FINE STRUCTURE OF THREAD CONNECTIONS IN THE ORB WEB OF *ARANEUS DIADEMATUS*[1]

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INTRODUCTION

Web-building spiders are valuable subjects for the study of behavior since the spider provides a record of much of its behavior through its web. Descriptions of the gross structure of the web and the behavior of the spider during its construction can be found in Savory (1952), Jacobi-Kleemann (1953), and Witt, Reed, and Peakall (1968). However, the gross structure is only part of the spider's creation. The threads from which the web is constructed are only several microns thick. Consequently, the unaided human eye can determine basically only the position of the threads.

Another part of the spider's creation is visible only with magnification. This is the fine structure of the threads where they connect to one another. Rapidly produced and possessing remarkable strength (DeWilde, 1943), thread connections are one of the more interesting accomplishments of the spider. However, little attention has been given to the fine structure of the web. Lehmensick and Kullmann (1957) and Friedrich and Langer (1969) examined spider silk by electron microscopy, but did not look at points of connection between threads. McCook (1889) and Nielsen (1931) have drawings of attachment disks for drag-lines made under low magnification. De-Wilde (1943) has a photomicrograph of a radius to frame connection, and Comstock (1948) has a drawing from a photomicrograph of a spiral to radius connection. Robbins (Savory, 1952) has a photomicrograph of a drag-line attachment disk and one of sticky spiral to radius connections, both at low magnification. Also, there is a photomicrograph of a spiral to radius connection from the hori-

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zontal web of *Cyrtophora citricola* in Kullmann's (1957) study of
this peculiar spider. However, we have been able to find no detailed
descriptions of thread connection fine structure.

In the study reported in this paper, we investigated the fine
structure of most of the types of thread connections which are found
in the web of *Araneus diadematus* Clerck. Within the web there
may be between 1000 and 1500 locations at which one thread is
fastened to another thread (Fig. 1). Mooring threads fasten the
web to some non-thread structure and may be continuous with
some of the frame threads (Witt, *et al.,* 1968). There are frame
thread to frame thread connections, forming Y's with the stem of
each Y being a mooring thread. Each radial thread is fastened to
a frame thread. Occasionally, a radius will be in the form of a
Y-structure at its peripheral end; the stem of the Y connects with
the hub; and each arm, or secondary frame thread (Peters, 1939),
fastens to either a frame thread or a radial thread. However, the
majority of the connections within the web are the viscid or sticky
spiral to radius connections in the trapping zone. Most of these
are at points at which the sticky spiral thread extends from both
sides of the radius. Occasionally, especially in the lower portion
of the web, the sticky spiral thread meets the radius but does not
continue on the other side. In the strengthening zone (Savory, 1952)
or notched zone (McCook, 1889), non-sticky spiral threads are
fastened to radial threads. The strengthening zone surrounds the
apparently disorderly network of threads in the hub (McCook,
1889). Non-sticky spiral thread to radial thread connections are also
present in the provisional spiral, a structure which is removed as
the sticky spiral is added. Each of these types of connections will be
described except for those at which a sticky spiral meets the radius
but does not continue on the other side.

<center>METHODS</center>

All thread connections surveyed in this study came from webs of
laboratory reared adult female cross spiders (*Araneus diadematus*
Clerck). Each spider was kept in a $51 \times 51 \times 9$ cm aluminum
frame with removable glass doors and was provided with one house
fly twice per week, water daily, and controlled conditions of light
and temperature (Witt. *et al.,* 1968). The age (3 to 4 months
since emergence from the egg cocoon), weight (88 mg to 134 mg),
and time between food consumption and web construction (1 to 8
days, with the majority at 1 day) were relatively constant for spiders
used in this study; and within these ranges for these factors, no cor-

