallest I have seen were 3 mm thick, somewhat concave on the outer side and somewhat convex on the inner. It can be seen, usually, that the close consists of two parts, built separately, and lying close to each other. In one nest the close was fourfold with all four parts quite close together; the close was 7 mm thick, a considerably large close for such a small insect. Neither with *S. sinuatus* F. nor *A. trifasciatus* F., which are rather bigger than *S. connexus* Curt., have I ever seen such big closes. But this wasp has very easy access to the clay, there is plenty of it 1 m beneath the roof where the wasps nest.

When the motherwasp builds a close it takes hold of the edge of the straw with her legs, and bends her abdomen under that, so that the centre of gravity comes just under the flat of support. By means of that she obtains what she needs without using her wings to keep her balance. Then she turns round slowly, and builds with her mandibles.

As soon as the female has finished a nest she at once begins to look for another.

5. The prey.

Like all other known *Symmorphus* species *S. connexus* Curt. uses larvae of Chrysomelides as food. Yet the food is very extraordinary, namely larvae of *Zeugophora subspinosa* F. (fig. 14). This species burrows in the leaves of Populus tremula, and it is rather astonishing that *S. connexus* Curt. takes this kind of larvae. How the wasp paralyses the larvae and gets them out of the leaves is still an unsolved problem. There were not many poplars in the neighbourhood, the nearest stood about 200 m away, but in spite of a thorough search I did not succeed in finding any of the two species that *S. connexus* Curt. uses as prey.

Another interesting feature is that this wasp, besides

using this larva of Chrysomelides as food, also uses a larva of a microlepidopteron, viz. *Gracilaria stigmatella* F. (fig. 15 and 16).*)

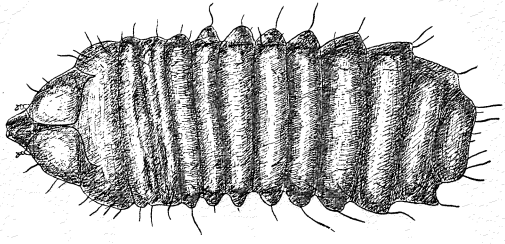
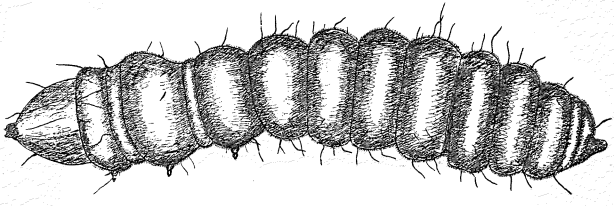


Fig. 14. *Zeugophora subspinosa* F. larva.



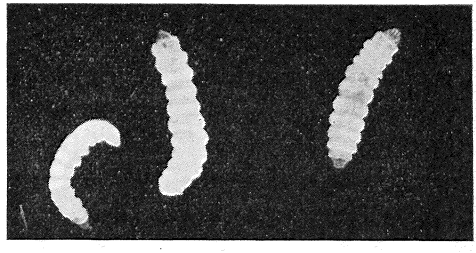


Fig. 15. } *Gracilaria stigmatella* F. larvae.
Fig. 16. }

This moth-larva burrows in the very same leaves as *Zeugophora subspinosa* F., and it is therefore to be deduced that *S. connexus* Curt. is not able to distinguish them from each other, but paralyses and takes both

*) I beg Mr. H. P. S. Sønderup to accept my best thanks for the determining of the prey.

species. They have both been found in the same chambers in no regular order.

However, this must be taken as an exception from the rule, that the *Symmorphus* species use larvae of Chrysomelids for food.

The time that it takes a wasp to fetch a prey-larva is from 6 to 30 minutes.

Number of minutes for a single hunt. .	6	7	8	9	10	11	12	13	14	15	16	17	18
Number of observations	2	3	0	0	0	0	0	1	1	2	0	1	1
Number of minutes for a single hunt. .	19	20	21	22	23	24	25	26	27	28	29	30	
Number of observations	1	1	1	0	1	1	0	0	1	1	1	2	

The prey is carried abdomen to abdomen. The female takes hold of the throat of the prey-larva with her mandibles, but she does not use her legs to keep the body of the larva close to her own. As a result the prey-larva hangs down almost vertically from the wasp, which has all her legs free to take hold of the straw in which she is nesting.

I have sometimes observed a wasp which was carrying her prey-larva land first on leaves of the small birch seen on the photograph (fig. 10) in front of the wall, and after a rest fly direct to the nest.

The weight of the prey seems to be rather heavy for the wasp, which does not fly as easily as without the burden. She often whirls to and fro in front of the eaves before landing with all her legs stretched forward. While she holds on with her legs, she pushes the prey in, and then follows herself. It takes her up to two minutes to push the larva right up to the joint.

As previously mentioned the fetching of prey is inter-

rupted by a longer or shorter resting-pause, during which the wasp stays in her nest.

The fetching of prey is commenced before the egg is hatched, and is continued till about 22 to 30 larvae have been provided. The number is usually 26 or 28.

A female *S. connexus* Curt. can easily carry in 28 prey-larvae in two days, and as the egg is not hatched

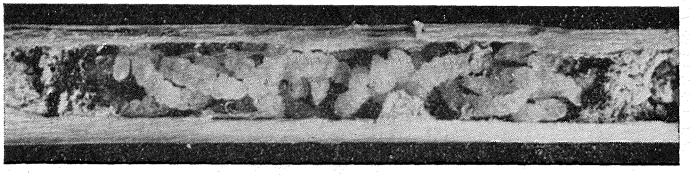


Fig. 17. Chamber in a nest of *Symmorphus connexus* Curt. Egg and prey.

Fig. 18. The nest containing young larva and prey.

till the third day after it has been laid, one might expect to find a fully stocked chamber with every egg. And that was what I actually found (fig. 17 and 18).

6. The development. — Egg.

The egg is laid, in some cases at least, in the night, as may be concluded from the following observations.

July 13, 1941.

At 9:57 a. m. I marked a female *S. connexus* Curt. by painting it yellow. When she was caught she was just closing her nest. At 12:25 p. m. she reappeared and was looking for her old nest, which I had removed, and as she could not find it,

she disappeared again. At 3:17 p. m. she was out looking for a new straw that could be used for nestbuilding. She made up her mind, and at once began to clean it out, sometimes interrupting her work to take a little flight to get to know the surroundings.

Till 4:03 p. m. she kept coming and disappearing, apparently, without any distinct purpose. Then she came home with clay in her mandibles. After some vain searching she found her nest, and remained there for 3 minutes, busy building the top of the first chamber. At 4:11 and 4:19 p. m. she returned with more clay, and at 4:45 p. m. she came back without any. After that I had to stop the investigations for that day.

July 14, 1941.

At 10:15 a. m. the "yellow" wasp was seen carrying in prey, and she spent $1\frac{3}{4}$ minutes in pushing it from the outlet of the nest to the chamber with the egg which I presume she had laid during the night.

July 15, 1941.

In the morning prey was carried in. In the afternoon the wasp built a clay-wall.

July 16, 1941.

At 9:10 a. m. she was seen carrying prey-larvae into the nest again, and she was doing so all the morning. It must be concluded then that the egg had been laid the night between the 15th and 16th of July.

The egg is of the ordinary aspect of an *Odynerus*-egg, suspended by a thread from the top of a chamber (fig. 19). The thread is rather long, about $^1/_3$ of the length of the whole egg. On the whole it seems that the species which build in thatch have rather a long thread carrying the egg, in contrast to the sand, clay and tree-building species (Tetens Nielsen (1942), Adlerz (1907)).