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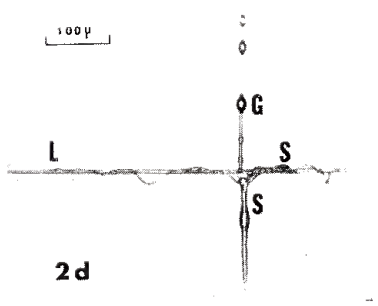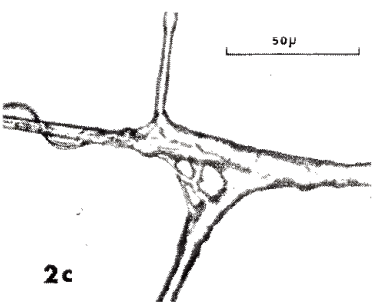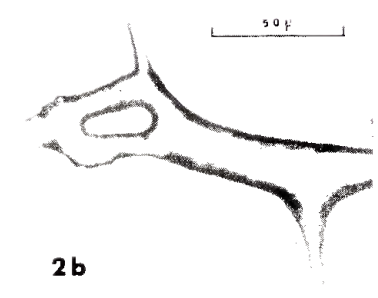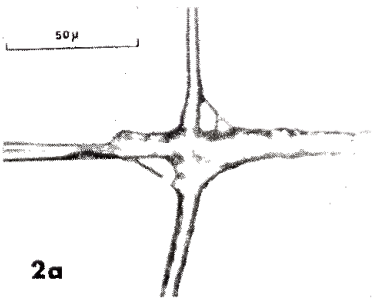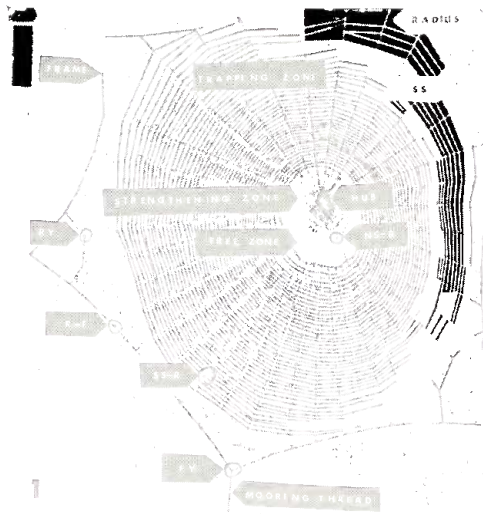
relation was apparent between these factors and structural features of the connections.

The day before the connections in a spider's web were to be looked at, the glass doors were removed, and the old web was destroyed. The new web, built by the spider early the next morning, was treated as in Witt *et al.* (1968) except that the threads were not coated in any way. Afterwards several thread connections from the web were examined.

In the web, threads are stretched tight into straight lines. When placed on a glass slide, threads with sticky globules often remained straight; but the globules were usually destroyed. Threads without globules curled and twisted when placed on a slide. To obtain a less distorted connection to study under a microscope, Permount mounting medium (Fisher Scientific Company) was streaked into a circle on a glass microscope slide, forming a basin. The slide was then placed against the web so that the threads surrounding the connection would stick to the Permount. Thus, the connection was suspended above the slide by the ridges of the circle of Permount. The threads were then burned loose from the outer edges of the circle by a surgical cauter, and the slide was taken away. The slide was always made on the same day that the web was built.

Within a week of preparation of the slide, the connection was viewed under a Leitz Labolux D microscope; and negatives were made on Panatomic X sheet film using a Brinkmann Mark V camera with various objective lenses on the microscope. That structural

Fig. 1. The vertical orb web of *Araneus diadematus* with labeled structures. The scale, consisting of a weight suspended by cotton threads 20 mm apart, indicates size and vertical direction. Abbreviations: SS, loop of sticky spiral; SS-R, sticky spiral to radius connection; NS-R, non-sticky spiral to radius connection; R-F, radius to frame connection; FY, frame Y-structure; RY, radial Y-structure.

Fig. 2a-d. Examples of sticky spiral (SS) to radius connections. In these photomicrographs, SS's run vertical; radii, horizontal. Radius is fastened to frame to right of page. Up and down on page corresponds to up and down, with respect to gravity, in web. a. Zero junction: points where SS joins radius on one side is directly across from where it joins at other side. Note sleeves on radius at both frame and hub side of SS. b. Smooth non-zero junction: there is space, smooth in appearance, along radius between points at which SS joins each side of radius. Idiosyncrasies such as the doughnut-shaped structure in this SS-R made generalization about structure difficult. c. Non-zero junction with rough appearance. d. Note sleeves (S) on radius at frame side of SS and on SS, loose strands (L) on radius, and globules (G) on SS.

variations of the connection were not due to the amount of time which elapsed between slide preparation and exposure of the negative was shown by comparing photomicrographs with the slides after more time had elapsed. After several weeks to a year, essentially no changes in structure were discovered except for frequent disappearance and fusion of globules on the sticky spiral.

Various measurements and counts were made from the negatives and prints. Since 1 μ was close to the limit of resolution on the photomicrograph, measurements in this range should be considered approximations. The thickness of a thread associated with a connection was usually measured at a distance of 150 μ from where the thread joined the other thread. In most cases, threads were fairly uniform in thickness at this distance. Closer to the other thread, thickness had a greater tendency to vary, and measurements were complicated by features of the connection. When the thickness of a thread at 150 μ was obviously not typical for that thread, as for example, when a sticky spiral had a globule on it at this point, the thickness was measured somewhat further from the connection. When strands were counted at a connection, "separate strands" were defined as strands with a visible space between them in the photomicrograph. However, sometimes an estimation of the number was used because some strands were hidden by others, and some were out of focus.