The egg of *S. connexus* Curt. is almost the same size as that of *S. sinuatus* F., though the latter wasp is considerably bigger than the former.

The egg is hatched on the 3rd day after it has been laid, and the larva remains, during the first hours, hanging by the thread and the egg-shell (fig. 20). I have

discovered that it is very difficult, unfortunately, to hatch the egg in imprisonment. I have only succeeded in doing so twice, and in both cases the wasp-larva died quite young. In other cases there are seldom any difficulties in hatching wasps' eggs and young larvae.

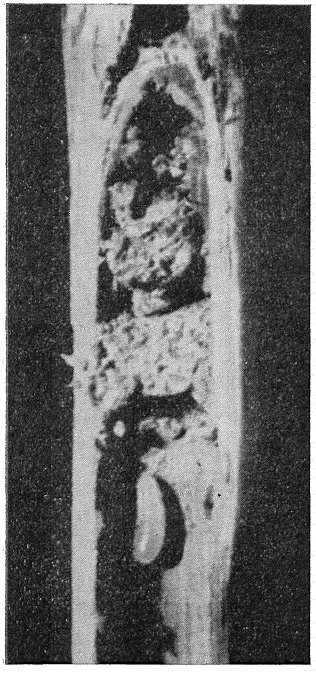


Fig. 19. Egg of *Symmorphus connexus* Curt. suspended from the top of a straw.

Fig. 20. Newly hatched larva of *Symmorphus connexus* Curt. still hanging by the eggshell.

The development. — Larva.

The newly hatched larva is pale, somewhat pink and chubby, and the mouth-parts are not yet darkened all over. However, the mandibles are able to pierce the cuticle of the prey, and they are constantly being moved.

The head and the first four segments are bent towards the abdomen. The division in segments is a little difficult to distinguish, as the cuticle is still very smooth. Stigmata cannot be seen at all.

The hatched larva at once begins to suck out the nearest prey-larva, and grows very quickly. It is coloured greyish brown by the food like many other wasp-larvae, not yellow or white, as might be expected because the prey is yellow and white.

A larva which was hatched on July 22nd had eaten everything on the 28th, and had thus been 6 days in consuming about 26 prey-larvae.

Another wasp-larva from the same nest was hatched on the 23rd, and on the 24th was given the prey from a chamber in which the egg was not hatched. On the 29th of July the wasp-larva had eaten all it wanted, and of about 50 larvae it had left only 8.

This nest was very interesting because of the order in which the prey was found in the four chambers. In the innermost, i. e. the oldest chamber, there were only very few *Zeugophora,* all the rest were *Gracilaria.* In the next chamber were mostly *Gracilaria,* in the last but one mostly *Zeugophora,* and in the last and outermost chamber only *Zeugophora.* Judging from what I have seen, on the whole, I am inclined to think that this regularity has been produced quite accidentally.

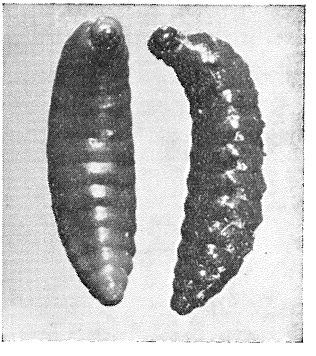


Fig. 21. Grown-up larvae of *Symmorphus connexus* Curt. The larvae have darkened somewhat in the liquid of preservation.

The grown-up larva is about 8 to 9 mm long, 3 mm thick, and 4 mm broad. The shape is long-stretched with the head and 3—4 segments

bent a little forward. The larvae shown on fig. 21 are a little shrunk by the liquid of preservation. In reality the segments are not to be seen so clearly, because the cuticle is more stretched.

The development. — Cocoon.

The day after the last prey-larva has been sucked out, the wasp-larva begins to spin a brown plate (German: Gespinstdeckelchen), in the same way as *Symmorphus sinuatus* F. and *Anchistrocerus trifasciatus* F. The spin-plate is spun up to and joined to the outermost clay-wall, and to that the cocoon is spun. The spin-plate is rather strong and tough. When the larva has finished the spin-plate, it proceeds with the cocoon at once. This is a wall-cocoon (German: Wandkokon, French: cocon jointe). The cocoon is spun very strongly together with the walls of the chamber, so that it might quite easily be destroyed when the nest is opened. The cocoon is very thin, whitish-yellow, rather tough, formed like a cylinder with rounded off ends. At the end nearest the entrance it is spun to the spin-plate, and at the other end it is spun together with the clay-wall. Inside the cocoon shines with quite a silky gleam. It is about 8 or 9 mm long and $2\frac{1}{2}$ to $3\frac{1}{2}$ mm broad according to the inner diameter of the straws. Sometimes there is no spin-plate, and then there may be a space between the cocoon and the clay-wall at the bottom of the chamber, with a few threads from the cocoon to keep it in place. Only in a single case have I found a chamber with a praepupa, which had spun no cocoon at all.

When this work has been done, the larva excretes, so that the excreta are to be found inside the cocoon at the farthest end.

The development. — Pupa.

In 5 or 6 days the grown up larva changes to a praepupa (fig. 22). This is stretched, with only the head

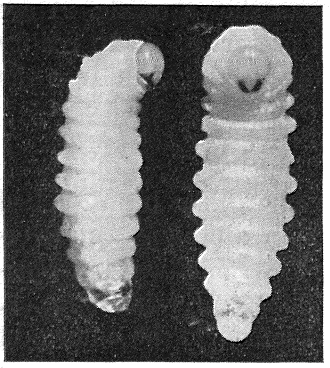


Fig. 22. Praepupae of *Symmorphus connexus* Curt.

and the two first segments bent towards the abdomen, so that the head is bent at an angle of 90°. On the sides of the 2nd to 10th segments there are sidepads (German: Seitenwülste), and the same segments have also backpads (German: Rückenwülste). The stigmata are near the caudal end of the 1st and 2nd segment and near the cranial end of the 4th to 11th segment, as with *Symmorphus sinuatus* F. The colour of the praepupa is white, almost like *Anchistrocerus trifasciatus* F.

7. Involuntary progressive feeding of the larvae.

First I am going to finish the example from page 317. On the 16th I saw the "yellow" wasp carrying prey. It might then be concluded that she had laid egg number two during the second night after the first egg was laid. On the 17th it rained the whole day, and on the 18th I was prevented from making any investigations. Most of the day it was rainy weather, so there had been little opportunity for the wasp to work that day. On the 19th the depth of the nest was still 53 mm. On that day she carried prey in. On the 20th it rained again the greater part of the day and on the 21st the sun did not appear till 5:00 p. m., but on the 22nd at 9:15 a. m. the nest was closed.

In the few hours of sunshine on the 20th and 21st the wasp had provided the rest of the prey for cham-

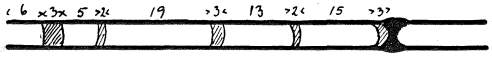


Fig. 23. The nest shown in fig. 11, 12, and 13, on July 22nd.

ber 2, closed it with a 2 mm thick clay wall, built a partition-wall of 3 mm and built the outermost close (fig. 23).

Accordingly, for chamber 1 she had provided all food in one and a half days and then built the partition-wall. This is what Roubaud (1916) calls "approvisionnement banal, en masse", and this is the most common thing among the *Odynerus* species, according to my own observations.

But the providing of prey for chamber 2 was a most interesting case, because the wasp must have fed her own larva. The egg in chamber 2, which was laid before the morning of the 16th, had been hatched before the afternoon of the 19th, when I saw the female carrying prey to that chamber.