The reader may refer when necessary to the following list, in alphabetical order, of abbreviations which will be used in this paper; FY, frame Y-structure; NS, loop of non-sticky spiral from the strengthening zone; NS-R, non-sticky spiral to radius connection from the strengthening zone; PS, loop of provisional spiral; PS-R, provisional spiral to radius connection; R-F, radius to frame connection; RY, radial Y-structure; SS, loop of sticky spiral; SS-R, sticky spiral to radius connection.

RESULTS

The microscope reveals a wealth of structural detail at thread connections from which many component features can be abstracted, and the complexity and variability of which make description difficult. Some features of the structures will be pointed out in the following sections; and sample photomicrographs will be presented. Various descriptive statistics (percentages, means, coefficients of variation, and ranges) will be used to provide an impression of the prevalence of certain features and the central tendency and variability of meas-

Table 1

Frequency of some structural features of sticky spiral to radius connections (SS-R's). For each feature, 49 SS-R's from 15 webs built by 8 different spiders were observed. Note that each SS-R had a sleeve on the radius at the frame side of the junction and that SS'S never had loose strands.

Feature	Percent of SS-R's having the feature
Zero Junction	22.4
Sleeve on Radius at Frame Side of Junction	100
Sleeve on Radius at Hub Side of Junction	46.9
Sleeve on SS	55.1
SS and Radius Both Single Stranded at Junction	36.7
Loose Strands Along Radius	35.5
Loose Strands Along SS	0

urements made on various features. We will draw attention to some of the questions suggested by these observations, and possible directions for further research will be indicated with hypotheses concerning function and origin of the structures.

Sticky Spiral to Radius Connections:

In reading the following section, the readers may refer to Table 1 and Table 2 for data pertaining to SS-R's.

We will define a "junction" as the space along a thread at which another thread is fastened to it. By "connection" we will mean

the junction plus the threads in the immediate vicinity of the junction.

The point at which the SS joined one side of the radius was either directly across from where it joined the other side (zero-junction) (Fig. 2a) ; or there were varying amounts of space (the junction) along the radius between these points (non-zero junction) (Fig. 2b), causing the SS to have a disconnected appearance. In contrast to the SS's, radii always appeared as continuous, nearly straight lines at SS-R's. Junctions were smooth (Fig. 2b) or rough (Fig. 2c), with many gradations between. The smoother junctions were more prevalent.

It would be interesting to know in what way, if any, the length and roughness of the junction are related to the functioning of the web. For example, do these features affect the strength of the connection or the transmission of vibrations along the radius?

The radius at the frame side of all SS-R's and, less frequently, the radius at the hub side of a SS was rougher in appearance and thicker adjacent to the junction than the same thread further away from the junction. These areas will be referred to as sleeves (Fig. 2d). For any given junction, the sleeve on the radius at the frame side was at least 25 μ longer than the one on the radius at the hub side; and usually it was longer than the one on the SS.

Perhaps threads are strengthened by sleeves, and the prevalence and length of sleeves are related to the magnitude of the tensions they must withstand in the web. Measurements of these tensions would be useful. At some SS-R's, the SS joined the radius as a single strand at both sides of the junction (Fig. 2b and 2d). Other SS-R's consisted of various numbers of strands (Fig. 2a, 2c, and 2e), often interconnected and variable in thickness. Perhaps the presence of many strands at a junction functions in the dispersal of stresses or to increase elasticity.

If the presence or absence of non-zero junctions, sleeves on the radii at the hub side of junctions, sleeves on SS's, and many strands at the connection improve the web in some way, why do some SS-R's have these characteristics while others do not?

Many SS-R's had idiosyncrasies, the description of which will not be attempted here. The doughnut shaped structure in Fig 2b is an example. It does not seem likely that these structures have a specific function since any one of them occurred at only a single SS-R. They are probably artifacts of the forces acting on the connection during its formation. Thread connections, especially SS-R's, are produced at a very rapid rate. The spider produces over a thousand

Table 2

Descriptive statistics for some structural features of sticky spiral to radius connections (SS-R's). SS-R's were rather variable with respect to these features, as indicated by the coefficients of variation. Note the differences in sleeve length on the radius at the different sides of the junction and the differences in thread thickness for the radius and SS. Thread thickness was measured at both sides of the junction.

Feature	Mean	Coefficient of Variation	Range	Number of Measurements	Number of Webs Examined	Number of Spiders Used
Length of Junction	27.8 μ	98	0 μ-100 μ	49	15	8
Length of Sleeve on Radius at Frame Side of Junction	106.6 μ	39	37 μ-200 μ	48	15	8
Length of Sleeve on Radius at Hub Side of Junction	57.2 μ	54	25 μ-100 μ	23	9	8
Length of Sleeve on SS	43.6 μ	59	7 μ-125 μ	37	13	6
Number of Strands at Junction	10.0	100	4-42	49	15	8
Distance Between Junction and Nearest Globule	49.3 μ	52	6 μ-112 μ	37	11	6
Number of Globules Within 300μ of Both Sides of Junction	6.5	54	0-12	49	15	8
Thickness of Radius	5.8 μ	16	3 μ-9 μ	96	15	8
Thickness of SS	3.7 μ	25	3 μ-5 μ	98	15	8

SS-R's in approximately ten minutes. Taking this into consideration, it is not surprising that there is a great deal of variation in connection structure and that SS-R's have idiosyncrasies.

Globules (Fig. 2d), presumably containing the viscid material, were seen on SS's in the vicinity of the junction, but none were seen on radii. There was a variable amount of space between the junction and the nearest globule. Observations of SS's at positions other than the vicinity of SS-R's produced the impression that the space density of globules (number of globules within a given length of thread) was rather constant. In contrast, the number of globules within 200 μ of both sides of the radius at a SS-R was quite variable.

Stretching the SS is the probable cause of the accumulation of viscid material into globules (Savory, 1952). The radius may interfere through being a discontinuity in the stretched line and, in this way, be responsible for the less uniform distribution of globules near the junction.

It is believed that the ampullate gland produces the silk for the radii and the baseline of the SS's, with the aggregate glands producing the viscid material (Peakall, 1969). However, the radial thread is not simply equivalent to a viscid spiral thread minus the viscid material because the radial threads we observed were generally thicker than SS's, although both had the same minimum thickness. Also, DeWilde (1943) found that viscid spiral threads are much more extensible than radial threads, and we observed loose strands (Fig. 2d) along the radii in the vicinity of SS-R's but never on SS's.

Connections from the Strengthening Zone and Provisional Spiral to Radius Connections:

Table 3 and Table 4 contain data pertaining to NS-R's. The motion pattern of the spider differs during construction of NS-R's and PS-R's on the one hand and SS-R's on the other. The fourth pair of legs are relatively motionless and touching the radius as a NS or PS is fastened to a radius. However, as the spinnerets touch the radius in generating a SS-R, one of the fourth legs stretches the SS. In comparison to NS-R's and PS-R's the construction of SS-R's apears slow and deliberate (Savory, 1952). There are also differences in the fine structure of these connnections.

Junctions of NS-R's (Fig. 3) were usually much longer than those of SS-R's. There were no zero junctions. In contrast to SS-R's, neither radial nor spiral threads ever appeared as continuous lines at NS-R's. This created the notched appearance of the strengthening

Table 3

Frequency of some structural features of connections from the strengthening zone (NS-R's). For each feature 18 NS-R's from 2 webs built by different spiders were observed. Comparing this table with Table 1, note the absence of zero junctions, the decreased frequency of sleeves on radii, and the presence of loose strands along the NS.

Feature	Percent of NS-R's having the Feature
Zero Junction	0
Sleeve on Radius	5.5
Sleeve on NS	22.2
NS and Radius Both Single Stranded at Junction	5.5
Loose Strands Along Radius	11.1
Loose Strands Along NS	11.1

zone. Also, unlike SS-R's, the junctions of NS-R's always had a rough appearance.

NS-R's had sleeves on radial or spiral threads less often than SS-R's. Unlike some SS-R's, there was a sleeve on no more than one strand at any one NS-R.

As at SS-R's, a spiral thread at a NS-R often joined the radius as several strands. However, some SS-R's had many more strands than were found at NS-R's.

Only two PS-R's (Fig. 4a) were looked at, and they resembled NS-R's in length and roughness of the junction, in configuration of threads, and in having sleeves and a number of strands.