This is an example of what Roubaud calls "approvisionnement progressif, continu". Furthermore, Roubaud shows that the differences between the two methods of provisioning are not so great as might be thought. He says, "L'une et l'autre font usage, suivant les circonstances saisonnières, tantôt d'un approvisionnement hâtif, en masse, tantôt d'un approvisionnement ralenti, au jour le jour. Il y a tous les passages entre les deux modes."

And here we see that in case of bad weather the provisioning may be different for two chambers in the same nest.

It is quite interesting that this evidence of adaptability of habits which Roubaud found in *Synagris* species is also to be observed in *Odynerus* species. As far as I know this has not been described earlier.

8. Parasites.

I have found no parasites at all. There were, as in most places, many Chrysises, but I never saw a single one enter the small straws used by *Symmorphus connexus* Curt., neither did I find any parasites in the nests.

IV.

Preferendum temperatures of *Odynerus* nesting in thatch.

In order to study the climatic conditions governing the thatch-nesting *Odynerus* I have, as preliminary experiments, investigated the preferendum temperatures by means of the method formerly used in this laboratory, and described by Tetens Nielsen (1938). A brief description of this method will be given here.

Into one container is poured water, which is maintained at a temperature of about 60°. Another container is filled with a mixture of ice and salt, and this arrangement gives a gradient of temperatures along the copper tube of about 2° to 50°. The temperature is controlled by means of thermometers inserted into the tube.

The method of finding the preferendum temperatures is as follows. The animal is put into the tube and from a given point of time the temperatures are read every half minute for instance, and at the same time the locality of the insect is observed. When a sufficient number of readings have been taken it can be calculated which intervals of temperatures the insect prefers.

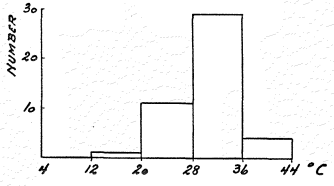
The *Anchistrocerus callosus* ♂ I used for the experiments was from the same roof as the *Symmorphus connexus* ♀, while the *Symmorphus sinuatus* ♂ was from the roof of the laboratory.

The results of the experiments may be set up in the following graphs.

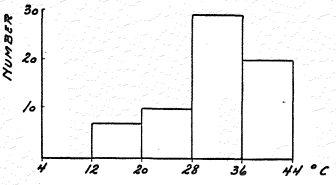
The abscissae indicate the temperature in centigrades and the ordinates the number of times the animal has been observed.

The graphs show that none of the three wasps are in activity until the temperature has reached 20° C. Further, that none of the insects have a marked prefe-

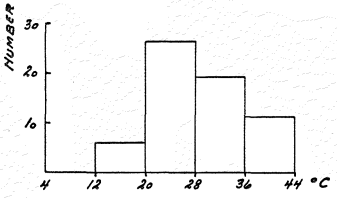
rendum temperature, but that they actually work when the temperature is approximately between 20° and 40° C. The temperature in roofs does not vary so much as in sand, so the result of the observations is as might be expected beforehand.



Graph 1.



Graph 2.



Graph 3.

Graph 1 showing the preferendum temperature of *Anchistrocerus callosus* Thoms.; Graph 2, the preferendum temperature of *Symmorphus sinuatus* F.; Graph 3, the preferendum temperature of *Symmorphus connexus* Curt.

It is of some interest to compare this result with the data known for aculeate Hymenopteres nesting in sandy soil. These insects have a much higher preferendum temperature than the thatch-nesting wasps because of the extremities of temperature and humidity to which they are exposed. (Adlerz 1912, and Chapman 1926).

Mr. Tetens Nielsen informs me that experiments which he is going to publish in due course have shown a preferendum temperature of *Bembex rostrata* F. of about 34° to 37° C., which is very near that which he has found for *Psammochares fuscus* L.