Is the manner in which the structure of NS-R's and PS-R's differs from the structure of SS-R's related to differences in movement pat-
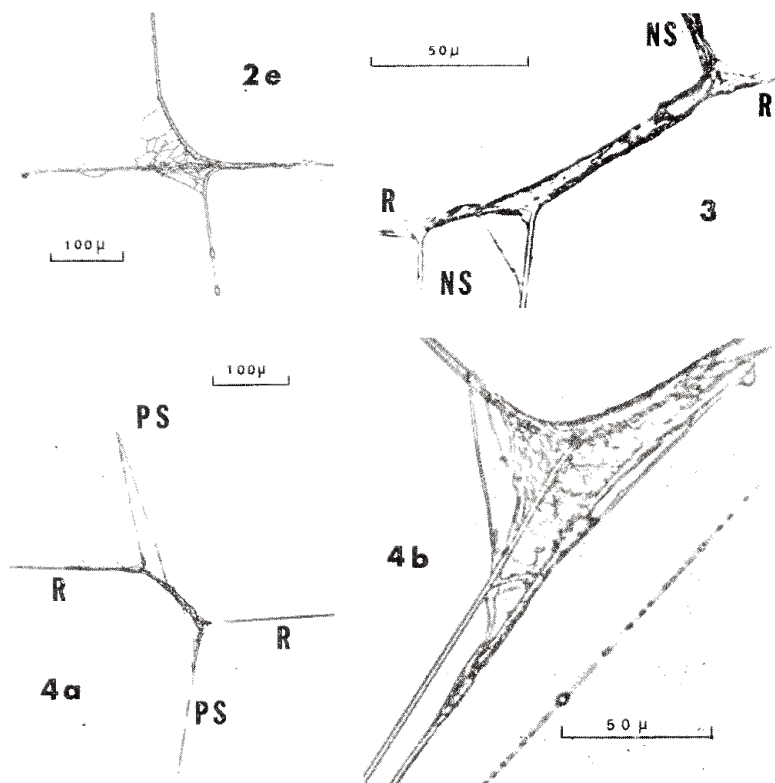
Fig. 2e. Sticky spiral to radius connections. Many strands connecting SS to radius.

Fig. 3. Typical non-sticky spiral to radius connection from strengthening zone. Sleeves can be seen on spiral (NS) at one side of radius (R); NS at other side consists of 3 strands. There is rough appearing space between points at which spiral joins each side of radius, and radius is out of line.

Fig. 4. Provisional spiral (PS) to radius (R) connection. a. Notice resemblance to NS-R's (Fig. 3). b. Globules can be seen on one of the strands.

terns during web construction? The spinnerets are capable of "to and fro" and complex rotary movements (Wilson, 1969). It would be interesting to observe these movements during the construction of each type of thread connection. For example, there may be differences in construction procedures on this level which can be related to the manner in which the fine structure of SS-R's differs from that of NS-R's and PS-R's. Also such observations might provide information about the origin of some of the structures at thread connections.

The production of radii, NS's, and PS's, is attributed to the ampullate glands. The aggregate glands, to which production of the viscid globules is atributed, are not believed to be involved (Peakall, 1969). Some spiral and radial threads at NS-R's and PS-R's resembled radii at SS-R's in having loose strands and no globules. However, one PS-R had tiny globules, smaller than those on SS's on a thin (0.5 μ — 1 μ) strand (Fig. 4b). How were these produced, and what glands were involved?

Table 4

Descriptive statistics for some structural features of connections from the strengthening zone (NS-R's). For each feature 2 webs built by different spiders were observed. NS-R's were rather variable with respect to these features, as indicated by the coefficients of variation. Comparing this table with Table 2, note the increased length of the junction and the decreased thickness of the radius. Thread thickness was measured at both sides of the junction.

Feature	Mean	Coefficient of Variation	Range	No. of Measurements
Length of Junction	137.4 μ	29	75 μ-225 μ	18
Number of Strands at Junction	8.9	49	4-22	18
Thickness of Radius	3.9 μ	41	1 μ-7 μ	35
Thickness of NS	3.1 μ	29	2 μ-5 μ	32

Table 5

Descriptive statistics for some structural features of radius to frame connections (R-F's). For each feature 5 webs built by 4 different spiders were observed. R-F's were rather variable with respect to these features, as indicated by the coefficients of variation. Note that frame threads at R-F's were thicker than threads at SS-R's and NS-R's (see Table 2 and Table 4).

Feature	Mean	Coefficient of Variation	Range	No. of Measurements
Length of Sleeve	158.7 μ	38	100 μ-250 μ	8
Number of Strands in Radius	34.1	24	19-45	8
Thickness of Frame	8.4 μ	27	5 μ-12 μ	13

It is interesting that a spiral to radius connection of another species, *Cyrtophora citricola* (Kullman, 1957) greatly resembled NS-R's of *A. diadematus*. It had a similar configuration of threads, a non-zero junction, the spiral thread joining the radius as several strands, and a loose strand on the spiral thread.

The Hub:

When the spider completes the sticky spiral, she removes the threads at the hub and adds new ones. Here she sits when the web is completed and from time to time fastens more threads.

At the only hub we investigated, there were thread connections resembling NS-R's (Fig. 5a). Others were compound, with threads radiating from the junction in more than 4 directions, probably the result of two or more connections being made at the same place at different times. The shapes of some junctions from the hub (Fig. 5b) were quite unlike the shapes of those from any other observed type of connection. There were many loose threads and strands of thread (Fig. 5a), perhaps the effect of changing tensions as the spider moved about the hub. The discovery of globules on threads

at the hub (Fig. 5b) resembling those on SS's, raises the question of which glands are in operation as the hub is formed.

Radius to Frame Connections and Y-Structures:

In reading the following section the reader may refer to Table 5 (R-F's) and Table 6 (FY's). In general appearance, R-F's and Y-structures resembled each other more than they resembled other types of connections in the web. However, many of the structures we have already mentioned in the discussion of other types of thread connections were also found at these connections.

We examined 8 R-F's, 5 FY's, and one RY. Each R-F (Fig. 6) and FY (Fig. 7) had one sleeve. Those at R-F's were on the frame; those at FY's were on the stem of the Y. The RY (Fig. 8) had 2 sleeves. One was on the stem, and one was on an arm. Sleeves at R-Fs, FY's and the RY were generally as long or longer than those at SS-R's.

R-F's and the RY had many interconnected strands. Each R-F consisted of a multi-stranded radius fastened to a single stranded frame, except for two at which the frame was split into 2 strands at one side of the junction. Each FY consisted of a multi-stranded frame thread (one of the arms) fastened to a single stranded frame thread (one arm and the stem). One arm of the RY consisted of 2 strands at the junction. Beyond the sleeve, the stem of the RY was split into several intertwined strands.

Some frame threads at R-F's and FY's were thicker than any other threads from the web. The thickness of the arms of the RY ($7 \ \mu$) was in the range of thickness ($3 \ \mu$ - $9 \ \mu$) found for radii at SS-R's.

Does the strength of a thread increase as its thickness increases? This seems likely because, generally, thread thickness corresponded directly with the importance of the supporting function of the thread (i.e., how large a portion of the web would collapse if it broke). Frames were thickest; radii from the trapping zone and at the RY were next; and radii and NS's from the strengthening zone, PS's, and SS's were thinnest.

Drag-line Attachment Disks:

Whenever the spider moves about outside of its web, it continually plays out a drag-line which it periodically fastens to the substrate. The ampullate gland which is involved in the production of the scaffolding of the web (frames, radii, NS's, and PS's) is also involved

in producing the dragline (Peakall, 1969). We examined two drag-line attachment disks (Fig. 9) which were obtained by having spiders drop from glass microscope slides. Although these are not connections from the web, it would seem likely that mooring thread to non-thread substrate connections are closely related, if not equivalent, to drag-line attachment disks.

The production of the drag-line attachment disk is attributed to the piriform glands (Peakall, 1969). Threads between 0.5 μ and 1 μ thick can be seen emerging from the spools of the piriform glands in Fig. 10. The thinnest strands which could be resolved at the attachment disks were in this range of thickness (Fig. 9b). This thickness also corresponded to the thinnest strands of connections from the web. In particular, R-F's, FY's, and some SS-R's had many strands in this range of thickness. This raises the question of whether the piriform glands are involved in the formation of each of these types of connections. One might hypothesize that some thread connections in the web are equivalent to drag-line attachment

Table 6

Descriptive statistics for some structural features of frame Y-structures (FY's). For each feature, 5 FY's from 3 webs built by 3 different spiders were observed. FY's were rather variable with respect to these features, as indicated by the coefficients of variation. Comparing this table with Table 5, note the similarities between R-F's and FY's.

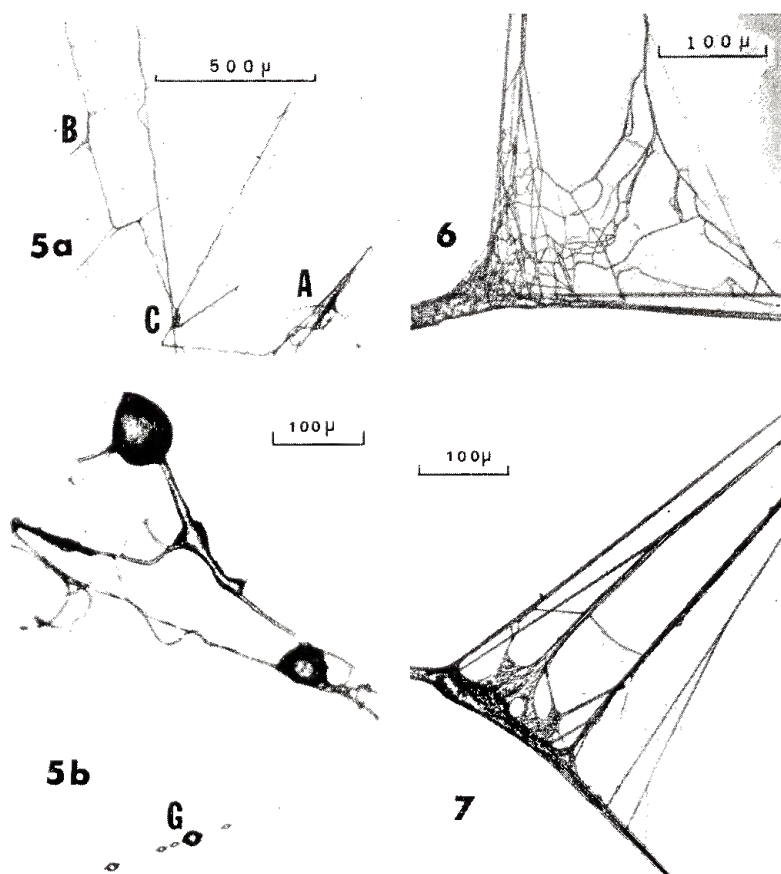| Feature	Means	Coefficient of Variation	Range
Length of Sleeve	74.8 μ	95	22 μ-180 μ
Number of Strands at Junction	15.6	60	9-32
Thickness of Stem of Y	10.4 μ	24	7 μ-14 μ
Thickness of Single Stranded Arm of Y	8.8 μ	19	7 μ-10 μ