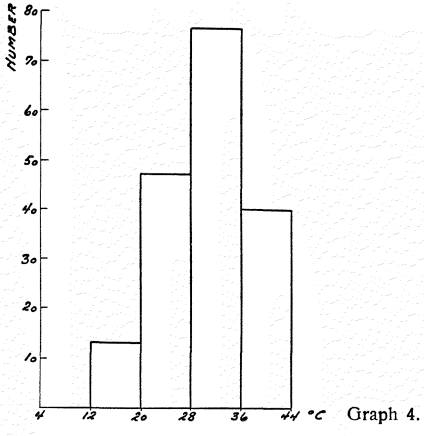
However, the graphs for the three wasps show diffe-

rences. It might seem curious that *A. callosus* prefers a higher temperature than *S. connexus*, since the latter has its period of activity in July, whereas *A. callosus* builds its nests in May. But there are different conditions to consider which might offer an explanation.

Wesenberg-Lund's Wall is surrounded on the three sides by trees, most of them birches, which, in the month of July, throw the greater part of the roof in shade for a large part of the day. The birches come into leaf at the beginning of May, but the thin leaves do not give the same shade as later on, in the month of July.

S. sinuatus F. seems to be somewhat more warmth-loving than *S. connexus* Curt. The roof in which *S. sinuatus* F. nests does not lie in shade, but receives the sunshine from morning till evening.

Most likely, however, the differences between the three species, are not reliable, and therefore it is justifiable to pool the results of all the experiments.



Graph 4.

Graph 4. The results of the experiments for the three mentioned wasps pooled to one graph showing the preferendum temperature of thatch-nesting wasps.

It shows that the thatch-building species having no marked interval of preferendum temperature, are actually able to work all day on fairly sunny and warm days. When the sun strikes the roof, and the thermometer shows abt. 30° C. in the shade, it is too hot for the wasps; they disappear into their nests or into other shady places till the temperature becomes more suitable.

V.

Comparison of the biology of the thatch-nesting species of *Symmorphus*.

Tetens Nielsen's and my own observations show that *Symmorphus suecicus* Sauss., *S. sinuatus* F., and *S. connexus* Curt. may replace each other, and *S. bifasciatus* L. belongs to the same group (Adlerz, Aurivillius). Therefore a comparison of the biology of these four species is given as a table, including our present knowledge of the most outstanding points of the biology of these species.

Symmorphus	*bifasciatus*	*suecicus*	*sinuatus*	*connexus*
Distribution	N. Germany, Denmark, Sweden	Denmark, Sweden, Finland	Germany, Denmark, Sweden, Finland	Germany, Denmark
Swarming period	Middle of June to beginning of July	First 10 days of July	First 10 days of July	First 10 days of July
Number of chambers in each nest	1—3	1—8	1—8	2—8
The inner diameter of straws used (mm)	?		3—6	$2\frac{1}{2}$—$3\frac{1}{2}$
The length of chambers (mm)	?	10—20	9—18	8—16

Symmorphus	*bifasciatus*	*suecicus*	*sinuatus*	*connexus*
Atriums (d = divided) (u = undivided)	12—50, u. d.	abt. 20, u.	11-116, u. d.	17—52, u. d.
Empty spaces (mm)	?	Not found	3—21	1—4
The prey-larvae	Phyllo-dectes	Phyllo-dectes	Chryso-melidae	Zeugophora, Gracilaria
Method of carrying the prey	In mandibles	Mandibles and legs	Mandibles and legs	Mandibles
Number of prey-larvae	6—12	12—15	10—17	22—30
Position of stigmas of the larva	?	?	1—2, 4—11	1—2, 4—11
Cocoon	?	Wall-cocoon	Free-cocoon	Wall-cocoon
Number of sidepads (s) and backpads (b)	s. ? b. ?	s. ? b. ?	s. 4—12 b. 1—12	s. 2—10 b. 2—10
Parasites	Mellitobia	Mellitobia	Mellitobia, Chrysis ignita, viridula	No parasites found

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