Fig. 5. Thread connections from hub. a. Notice loose thread (A), connections resembling NS-R's (B) (Fig. 3), and compound connections (C). b. Junctions of unusual shapes. Also note globules (G), which resemble those on SS's in Fig. 2.

Fig. 6. Typical radius to frame connection. Radius, consisting of numerous strands, runs vertical; frame, horizontal. Frame can be seen to have sleeves at one side of radius and to consist of two strands at other side.

Fig. 7. Typical frame Y-structure. Multi-strand frame fastened to single strand frame.
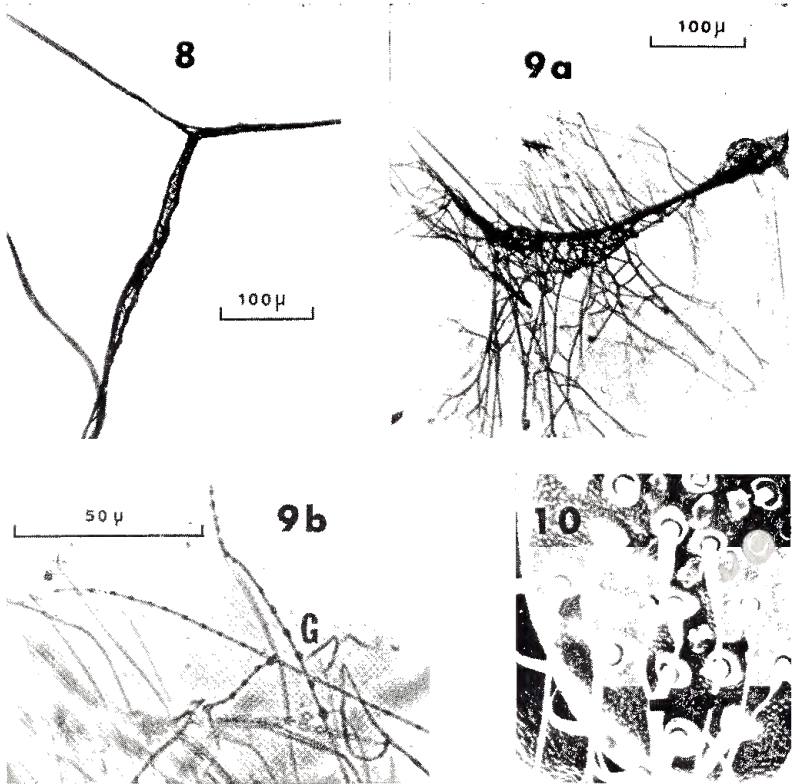
Fig. 8. Radial Y structure. Sleeves can be seen on stem and one arm of Y. Note that beyond sleeve on stem, radius is split into several strands.

Fig. 9. a. Drag-line attachment disk with numerous strands of thread. b. Higher magnification. Note globules (G).

Fig. 10. Scanning electron micrograph of anterior spinneret showing numerous spools which open from piriform glands. Arrow indicates thread between 0.5 μ — 1 μ in diameter, coming from spool .1200$\times$. Photomicrograph courtesy of Rainer Foelix, N. C. Department of Mental Health, Raleigh, N. C.

disks except that each thread is fastened to another thread rather than to a non-thread substrate. However, the number of strands (over 100, counting only those which touch the drag-line) at drag-line attachment disks (Fig. 9a) greatly exceeded the number at any connection from the web. Also, globules which, with the exception of one PS-R, were never observed on the minute strands of connections from the web, were found on some $0.5 \mu — 1 \mu$ thick strands at drag-line attachment disks (Fig. 9b). Are they involved in fastening the disks? What glands produce them?

FORMATION OF JUNCTIONS

How are threads fastened together at thread connections? By what mechanism is the junction formed?

Within the glands, the silk is fluid. Eisner and Peakall (priv. comm.) have photomicrographs, taken under polarized light, of silk being pulled from the ampullate gland which indicate that the silk is already highly ordered at the spigot. Apparently the transformation into a solid is at or previous to this point. Wilson (1969) hypothesized that the control valve, located inside the spinneret and behind the spigot, is the site of the transformation for the ampullate gland.

One hypothesis for junction formation is that there is a cementing substance which fastens threads together. As the spinnerets touch the old threads, to which the new thread will be fastened, the cementing substance, from another gland, is added to the solid silk coming from the ampullate gland. If this hypothesis is true, then what is the cementing substance? Should we expect each type of connection to be equipped with the same type of cement?

At SS-R's, the cement is apparently not simply the viscid material from the aggregate glands. This conclusion is supported by two observations: 1) When SS-R's were immersed in water, the globules on the SS were washed off; but the junction remained secure. 2) Artificial sticky spiral to frame connections and SS-R's were produced by placing a frame or radius over a Permount basin, then placing a SS from the same web across it. Never securely fastened, the SS at these connections could always be moved in any direction on the frame or radius. SS's which cross but are not fastened to radii are common in the horizontal web of *Uloborus diversus* (Eberhard, 1969), and we found them in webs of *A. diadematus* after the spider had ben administered a central stimulant (dextro-ampheta-

mine sulfate, 100 mg/kg). However, they do not normally occur in the vertical web of *A. diadematus.*

Possibly the material from the piriform glands is a cement. Does it cement the drag-line to the substrate through fusing to both, or are the threads from the piriform glands themselves cemented at one end to the dragline and at the other to the substrate?

Stretching may be responsible for solidification of fluid silk through causing filaments to slide past one another, assuming positions which allow for a greater degree of cross linkage (Lucas and Rudall, 1968). Another hypothesis of junction formation is that fluid silk for the new thread fuses with the old thread as it solidifies. As the spinnerets sit on the old thread, some fluid silk departs from the spigot of the ampullate gland (and the spigots and spools of any other gland involved). Solidification does not occur because there is insufficient stretching of the material. When the spinnerets are lifted and sufficient stretching occurs, the new silk solidifies and is fused to the old thread.

More information will be necessary before we can choose between these hypotheses. Perhaps different mechanisms occur at different types of connections. Also, it may become necessary to somehow modify or combine these hypotheses.
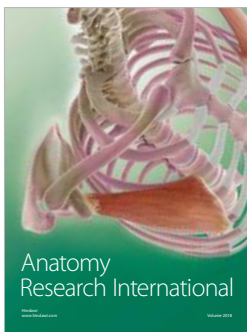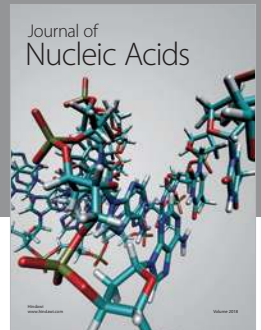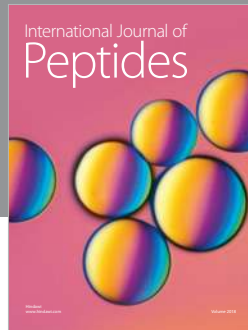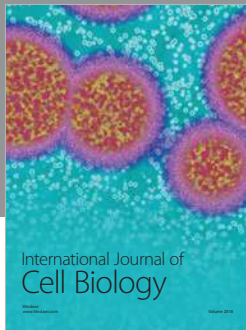
SUMMARY AND CONCLUSIONS

The fine structure at thread connections in the web of *Araneus diadematus* was examined by photomicroscopy. Characteristic structures were discovered for each connection type including presence of sleeves on threads, various lengths of junctions, various numbers of strands, and different distributions of globules. Possible functions and origins of structures were discussed. There was a discussion of two hypotheses related to connection formation: a) threads are cemented together, and b) new thread, while in a semi-solid state, fuses to old thread.

This survey is only a modest beginning in the direction of studying the fine structure of thread connections. With a more extensive and systematic investigation, rigorous statistical comparisons could be made of different types of connections and of the same type of connection from different regions of the web. Structure could be compared for spiders of different age, weight, and species. Viewing the fine structure of connections has led to many interesting questions. Some were mentioned in this paper; others have probably occurred to the reader. Hopefully, these will be pursued further in future studies.

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